

Ecology of the Bushpig
Potamochoerus porcus Linn. 1758
in the Cape Province, South Africa

by

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DECLARATION

I the undersigned hereby declare that the work contained in this dissertation is my own original work and has not previously in its entirety or in part been submitted at any university for a degree.

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ABSTRACT

Bushpig sociology, energetics, reproduction and population dynamics were studied over an 8-year period in the Cape Province, South Africa. The social organization was found to be strikingly different from that known from other suid species. The basic social unit is a unimaternal family group, occupying a resource-based territory, with a monogamous mating system. This form of social organisation is related to the dispersed nature of food resources, to which it provides exclusive access. It is reminiscent of canid social systems. Agonistic behaviour, communication and maternal behaviour were studied as the opportunity arose. The average home range size was 7,2 km², ranging from 3,8 to 10,1 km². Home ranges were often traversed within 1-4 days, as part of territory patrolling. The average diel ranging distance was 3 km. Bushpig were active during both night and day and exhibited a basic bimodal rhythm. The main phase of intensive foraging occurred from before dusk to midnight, with a secondary activity peak after dawn. Activity schedules were geared to avoid extreme ambient temperatures. Temperature regulation and water use were investigated, with particular reference to thermoregulatory behaviour (nest building), pelage characteristics, body core temperature dynamics, thermoneutral zones and resting metabolic rates. The thermoneutral zone for 10 kg bushpig juveniles was estimated to lie between 13° and 30°C and that for adults between 8° and 25°C. Foraging behaviour, diet and its nutrient content were investigated. Regional differences in the nutritional quality of bushpig diets in the Eastern and Southern Cape were associated with the predominance of nutrient-rich and nutrient-poor substrates respectively. These in turn were reflected by divergent life history features in the populations from the two regions. Patterns of growth and energy storage were described and the value of various parameters (e.g. mass to size ratio, fat depositions, blood composition) to evaluate condition was investigated. In studying reproductive biology, sexual maturation, female reproductive cycles, prenatal litter statistics, foetal development, lactation, breeding seasonality and reproductive turnover were the main aspects addressed. The role of food quality, body condition and social status in determining reproductive success was discussed. Bushpig population density estimates in the Southern Cape ranged between 0,3 and 0,5 animals/km². The dynamics of Southern and

Eastern Cape populations were found to differ. The differences are consistent with the hypothesis that social organisation is determined by the distribution and availability of food, while diet quality shapes life history tactics. A life history model was developed which links edaphoclimatic environmental conditions with diet quality, metabolic turnover rate and, ultimately, life history features. In the concluding chapter some of the managerial implications of the research findings are discussed.

OPSOMMING

Die sosiologie, fasette van die energiebalans (temperatuurregulering, voeding), voortplanting en bevolkingsdinamika van bosvarke is in die Kaapprovinsie (Suid-Afrika) oor 'n tydperk van 8 jaar bestudeer. Dit kon bewys word dat die sosiale organisasie van die bosvark van dié van ander varksoorte verskil. Die basiese sosiale eenheid bestaan uit 'n familiegroep wat slegs 'n enkele telende moederdier bevat. Ruimtelike organisasie is gebaseer op 'n stelstel van voedingsteritoriums. 'n Monogamiese paringstelsel kom voor. Die yl verspreiding van voedsel word as die onderliggende rede vir die sosiale organisasie beskou. Gedragspatrone (kommunikasie, aggressie, grootmaak van kleintjies) is bestudeer soos die geleentheid voorgekom het. Heelwat ooreenkomste is gevind tussen die sosiale organisasie van die bosvark en lede van die hondefamilie. Die gemiddelde woongebiedgrootte is 7,2 km² (tussen 3,8 en 10,1 km²). Woongebiede word gewoonlik binne 1-4 dae deurkruis en dus soos territoria gepatroleer. Die gemiddelde daaglike bewegingsafstand was 3 km. Bosvarke was beide gedurende die nag en die dag aktief en het 'n bimodale aktiwiteitsritme gevolg. Die hoofaktiwiteitsfase van intensiewe voeding het tussen sonder en middernag plaasgevind, met 'n sekondêre fase na sonop. Soedoende is temperatuurruiterstes vermy. Temperatuurregulering en watergebruikspatrone is bestudeer, insluitend temperatuurreguleringsgedrag, haarkleedeienskappe, liggaamskerntemperature, termoneutraliteit en metaboliese omset. Voedingsgedrag, voedsel en die voedingswaarde daarvan is ondersoek. Verskille tussen die Oos- en Suid-Kaap in die kwaliteit van voedsel hang saam met die laer vlak van voedingsstowwe in die gronde van die Suid-Kaap. Bosvarkbevolkings in die twee streke toon verskille in populasiedinamika wat hieraan toegeskryf kan word. Groei- en energiestoorpatrone is beskryf. Die moontlikhede is ondersoek om kondisie te evalueer met behulp van parameters soos massa tot grootte-verhoudings, vetneerleggings en bloedwaardes. Aspekte van voortplantingsbiologie, soos geslagsrypheid, vroulike voortplantingssiklusse, vorgeboortelike werpselgroottes, foetale ontwikkeling, laktasie, seisoenaliteit en voortplantingsomset is behandel. Die rol van voedselkwaliteit, kondisie en sosiale status by die bepaling van voortplantingsukses word bespreek. Skattings van die bevolkingsdigtheid van bosvarke in die Suid-Kaap het gewissel tussen 0,3 en 0,5 diere per km². Op grond van die verskille in bevolkingsdinamika tussen bosvarke in die Suid- en Oos-Kaap is 'n model ontwikkel om die

verband tussen bevolkingsregulering en lewensstrategieë (life history tactics) te verklaar. Hiervolgens het voedselbeskikbaarheid die tipe sosiale organisasie bepaal terwyl die lewensstrategieë van bevolkings die gevolg is van voedselkwaliteit. Die model stel voor 'n verband tussen groeipleksomstandighede, voedselkwaliteit, metaboliese omset en bevolkingsdinamika. In die laaste hoofstuk word sommige van die bestuursimplikasies van die navorsingsbevindinge bespreek.

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List of abbreviations

| | | | |
|--------|--|-----------|-------------------------------------|
| ad | : Adult | PCF | : Percentage crude fibre |
| ADF | : Acid-detergent fibre | PCP | : Percentage crude protein |
| ADL | : Acid-detergent lignin | PCV | : Packed cell volume |
| AIA | : Acid-insoluble ash | P/E | : Protein/energy ratio |
| a.s.l. | : Above sea level | PEE | : Percentage ether extract |
| BMR | : Basal metabolic rate | PFC | : Percentage of forage class |
| C | : Conductance | PTD | : Percentage of total diet |
| CAM | : Crassulacean acid metabolism | RBC | : Red blood cells |
| CM | : Minimum conductance | RMR | : Resting metabolic rate |
| CSIR | : Council for Scientific and Industrial Research | RMT | : Relative medullary thickness |
| DAPA | : Diaminopimelic acid | RNRI | : Relative nutrient retrieval index |
| df | : Degrees of freedom | RP | : Reproductive proportion |
| F | : Female | s | : Standard deviation |
| FP | : Farrowing proportion | sad | : Subadult |
| Hb | : Haemoglobin | Ta | : Ambient temperature |
| J | : Juvenile | Tb | : Body core temperature |
| M | : Male | TPR | : Turnover potential ratio |
| MBP | : Mean bulk percentage | UD | : Utilization distribution |
| MCP | : Minimum convex polygon | VFA | : Volatile fatty acid |
| MTR | : Metabolic turnover rate | W | : Body mass |
| n | : Sample size | \bar{X} | : Mean |
| NFE | : Nitrogen-free extract | Y | : Yearling |
| NS | : Not significant | y | : Year |
| PA | : Percentage ash | | |
| PC | : Principal component | | |

1. PREFACE

1.1 Introduction

A decade ago Kingdon (1979) still considered the bushpig as one of the least known of the larger African mammals (also Sowls and Phelps 1968, Leuthold 1977). This state of affairs was linked to the habitat preference and nocturnal habits of the species (Milstein 1971, Frädrieh 1974, Kingdon 1979, Ghiglieri *et al.* 1982).

The bushpig had attracted widespread attention primarily in its role as an agricultural problem animal. Attempts to eliminate bushpigs in some areas, led to concern from a conservation perspective (Oliver 1981). Taxonomic revision was identified as a priority and a prerequisite for any attempts to conserve the full diversity of the species (Oliver 1981). The conservation status of some subspecies in central and western Africa in particular is uncertain. The need for more information about the species was emphasized by increasing habitat fragmentation due to the expansion of agricultural development resulting from human population increases. This also led to an interest in the potential of the species as a source of protein.

A number of authors have dealt with the bushpig as an agricultural problem animal (Thomas and Kolbe 1942, Sowls and Phelps 1968, Milstein 1971, Kingdon 1979, Walker 1986, Cooper and Melton 1988). Earlier accounts of the natural history of the species include those of Phillips (1926a), Thomas and Kolbe (1942), Jobaert (1958), Maberly (1967), Attwell and Bearder (1976) and Breytenbach (1979). Short papers on specific aspects were published by Ewer (1958a: skull features), Parkes (1966: testis histology), Sowls and Phelps (1966: body temperature in juveniles), Scotcher (1973: diurnal feeding) and Jones (1978: scent marking gland).

The taxonomy of *Potamochoerus* received attention by, *inter alia*, Gray (1868), Lönnberg (1910), Von Boetticher (1933), Haltenorth (1963) and finally by Ansell (1971) who recognized 13 subspecies on the basis of the incomplete data available. Reviews of the phylogeny of African

suids also refer to the bushpig (White and Harris 1977, Cooke and Wilkinson 1978, Harris and White 1979).

Sowls and Phelps (1968), Skinner, Breytenbach and Maberly (1976) and Ghiglieri *et al.* (1982) give general accounts of aspects of bushpig biology. As a consequence of veterinary import restrictions, African and Asiatic suid species are scarce in American and European zoo collections and the opportunity of studying bushpigs in captivity is limited (Frädrich 1974). Gewalt (1988) reported on the experiences and problems of breeding bushpigs in limited zoo populations. Available information on free-ranging bushpigs was reviewed by Kingdon (1979) and summarized by Smithers (1983). Since Kingdon's review a number of publications have appeared, focusing on diet and feeding habits (Breytenbach and Skinner 1982, Jones 1984, Melton, Cooper and Whittington 1989). As part of the present study, Seydack (1983) investigated age assessment.

Despite the work already done, knowledge of the bushpig remains relatively limited and inadequate for the requirements of sophisticated natural resource management. A comprehensive data base is of particular importance for multipurpose forest management, be it in the context of population control, utilization or conservation (cf Seydack 1982, 1987). The present study was aimed at providing this data base for the bushpig in the Cape Province, South Africa. The study area is fully described in Chapter 2.

1.2 Objectives

The aims of this study were defined rather broadly. They were to provide basic information on the biology of the bushpig (vital statistics) and to promote an increased understanding of its ecology. Since it was to be the first comprehensive scientific study of the species, such a broad spectrum approach was deemed appropriate.

The information presented here is of both theoretical and practical value. Its academic interest lies in providing a basis for interspecific comparisons and for the interpretation of interregional environment/animal interactions. The results of this study are also

intended to be of use to natural resource agencies involved in management of the species for conservation, utilization or control. In order to achieve these objectives the approach was to cover as wide a field (Fig. 1/1) in as great a depth as possible within the constraints of time, funds and logistics.

1.3 Methods

The main methods applied in most of the study are outlined below. Methods pertaining only to specific aspects are described in the relevant sections.

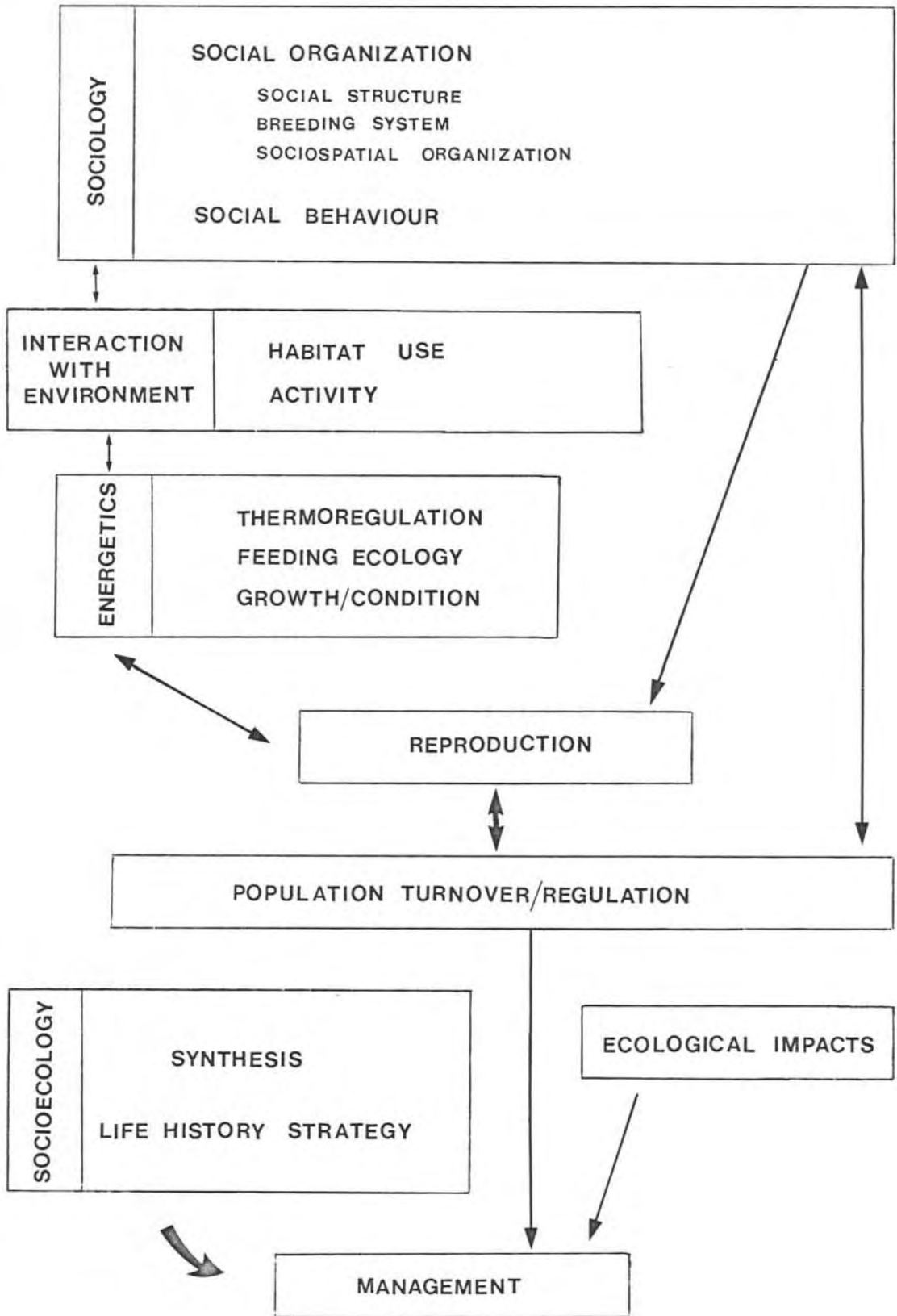
1.3.1 Capture programme

1.3.1.1 Equipment and layout

Bushpigs were captured in corrals. By using corrals rather than box traps it was possible to capture complete social units, with a minimum of resistance to entering the traps. Two types of corrals were used. Both consisted of five sections forming a pentagon, with the side opposite the sharpest angle being used as the trap door (Plate 1a)

The original type consisted of four fixed 3,8 x 1,2 m sections and a 2,6 x 1,2 m trap door. The sections were formed by frames, reinforced with cross-bars spaced at varying distances apart and covered with a double layer of diamond mesh wire (64 x 64 mm mesh, 2 mm in diameter). These corrals could be easily dismantled, transported and re-erected on new sites. Their height of 1,2 m was however found to be insufficient and they were thus heightened with wire mesh for another 0,6 m. In order to reduce the time taken to shift corrals, another type was also used. It consisted of four sections of 4,0 x 1,5 m reinforcing mat (10 x 10 cm mesh; 5 mm steel rods) and a 3,0 x 1,5 m trap door section of the same material. Both types had to be tied or weighed down with logs. Bushpigs tended to smash the second type of corral unless it was reinforced with logs fastened along the sides at approximately the height of a charging animal. Since it was more rigid and less visible,

FIG.1/1: STUDY CONCEPT



charging bushpigs tended to damage themselves more than in the mesh wire frame-type, where animals were seldom hurt.

The trap door was hinged at the upper corners of two adjacent sections and held open by a rope. This led over a forked support to the bait spot in the far corner of the corral where bait was placed. The rope was fastened to a cross-stick (ca 30 cm) held down by the side of the corral at one end and a stone on the other. The trap closed when the cross-stick was dislodged by animals feeding on the bait. This consisted of crushed maize and pig growth meal pellets. Bait was placed in a number of spots inside the corral so as to ensure a time lag between entering and triggering, thereby facilitating capture of entire groups.

Corral sites were selected with the aid of a 500 x 500 m square grid overlaying the relevant portions of Goudveld State Forest, one in each accessible square of the grid (i.e. for every 25 ha). This yielded a total of 151 sites (Fig. 1/2). A replicate capture programme was carried out on Diepwalle State Forest with a somewhat different layout. Here corral sites were spaced approximately 500 m along all roads traversing the study area, giving a total of 61.

The regular capture programme was undertaken between December 1980 and March 1985. The number of capture corrals in operation was increased progressively from an original 5 to a total of 41. For the period August 1982 to June 1983 seventeen of these were operated at Diepwalle. The shifting schedule provided for the full coverage of the study area over the period of one year, i.e. when 25 corrals were operated they remained at the same sites for 8 weeks. The capture programmes as outlined, covered areas of approximately 8 600 and 5 200 ha on Goudveld and Diepwalle respectively.

Corrals were checked daily during the morning. For certain periods a second visit in the late afternoon was necessary to replace the bait taken by baboons, monkeys or birds during the day.

PLATE 1

- a. Capture corral
- b. Study enclosure: viewed from inside of forest (Goudveld)
- c. Enclosure fence
- d. Hand-reared bushpig male (TE3)

PLATE 1

a



b



c

d



PLATE 2

- a. Bushpig family in enclosure A (Goudveld; 1984) From L to R: juvenile, yearling TD12 (F), juvenile, alpha sow TD2, juvenile, alpha boar TD5.

- b. Bushpig family in enclosure A (Goudveld: 1984) From L to R: yearling TD12 (F), alpha boar TD5, juvenile, male TD1, juvenile, male TD7, alpha sow TD2.

- c. Alpha sow TD2 and alpha boar TD5 in enclosure A (Goudveld),

a



b



c



1.3.1.2 Immobilization

Doses of M99 (Etorphine) similar to those recommended for warthog by Harthoorn (1973) were found appropriate for bushpig. A dose of 1,4 mg of M99 was used for the weight range 40 - 70 kg and 1,6 mg for heavier animals. For animals weighing between 15 and 40 kg doses ranging from 1,0 to 1,4 mg were used. Individuals of less than 15 kg were handled manually. The M99 was used in combination with acetylpromazine (ACP) as an analgesic, made up as follows: 20 mg M99 + 5 ml ACP (2,5 mg) + 15 ml buffer solution. A major factor in the choice of M99 was the low drug volume involved (< 1,6 ml). This facilitated darting effectiveness with drug administration by means of a blowpipe. M50-50 (diprenorphine) was injected intramuscularly as an antagonist.

The immobilizing agent was administered in syringe projectiles with a blow pipe (Bubenik and Bubenik 1976; as adapted by D. Pepler, Faculty of Forestry, University of Stellenbosch). This darting system proved quite efficient under the conditions of operation encountered, i.e. one or more violently active animals in a capture corral. Averaged over more than 600 immobilizations 1,4 darts were required per animal (comparable to 1,3 shots/immobilization of caribou from the ground and 1,9 shots from the air by Fuller and Keith 1981). Malfunctions mostly resulted from needle breakage on impact, bounce-offs or insufficient penetration and premature loss of the dart with delayed drug injection or absorption (subcutaneous fat).

The behavioural and physiological reactions were typical for the drug used (Lynch and Hanson 1981): initially stumbling, loss of alertness, hackneyed gait, preceded by a period of hyperactivity, lying in sternal recumbancy, vocalization and elevated body temperatures. Induction times varied between 3 and 10 minutes and the animals remained tractable for periods ranging from 30 to 120 minutes. Accidentally applied double doses or additional injections to lengthen the tractable period did not appear to increase the risk of mortality, confirming the broad safety margin attributed to M99. Recovery periods after administration of the antidote seldom exceeded 5 minutes.

Three percent of the immobilizations resulted in death of the animal (n = 18). A mortality of 2,9% is reported by Alford *et al.* (1974 *op*

cit. Lynch and Hanson 1981) in a variety of species when M99 was used as immobilizing agent. In this study the causal factors could not be objectively confirmed, but hyperthermia (n = 11), stress (n = 4) and poor condition (n = 3) were suggested by correlations with ambient temperature, state of anxiety and physical condition of the animals involved.

1.3.1.3 Parameters and procedures

In addition to capture date and locality, the mass, sex, age and condition was recorded for each individual, as well as the presence of fighting wounds. At first capture the animals were marked by tattooing a number into the non-pigmented part on the inside of the ear. The number series consisted of a letter of the alphabet followed by a numeral, with a "C" added in front for differentiation with the numbering system of captured individuals from that of culled or captive animals (e.g. CA1 or CT7). A recognizable visual pattern was cut into the coat for temporary individual recognition during subsequent capture events, thereby avoiding repeated immobilization solely for identification purposes. These marks usually lasted for the duration of any particular capture corral placement (up to 4 months).

Age was documented by dental photography, completion of molar wear forms (Seydack 1983) or the recording of dental formulae. For the purpose of this dental inspection the jaws were parted with the aid of two slings inserted behind the upper and lower canines and pulled in opposite direction by holding the one sling down with the foot and pulling the other upwards.

An assessment of condition was done by feeling and noting body conformation like the protrusion of ribs, spine, or pelvic girdle bones. Blood samples were taken for the determination of metabolic and hormonal parameters. The skin was incised across and at right angles to the cephalic vein and then punctured with the scalpel. Separate tubes were collected for the hematological assays, glucose (EDTA and fluoride as anticoagulants respectively) and for blood serum for the analyses of blood chemistry and hormone levels. The samples were stored for up to

24 hours in the refrigerator, before processing at the local medical laboratory.

1.3.1.4 Extent of data

The capture programme entailed a total of 34 000 capture days (number of operative capture corrals x days in operation) for Goudveld and 4 862 days on Diepwalle. This effort resulted in 329 and 42 capture events, involving 86 and 22 different bushpig individuals for Goudveld and Diepwalle respectively.

Average recapture rates, defined as the average number of captures per individual, were 3,92 (Goudveld) and 1,91 (Diepwalle). The record number of captures of the same individual was 36 for bushpig CL2 which occurred over a period of two years. A group of 9 animals was the largest group caught during the same capture event, i.e. in a single capture corral. The number of captures per unit of capture effort were similar for Goudveld ($34\ 000 \div 329$) and Diepwalle ($4\ 862 \div 42$): 103 and 116 days per capture event respectively.

1.3.2 Post-mortem sampling

1.3.2.1 Source and extent of post-mortem material

Biological samples and information from culled animals were obtained either from research hunts on state forest land or from sport or control hunting on private land. In the first case, animals were shot at pre-baited spots or trapped, while private hunts were undertaken with the help of dogs. Post-mortem sampling was also carried out on all animals which died as a result of immobilization. The number of culled animals which became available for sampling during the course of the study are shown in Table 1/1.

| TABLE 1/1: CULLED BUSHPIGS AVAILABLE FOR BIOLOGICAL SAMPLING PER YEAR AND REGION | | | | |
|--|---------------|---------|--------------------------------|-----------------|
| YEAR | SOUTHERN CAPE | | EASTERN CAPE (PRIVATE LAND) | ANNUAL TOTAL |
| | STATE | PRIVATE | | |
| 1978 | 43 | 5 | - | 48 |
| 1979 | 15 | 11 | - | 26 |
| 1980 | 39 | - | - | 39 |
| 1981 | 53 | - | - | 53 |
| 1982 | 12 | 4 | 65 | 81 |
| 1983 | 30 | 17 | 39 | 86 |
| 1984 | 28 | 23 | 35 | 86 |
| 1985 | 6 | 6 | 14 | 26 |
| 1986 | - | 6 | 3 | 9 |
| TOTAL | 226 | 72 | 156 | 454 |

1.3.2.2 Sampling programme

The original scope of the study was more limited than it became later and the type of post-mortem samples taken thus changed as the study progressed. A complete collection of all items was not always achieved, particular during the initial stages due to a variety of circumstances and collectors.

For each culled animal the date, locality and vegetation type, as well as group composition, was routinely noted. Selected body measurements, body mass parameters, such as live weight, field-dressed weight, carcass weight, female reproductive status (pregnant, lactating, anoestrus) and condition were recorded. The development of the sampling programme was as follows:

- 1978/79 Collection of male and female gonads, skulls, stomach contents and liver samples.
- 1980 Blood samples were added to the list of items to be collected.
- 1981 Stomach content mass recorded.
- 1982 Humerus and femur bones for bone marrow, skin samples.

- mid 1983 Sampling as per collection form (Figure 1/3). Additional items here were fat layer measurements at selected localities, stomach contents and rectal faeces for Weende analyses and gastric and caecal fluid samples for VFA determinations.
- 1986 The standard sampling programme was discontinued, but certain specific items were collected, e.g. gland material for behavioural experimentation, digestive fluids for microfauna scanning or gastric fluid samples for pH determinations.

The information and samples obtained from each culled individual were identified by a numbering system containing a letter and a number, the letter denoting geographic origin as indicated below:

- B Bergplaas State Forest
- D Diepwalle State Forest
- E Witfontein State Forest
- EC Eastern Cape: Miscellaneous localities
- G Goudveld State Forest
- GB Farm south of Goudveld
- J Jonkersberg State Forest
- K Karatara State Forest
- L Farm Lancewood (George District)
- N Kransbos State Forest
- O Gouna State Forest
- OKA Eastern Cape: hunting group Oelofse
- OKC Eastern Cape: hunting group Coetzer
- OKW Eastern Cape: hunting group Wait
- R Kruisfontein State Forest
- S Saasveld: Groenkop State Forest
- SC Southern Cape: miscellaneous localities
- T Tsitsikamma Forest Region
- U Buffelsnek State Forest
- W Farm Quarrywood (Knysna District)
- Y Knysna township surroundings

FIG.1/3 : FIELD FORM : POST-MORTEM RECORDS AND COLLECTIONS

BUSHPIG NO.

A. INFORMATION

(a) Date: _____ (b) Sex: _____

(c) District/Farm: _____

(d) Vegetation type: _____

(e) Size: I) Length (snout to beginning of tail): _____
II) Hind foot length: _____
III) Weight: _____ kg

(f) Association:
I) Solitary
II) One of Numbers of others in sounder if culled: _____

(g) Condition:
I) Fat Average Lean
II) Subcutaneous fat layer thickness in mm:
Shoulder Thoracic Back
Peritoneal: _____

B. SAMPLE COLLECTIONS

(a) Sow:
I) Both ovaries (in formol saline)
II) All embryo's or foeti if pregnant (in formol saline)
III) If lactating, indicate no of active mammae
Boar: Both testicles

(b) Liver samples (two 2X2X5 cm pieces in prescribed bottle)

(c) One longbone of hind quarters (boud) and shoulder (blad) each

(d) Skull, dental formulæ or wear class

(e) Feeding: I) Weight of stomach contents(-) = _____ kg
II) Stomach contents (medium plastic bottle, no preservative)
III) Stomach contents (large bottle; formol saline)

NOTE: Ensure correct labelling on all data and sampling items

C. REMARKS

Whenever the skull was not available for collection, parameters indicating age were recorded. Dental formulae, with comments as to the degree of eruption (piercing, erupting, erupted; measurements of erupted parts for lower incisivi and canines), were used up to the age when the third molar pierced the gum line (± 2 years). Third molar eruption and wear characteristics were noted for age determination up to the eruption of the last (5th) cusp of the upper third molar at approximately 4 years of age. Thereafter wear characteristics were recorded on molar wear rating forms (Seydack 1983).

1.3.2.3 Sampling techniques

The sampling procedure after culling and immediately thereafter is described below. Subsequent processing of samples and analyses are described in the relevant sections.

(a) Reproduction

From sows both ovaries and, when present, all embryos or fetuses were collected and preserved in formol saline (2 N commercial 40% formalin and 180 g NaCl made up to 20 N with water). Formol saline was used as a preservative to prevent organ distortion during storage. It was also used for samples where this was not a problem because of the practicality of carrying more than one preservative. With large fetuses a small abdominal cut was made to facilitate penetration of the preservative. Both testicles were removed from boars and cut to facilitate rapid penetration of formol saline.

(b) Feeding and nutrition

(I) A well-mixed 2,2 N sample of stomach contents was collected and preserved in formol saline for the analysis of food eaten.

(II) Samples of stomach contents and rectal faeces of up to 300 ml were obtained and stored at -10°C for subsequent Weende analysis.

- (III) Gastric, caecal and duodenal fluid samples, preserved in HgCl₂, were collected for the determination of volatile fatty acid concentrations.
- (IV) Samples from the caecum and upper colon were preserved in formalin for microfaunal studies.
- (V) Gastric fluid samples were collected from the pyloric and caudal regions of the stomach, separately or combined, for pH determinations.
- (VI) Two samples from the edge of the liver (each approximately 5 x 2 x 2 cm) were preserved in prebottled analytical formalin for trace element analysis.

(c) Condition

- (I) The depth of subcutaneous fat deposits was measured at three localities and one measurement was made of the peritoneal fat layer. The layers were incised with a scalpel and the maximum observed thicknesses measured or estimated in mm. Visual estimation was verified to be sufficiently accurate. Subcutaneous fat was measured on the dorsal shoulder and ventral thorax crests opposite the elbow and dorsally in the region where the tail begins.
- (II) One femur and one humerus bone was dissected out from each carcass of animals two years and older. These bones were frozen, crushed and the marrow columns transferred into plastic vials. Further storage was at temperatures below -10°C until marrow fat analysis was undertaken at the Saasveld Forest Research Centre.
- (III) Whole blood samples were collected for glucose level determinations (± 1 ml with fluoride as anticoagulant) and haematology analyses (1 - 2 ml with EDTA or heparin as anticoagulant). Samples of 40 ml blood for blood chemistry analyses were collected in 4 correctly-sized tubes for serum centrifugation. The samples were stored at $\pm 7^\circ\text{C}$ and sent to the State Laboratory (George) within 24 hours.

(d) Temperature regulation and water metabolism

- (I) Skin samples were collected from selected animals to cover the full seasonal and age ranges. From each animal four 4 x 4 cm samples were obtained. Skin sampling sites corresponded to mid-heights at the shoulders and haunches on both sides of the animal. A 4 x 4 cm template was placed on the inner side of the wet coat and the samples cut out carefully in order to avoid cutting any hairs. The hairs of each sample were subsequently cut off flush with the skin surface and placed in an envelope for counting and measuring.
- (II) One kidney was collected from selected animals and frozen for later morphological analyses (RMT assessment).
- (III) A limited number of 2 - 5 ml urine samples were collected and frozen.

1.3.3 Radio-tracking

1.3.3.1 Equipment

The receiving equipment consisted of 4 element, general purpose hand-held Yagi antennas and portable receivers. Three AVM receivers (LA12 - D5) were available initially (AVM Instrument Company, 6 575 Trinity Court, Dublin, California 94 566, USA). They were later supplemented with a receiver (Digitaal 224) produced by the National Electrical Engineering Research Institute, NEERI, of the CSIR (Pretoria).

The receivers operated in the 148 MHz frequency band. This frequency allowed the use of small, easily transportable receiving antennas, which facilitated tracking by vehicle and on foot. Frequencies in this range are associated with greater, though more variable range, but are more subject to reflectance and attenuation than lower frequency bands (cf Sargeant 1980).

PLATE 3

- a. Fitting of radio collar to sow CT2 (Goudveld 1984).

- b. Radio-collared sow TH2 near Van Loggerenbush (Goudveld 1984).

- c. During radio-tracking: Goudveld 1984.

a



b

c



The power source used for the AVM receivers was a 12V motor cycle type battery. The receiver/battery unit was mounted on a backpack for convenient transport when tracking on foot. The NEERI receiver was powered by an internal 9V battery.

Eleven-element yagi antenna (NEERI) were mounted at selected stations (e.g. fire look-out tower) to facilitate initial contact and accurate long-distance direction finding.

Since imported AVM transmitters did not perform at all under the prevailing conditions, transmitters designed and produced by NEERI were obtained. These had 3-transistor pulsers with a pulse on/off ratio of 1:40 and a pulse rate of 100/min (average current 0,4 mA). The electronic components and batteries were enclosed in a metal box (45 x 66 x 96 mm) filled with polyurethane. Lithium cells with thionile-chloride electrolyte were used. During storage the transmitters were deactivated with magnetic switches. Transmitters were "burnt-in" by the producer, i.e. they were subjected to extreme conditions of temperature fluctuations, while frequency, pulse duration and repetition rates were evaluated. In this way transmitters likely to perform poorly could be identified at an early stage.

Flexible, multistrand copper wire was used for the 50 cm long transmitting antennas which were placed within the neck collar belting. The antenna emerged at a corner of the metal box and was situated between the belt layers of the neck collar, held in place by contact adhesive and pop rivets. Two layers of thin conveyor belt were used, one running on either side of the transmitter box. Bolts and nuts were used on either side to secure the belt to the box. The transmitter/collar unit had a mass of about 750 g.

The collar was held in place on the animal with a harness, made from conveyor belting 40 mm wide and about 3 mm thick. The harness attachment was necessary in view of the cone-shaped body to head conformation of the bushpig. A girth strap was located just posterior to the animals front legs. A dorsally positioned strap connected the girth strap to the transmitter collar (Plates 3 a, b). The girth strap

belting was covered with a sheath of smooth ground sheeting material in order to minimize the danger of cutting into or abrading the skin.

Tightness of the harness fit was important. When too loose, the harness was thrown off or the animal became entangled, with one foot stuck between the neck collar and the neck. Harnesses fitted too tightly resulted in skin abrasion and infection. The problem of fitting was confounded by substantial changes in body condition, e.g. lactational weight loss. The ongoing capture programme resulted in the recapture of radio-collared individuals so that harness misfits could be rectified in virtually all cases ($n = 4$).

1.3.3.2 Tracking procedures

The tracking programme comprised two components. Positions of collared animals were determined by regular fixes from the ground or from the air in order to delineate home ranges. In addition movement tracking was undertaken. This entailed sequential half hourly position fixes over full 24-hour periods (Plate 3 c). In all, 166 animal locations were obtained by ground tracking and on 57 flights (38 flying hours) with a light fixed-wing aeroplane. Movement tracking involved 8 bushpigs from which data was collected over 59 x 24-hour periods.

When tracking, the aim was to locate the animal every half hour uninterruptedly for one to four successive 24-hour periods. Tracking was started at 15:00, the time of the day with the greatest likelihood of the animal being at rest. The weather and ambient temperature were recorded half-hourly. From the nature of the signal, and whether the animal was stationary or not, it was recorded as active or resting.

Two aspects were of particular importance for developing a good movement data base. Animals had to be located with reasonable accuracy and their positions followed with a minimum of interruption. The broken topography of the study area and the marked attenuation of signals by the dense forest vegetation, particularly when wet, resulted in frequent loss of contact. In order to overcome this and to maximise accuracy, a tracking strategy was selected which involved being highly mobile and staying reasonably close to the animal. The accurately mapped network

of roads and slippaths was of sufficient density to allow this approach. Most locations were made from distances of less than 1 km from the tracked animal and often from only a few hundred meters away.

Initial contact was made from a fire look-out or fixed-wing aeroplane. Tracking was carried out with two units, each consisting of two operators, a vehicle, receiver and antennas. Both units took directional bearings in synchrony and were in contact with each other by walkie-talkie. When an animal could not be located from a road, tracking was continued on foot by one or both tracking units. The direction to the tracked animal was determined by reference to a suitably placed test transmitter or linear, mapped features, e.g. a road. The bearing to the animal was obtained by a modified "null-average" method (cf Springer 1979). According to this method the approximate direction where the signal was loudest, was determined. The antenna was then turned away to either side and the directions marked where the signal strength declined rapidly. These two directions usually deviated to about the same degree from that producing the loudest signal but were better defined. The direction halving the angle between them was taken as the bearing to the tracked animal.

For locating animals from an aircraft, a whip antenna was fixed to the wing strut. When flying at a low altitude the attenuating effect of forest vegetation on signals facilitated pin-pointing transmitters, since it produced a steep gradient in signal strength, depending on the horizontal displacement of aeroplane and transmitter. Once the signal was picked up, the position of the transmitter was pin-pointed by dropping in altitude, traversing the area by flying at right angles and establishing the intersecting lines of maximum signal strength on a map (1/20 000 scale). The process was rounded off by verifying the accuracy of the location by overflying the proximate area above the position of the tracked animal at a low altitude.

The accuracy of radio tracking was assessed in a number of test cases. Locations determined from the air were usually within 200 m of the true positions. Ground tracking accuracy was variable, but for distances up to 1 000 m, estimates were within 50 - 100 m from the true positions.

1.3.4 Studies on captive bushpigs

The field study programme was supplemented by observations on captive bushpigs, some of them hand-reared, kept in enclosures under semi-natural conditions on Goudveld State Forest.

1.3.4.1 The study enclosures

The fence was constructed with 0,7 m wide corrugated iron sheets at the bottom and 0,8 m diamond-mesh wire above. Approximately 0,2 m of the corrugated iron sheet was sunk into the ground, resulting in a fence with a height of approximately 1,3 m. On average, the fence poles (10 cm in diameter) were spaced at 6,5 m, with two droppers in between. The corrugated iron sheet and mesh wire were supported by 6 strands of steel wire (Plates 1 b, c).

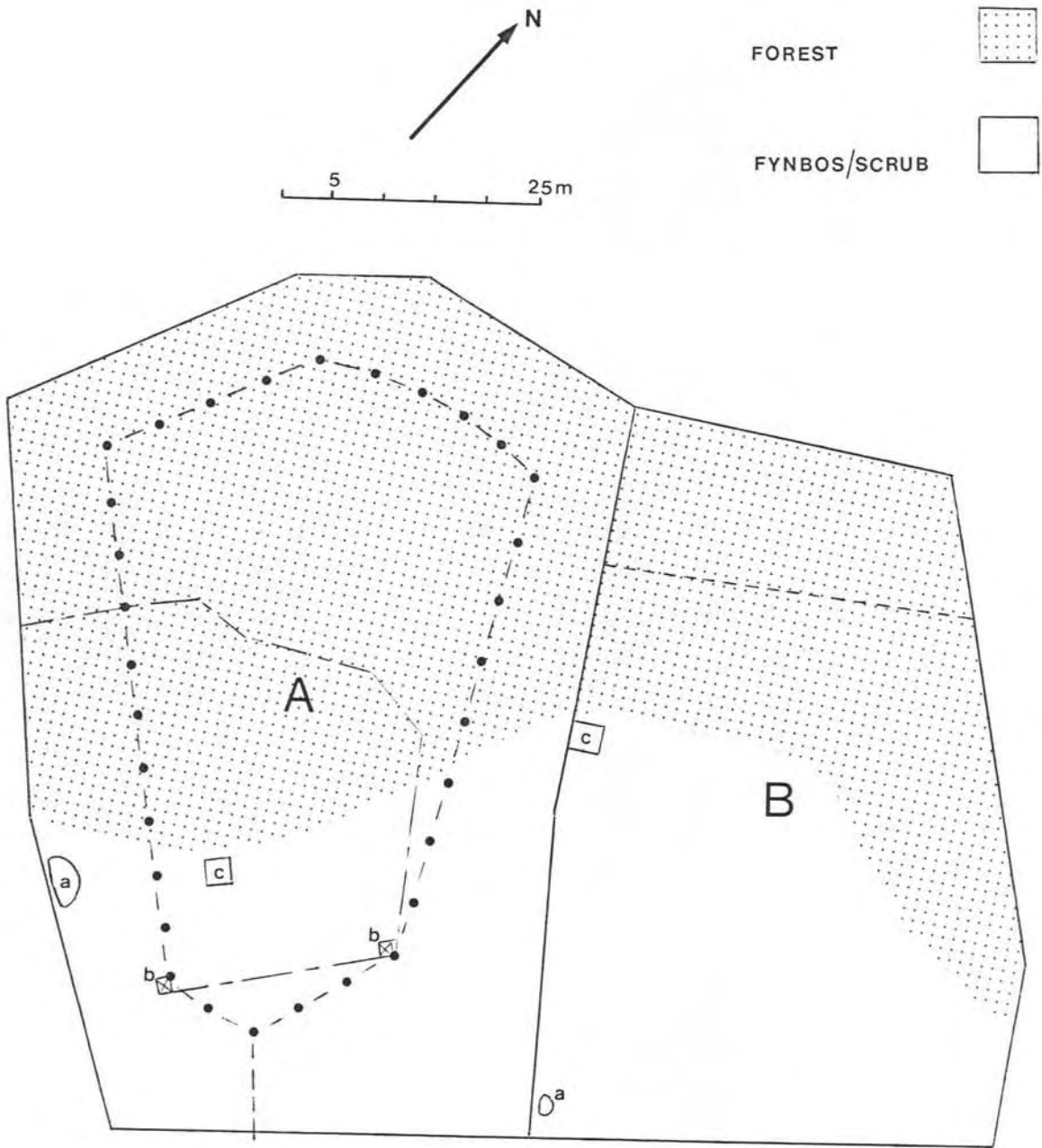
The main enclosure (A) was constructed during 1980, while enclosure B was added in 1983. They covered 4 000 and 2 660 m² respectively (Figure 1/4). Two types of natural vegetation were present in both enclosures: indigenous high forest (dryish medium-moist type; 2.4.2.1) and forest/fynbos ecotone. Both enclosures had small dams for drinking and wallowing and permanent corrals, enabling the animals to be captured when necessary.

Two observation towers were erected, as well as a walkway enabling observers to move about in safety out of reach of newly introduced bushpigs, which exhibited extreme aggression. In order to facilitate observations at night, a double-core electrical cable with 32 approximately equally spaced 100 watt globes was installed at a height of 2 - 3 m (Figure 1/4).

1.3.4.2 The enclosure study populations and their care

The initial population of enclosure A was formed by two groups: adult sow TD3 with two of her yearling offspring TD1(M) and TD2(F) from Bergplaas, and the adult pair TD5(M) and TD4(F) with two male juveniles TD6 and TD7 caught on Goudveld in the area surrounding the enclosure. Sow TD4 was killed by sow TD3 on introduction. TC2(M) was a transient

FIG.1/4: LAYOUT OF STUDY ENCLOSURES A AND B (GOUDVELD)



a Water holes

b Observation towers

c Capture corrals

●—● Electrical wiring with bulbs

----- Partitioning

----- Raised walking structure

occupant from the Hoekwill pen (Table 1/3). All other additions were litters born to the prevailing dominant sows TD3 and TD2 (Table 1/2).

| TABLE 1/2: OCCUPANTS OF STUDY ENCLOSURE A Goudveld State Forest (Plates 2 a, b, c) | | | | | | |
|---|------|-----|----------------|-----------------------|--------|--------------------------------------|
| DATE OF INTRODUCTION | NO | SEX | AGE (Years) | Occupancy terminated: | | |
| | | | | DATE | MOTHER | REASON |
| 29.11.1980 | TD3 | F | 11,4 | 13.1.1982 | | Shot (in poor health) |
| 29.11.1980 | TD1 | M | 1,0 | 5.1.1988 | TD3 | Released |
| 29.11.1980 | TD2 | F | 1,0 | 5.1.1988 | TD3 | Released |
| 1.1.1981 | TD4 | F | 10,7 | 2.1.1981 | | Fighting mortality (TD3 vs TD4) |
| 1.1.1981 | TD5 | M | 7,7 | 11.12.1985 | | Fighting mortality (TD1 vs TD5) |
| 1.1.1981 | TD6 | M | 0,1 | 18.5.1981 | | Immobilization casualty |
| 1.1.1981 | TD7 | M | 0,1 | 22.12.1986 | | Broke out of enclosure |
| 31.1.1981 | TC2 | M | 0,9 | 7.2.1982 | | Transferred to Saasveld enclosure |
| 11.1.1982 | TD8 | F | B O | 15.1.1982 | TD3 | Death due to inappropriate fostering |
| 11.1.1981 | TD9 | M | R | 13.1.1982 | | Exposure mortality |
| 19.9.1982 | TD10 | M | N | 22.9.1982 | TD2 | Cause of death unknown |
| 3.3.1983 | TD11 | F | | 1.1.1984 | TD2 | Cause of death unknown |
| Nov. 1983 | TD12 | F | IN | 26.11.1985 | TD2 | Broke out of enclosure |
| 23.10.1984 | TD13 | M | | 13.8.1986 | | Released |
| 23.10.1984 | TD14 | M | EN- | 13.8.1986 | TD2 | Released |
| 23.10.1984 | TD15 | M | CLO- | 13.8.1986 | | Released |
| 1.10.1985 | TD16 | F | SURE | 1.11.1985 | TD2 | Exposure mortality |
| 1.10.1985 | TD17 | F | | 3.11.1985 | | Exposure mortality |
| March 1986 | TD18 | M | | 5.1.1988 | TD2 | Released |
| March 1986 | TD19 | F | | 22.10.1986 | | Immobilization casualty |

Enclosure B was inhabited by three transient groups:

- (I) Adult pair DJ1(M) and DI1(F) captured at Diepwalle and transferred to Goudveld (26.6.1983). Both broke through into the adjacent enclosure A. Sow DI1 died of trauma from a combination of wounds sustained in fighting with sow TD2 and capture myopathy when she was subsequently immobilised. Boar DJ1 was involved in fighting during the post-lactational oestrus of sow TD2 and succumbed to wound sepsis.

- (II) Adult pair TH1(M) and TH2(F), captured at Saasveld and transferred to Goudveld (11.7.1984). Both were radio collared and released on Goudveld State Forest on 10.10.1984.
- (III) The territorial pair outside the enclosure, CT4(M) and CT3(F), were captured and placed into enclosure B on 24.6.1986. Transmitters were fitted to both on 24.10.1986. Sow CT3 then had colostrum in her mammae. They were released into their territory on 30.10.1986 and their movements monitored.

All enclosure populations were fed daily *ad libitum* with balanced pelleted rations (EPOL). Water was available throughout. In both enclosures shelters were provided, since natural refuges (lair) were limited, especially in enclosure A, which was comparatively densely populated.

1.3.4.3 Penned and hand-reared bushpigs

In addition to the occupants of enclosures A and B, a total of 16 captive bushpigs were available for study over variable time periods (Table 1/3). Four of these were hand reared (TB1, TE1-3, Plate 1 d).

1.3.4.4 Monitoring and observation programme on captive bushpigs

The study of captive bushpigs involved monitoring physiological and morphological parameters, behavioural observations and *ad hoc* experiments. The programme is outlined below, but the detailed description of the methods involved is dealt with under the various sections.

(a) The following aspects were monitored:

- (I) Growth. Mass and body dimensions of immatures were measured periodically, usually monthly, until adulthood. Selected individuals younger than 6 months were measured more frequently.

TABLE 1/3: PENNED OR HAND-REARED BUSHPIGS AVAILABLE FOR STUDY (1980 - 1986)

| Number | Sex | Age or age estimate at onset of captivity | Onset of Captivity or Inspection | Period available for study (months) | Remarks |
|--------|-----|---|----------------------------------|-------------------------------------|--|
| TA 1 | F | 8 months \pm 1 | 5/5/80 | 19 | Captured at Gouna and housed in the Hoekwil pen. Escaped. |
| TA 2 | M | 8 months \pm 1 | 5/5/80 | 19 | |
| TB 1 | M | Few Days | 10/80 | 9½ | Hand-reared (Dieprivier, George District) Escaped. |
| TC 1 | F | 6 months \pm 1 | 9/9/80 | 4 | Captured at Kruisfontein and housed in the Hoekwil pen. Escaped. As TC 1, but was transferred to the Goudveld enclosure on 31/1/1981 and to the Saasveld enclosure on 7/2/1982, from where he escaped. |
| TC 2 | M | 6 months \pm 1 | 9/9/80 | 5 | |
| TE 1 | M | 3 weeks \pm 1 | 24/10/81 | 20 | Received from Adelaide Nature Conservation Station Hand-reared and later transferred to the Goudveld pen. Died of drug-induced hyperthermia (19/6/83) |
| TE 2 | M | 3 weeks \pm 1 | 24/10/81 | 7 | |
| TE 3 | M | 4 weeks \pm 2 | 11/11/81 | 37 | Captured at Bergplaas. Hand-reared. Transferred to Goudveld pen. Immobilization mortality: 2/1/1985 |
| TE 4 | M | 16 months | 6/2/83 | 4 | Brother to TE 1 and TE 2. Housed in pen at Adelaide Nature Conservation Station. Last inspection: 4/6/1983 |
| TF 1 | M | Birth | 19/1/83 | 22 | Born 19/1/1983 in Adelaide pen. Transferred to Goudveld pen (14/6/1983). Released on Goudveld State Forest (6/11/1984) |
| TF 2 | M | Birth | 19/1/83 | 5 | |
| TF 3 | M | Birth | 19/1/83 | 22 | |
| TF 4 | F | Birth | 19/1/83 | 5 | |
| TF 5 | F | 28 months \pm 3 | 6/2/83 | 4 | Last inspection 4/6/1983. Housed in Adelaide pen and mother to TF 1 - 4 |
| TF 6 | M | 25 months \pm 3 | 6/2/83 | 4 | |
| TG 1 | M | 11 months \pm 1 | 1/4/83 | 2½ | Received from the Eastern Cape in a state of malnutrition. Died of drug-induced hyperthermia in the Goudveld pen (19/6/1983) |

- (II) Dental changes. Tooth eruption, replacement and wear were monitored for purposes of age assessment.
 - (III) Condition. Condition was monitored by measuring body mass and collecting blood for study.
- (b) The observation programme involved series of 24-hour observation periods in enclosure A and was focussed on temperature regulation, activity patterns and rearing behaviour. A total of 41 x 24-hour observation periods were undertaken.
 - (c) *Ad hoc* experiments to observe agonistic behaviour and aspects of olfactory communication were carried out in the enclosures.

1.4 Approach

The holistic approach underlying this study implied that a wide variety of topics was tackled, whereas the depth of investigation was partly determined by logistic constraints. The approach entailed study of the individual, its morphology, physiology and behaviour, in relation and with reference to both the social and physical environment (climate, vegetation, geology). The type of study generated mainly general purpose data from which laws of association could be derived by induction and interpretative hypotheses by retroduction. Induction only gives knowledge about the possible associations between classes of facts, whereas retroduction is the method of circumstantial evidence (Romesburg 1981).

Extended involvement of an observer in a subject allows the subconscious mind to absorb the total make-up of the subject and its unique features (cf Tinley 1977). This favours an intuitive understanding which must then be verified by the conscious acquisition of details and repeatedly reappraised against alternative interpretations. A rigorous scientific approach involves four stages: observations, hypotheses, predictions and tests (Krebs and Davies 1981). Sometimes it is possible to test between hypotheses simply by further observation or through intra- and interspecies comparisons, but often an experimental approach is required.

It may take years of research involvement before it is possible to ask truly good key questions about the behaviour or ecology of a species (cf Krebs and Davies 1981). The creation of hypotheses or hypothetical interpretations is therefore considered an important outcome of this research undertaking. It involves providing plausible, tentative explanations in agreement with and logically accommodating all the known relevant facts. If not adequately substantiated inductively or retroductively, they should be followed up by specific experimental research using the hypothetico-deductive method (Romesburg 1981). The hypotheses which have emerged from this study thus serve the important aim of directing future research to salient questions or issues.

This approach to the study was designed to provide both descriptive information, for direct use in description and management, and interpretative knowledge. The latter was intended to facilitate understanding; the appropriate use of the descriptive information and to serve as points of commencement for further research. The interpretative knowledge so gained would also be amenable to cautious extrapolation to beyond the narrow species-specific and regional confines of the study.

DISTRIBUTION OF
HABITAT ZONES
(PLATE 4)



MAP 2: PHYSIOGRAPHY OF STUDY AREA - SOUTHERN AND EASTERN CAPE

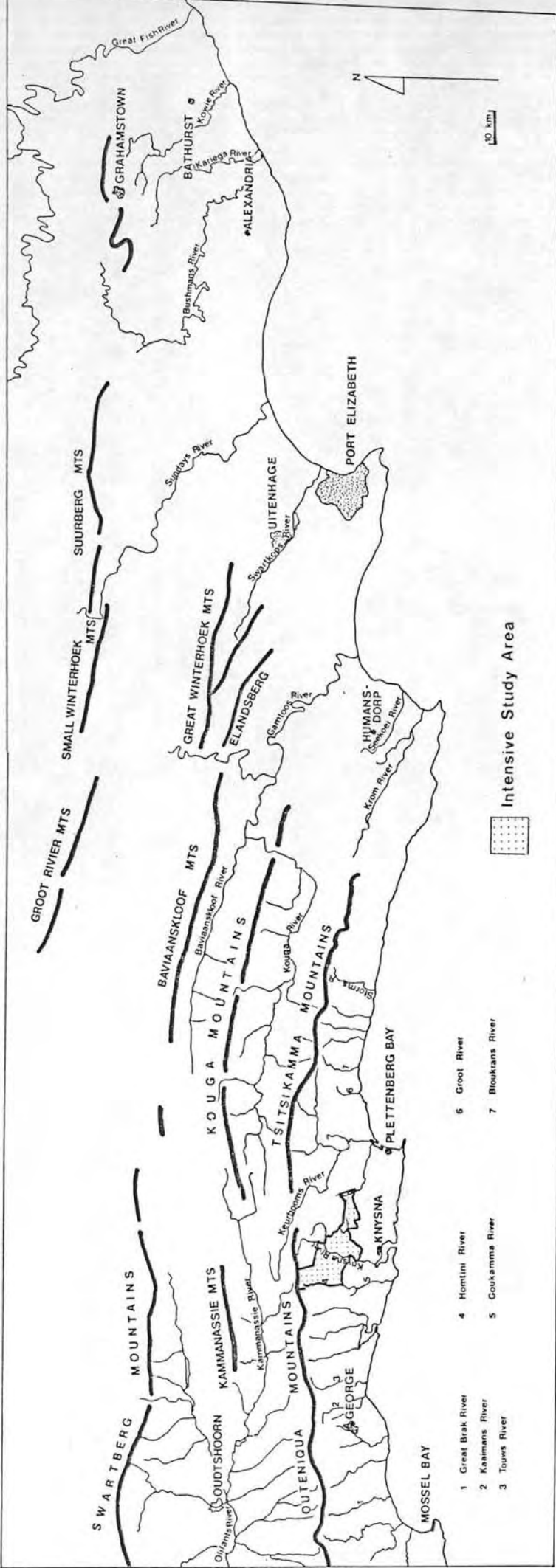


PLATE 4

Aerial photograph of Goudveld State Forest (Knysna district)

Scale: ca 1/75 000

Aerial photographs reproduced under Government Printer's Copyright Authority 8471 of 1 January 1986.

DISTRIBUTION OF
HABITAT ZONES
(PLATE 4)





- (II) Cape Fold Belt mountain zone (Elandsberg, Great Winterhoek, Suurberg mountains). The highest peak is the Cockscomb (1 758 ma.s.l.) in the Great Winterhoek range.
- (III) Coastal forelands south of the Fold Belt approximately bounded by the 300 m contour. They are dissected by the relatively broad north to south orientated valleys of the Sundays, Bushmans, Kariega, Kowie and Great Fish rivers.

These physiographic features are illustrated in Map 2.

2.2.2 Geology

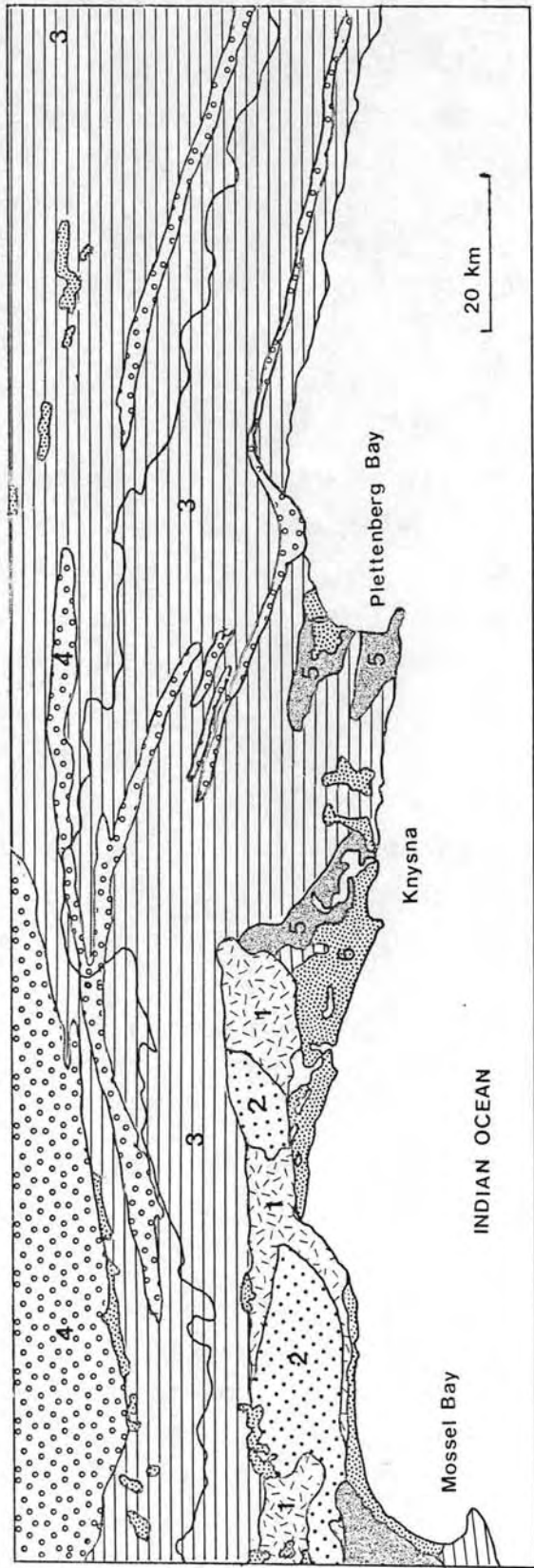
The geological stratigraphy of the Southern Cape includes (from old to young) pre-Cape deposits with subsequent granite intrusions, Table Mountain sandstone and Bokkeveld shales of the Cape Supergroup, followed by Enon deposits of the Cretaceous period and recent unconsolidated alluvial, aeolian and marine deposits of the Quaternary (Scriba 1984; Figure 2/1).

The Kaaibans Group (Pre-Cape Granite and Gneiss intrusions) gave rise to phyllites, quartzites, hornfels and schist deposits (Toerien 1979). Both these groups are intermittently exposed along the plateau from northwest of Knysna to north of Mossel Bay.

The mountain ranges and coastal plateau of the Southern Cape consist virtually entirely of sandstone of the Table Mountain Group of the Cape Supergroup (Donald and Theron 1983). Five formations are distinguishable: Peninsula, Cedarberg, Tchoando, Kouga, Baviaanskloof (Toerien 1979, Johnson 1976). The Peninsula Formation, a quartzitic sandstone, is the thickest (± 1 500 m) and normally forms the highest peaks and southern slopes. It is followed by the Cedarberg Formation, a narrow 35-50 m thick black shale band. The Tchoando Formation, a reddish-brown sandstone containing frequent subordinate shalebands, overlies the Cedarberg. It is exposed along the foothills of the coastal mountains and underlies most of the indigenous forests. The Kouga Formation (300-400 m) follows: a distinctly white, medium to coarse-grained sandstone. The Baviaanskloof Formation is formed by two dark-grey impure sandstones separated by a feldspathic zone. The

FIG.2/1 GEOLOGICAL FORMATIONS OF THE SOUTHERN CAPE

- 1. Malmesbury
- 2. Cape Granites
- 3. Table Mountain sandstone
- 4. Bokkeveld
- 5. Enon conglomerates
- 6. Unconsolidated deposits



(ex Scriba 1984; from Geological Map of R.S.A 1970)

Cedarberg, Kouga and Baviaanskloof formations are only represented by narrow bands and underly as such the indigenous forests of the Tsitsikamma coastal plateau (Scriba 1984).

The main formation of the Bokkeveld Group in the study area is the Gydo Formation. Its sediments consist of shales and siltstones (Toerien 1979). It is exposed in narrow bands associated with and overlying the Baviaanskloof and Kouga formations (Scriba 1984) and is particularly prominent in the intermontane valleys such as the Langkloof.

The Enon conglomerates (consisting of pebbles and rounded boulders) are found along the coastal plain north of Mossel Bay, at Knysna and Plettenberg Bay. Unconsolidated deposits of aeolian sand, dune sand, alluvial and marine terraces occur along the coast from Mossel Bay to Plettenberg Bay (Scriba 1984) and further east as described below.

Cowling (1982) characterizes the geology of the south-eastern Cape transition as follows:

"Rocks of the Cape Supergroup predominate in the area. Quartzitic sandstones of the Table Mountain Group (T.M.G.) comprise the mountains but also underlie considerable portions of the coastal plain. Argillaceous Bokkeveld beds occur extensively on the coastal plain.

Cretaceous fluvial, estuarine and marine sediments of the Uitenhage Group are found in the Gamtoos Valley. Coarse grained conglomerates and sandstones are the predominant rocks. The lower beds are finer and consist of fine sandstones with reddish marls and grey sandy clays.

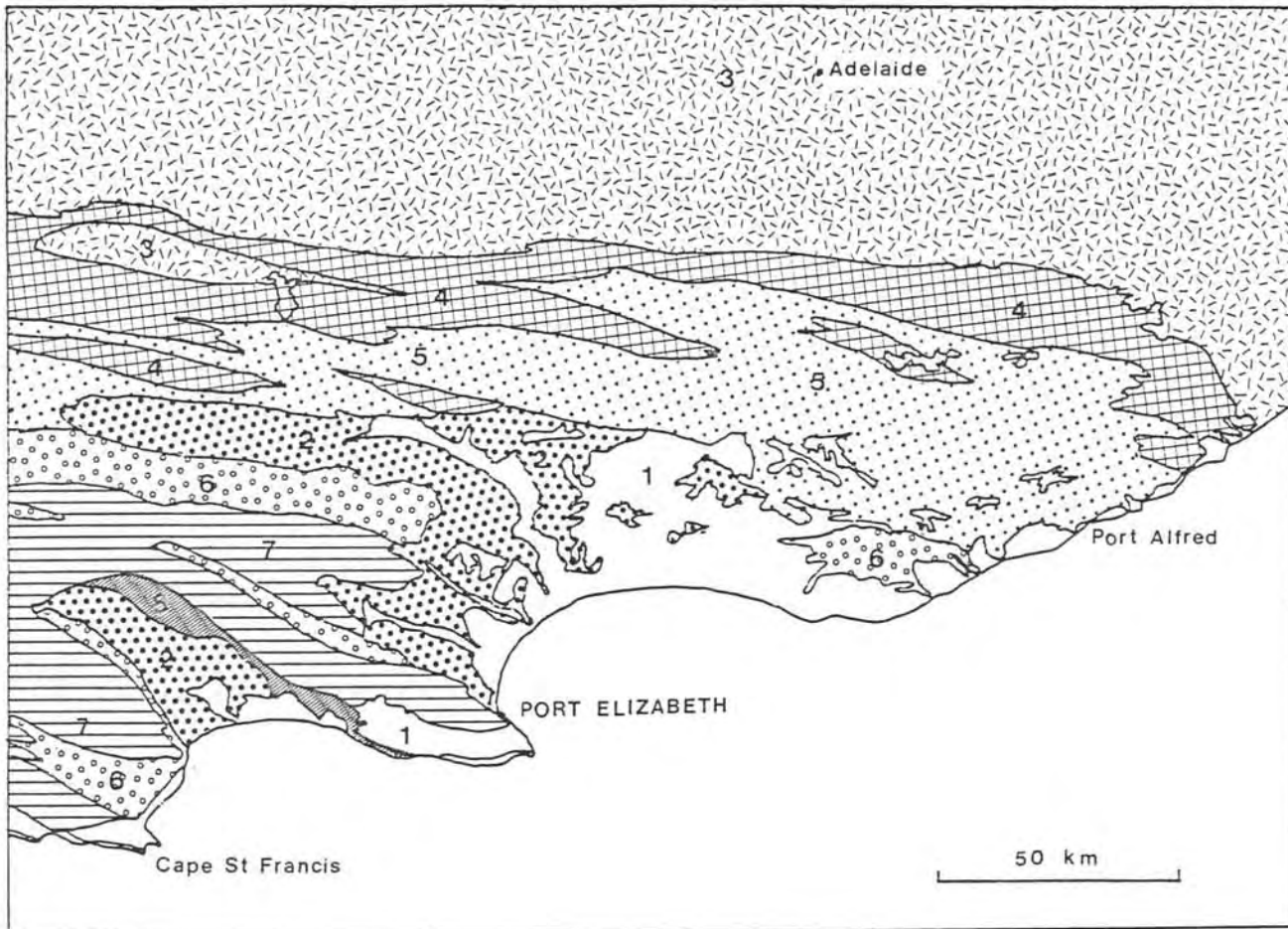
Quaternary deposits occur as alluvium in the major river valleys and as calcareous dune sands along the coast, where there are occasional exposures of calcrete."

The geological formations of the Eastern Cape, as delineated, belong to 5 units, from oldest to youngest (Rust 1986): Gamtoos Formation, Cape Supergroup, Karoo Sequence, Uitenhage Group and the Alexandria Formation (refer to Figure 2/2). Common rock types include sandstone, mudstone,

FIG.2/2 : GEOLOGY OF THE EASTERN CAPE

(Simplified from Geological Map of the Republics of South Africa, Transkei, Bophuthatswana, Venda and Ciskei and the Kingdoms of Lesotho and Swaziland, 1984, Department of Mineral and Energy Affairs)

- 1 ALEXANDRIA/NANAGA FORMATIONS
- 2 UITENHAGE GROUP
- 3 BEAUFORT GROUP
- 4 ECCA GROUP (incl. Dwyka Formation)
- 5 WITTEBERG GROUP
- 6 BOKKEVELD GROUP
- 7 TABLE MOUNTAIN GROUP
- 8 GAMTOOS FORMATION



conglomerate, shale and limestone. The geological features of the Eastern Cape are summarized in Table 2/1.

| TABLE 2/1: GEOLOGICAL FEATURES OF THE EASTERN CAPE | | | |
|--|---|--|---|
| UNIT | SUBUNIT | ROCK TYPE | LOCALITY |
| Alexandria Formation and younger sediments | | Limestone Sandstone Dune Sand | Active and fixed dunes along coastline. Fixed dunes up to 30 km from present shoreline. Alexandria district |
| Uitenhage Group | Sundays River Formation Kirkwood Formation Enon Formation | Shale Mudstone Sandstone Conglomerate | Basins of Gamtoos and Sunday rivers and Algoa Bay |
| Karoo sequence | Beaufort Group | Mudstone Sandstone | Karoo north of Cape Fold Belt outliers extending to coast in the Fish River valley |
| | Ecca Group (Dwyka) | Shale Mudstone Sandstone Tillite | |
| Cape Supergroup | Witteberg Group | Shale Siltstone Quartzitic sandstone | More hilly and rounded ranges (e.g. Albany / Bathurst) |
| | Bokkeveld Group | | Prominent in inter-montane valleys e.g. Elands Valley and extensive lowland areas around Humansdorp |
| | Table Mountain Group | | Bare and craggy ranges. Winterhoek Mountains |
| Gamtoos Formation | | Limestone Quartzite | Eastern foothills of lower Gamtoos Valley |

2.2.3 Soils

2.2.3.1 Soil types

Following Scriba (1984) six main soil types can be identified for the Southern Cape south of the coastal mountain ranges (Figure 2/3):

(I) Regic sands

Deep uniform sands of medium texture, frequently calcareous. Coastal dune areas around Mossel Bay and Plettenberg Bay, as well as coastal lakes area between Wilderness and Knysna.

(II) Duplex soils

The top soil is relatively permeable overlying a slowly permeable diagnostic horizon. The subsoil is normally gleyed. These are the soils typical of the coastal plateau (Schloms *et al.* 1983).

(III) Lithosols and lithocutanic soils

These soils usually have a rocky base with the parent material often exposed. They occur on the slopes of the foothills and the steeper river incisions and coast lines.

(IV) Podsoles

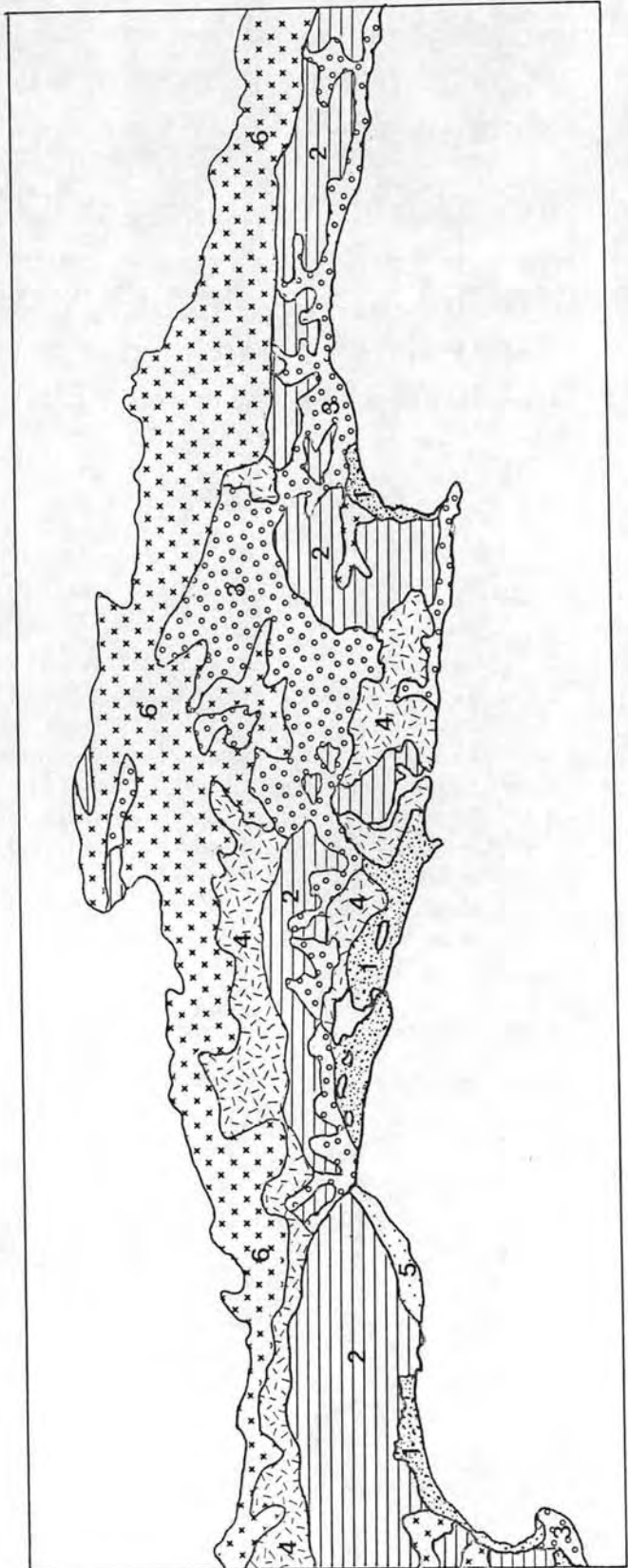
MacVicar *et al.* (1977 *op. cit.* Scriba 1984) describe podsoles as being characterized by the removal of aluminium, iron oxides and organic matter from the A-horizon by leaching and the deposition thereof as ferrihumics in the B-horizon. Podsoles occur along the foothills of the Outeniqua mountains and on the lower coastal plateau typically in areas of higher rainfall.

(V) Red apedal soils

These red or yellow-brown well-drained soils dominate along a narrow strip along the coast from Wilderness to Herolds Bay.

FIG.2/3 SOUTHERN CAPE SOIL TYPES

- 1. Regic sands
- 2. Duplex
- 3. Lithocutanic/lithosols
- 4. Podsols
- 5. Red apedals
- 6. Unconsolidated exposed rock



(ex Scriba 1984; from S.I.R.I. 1983)

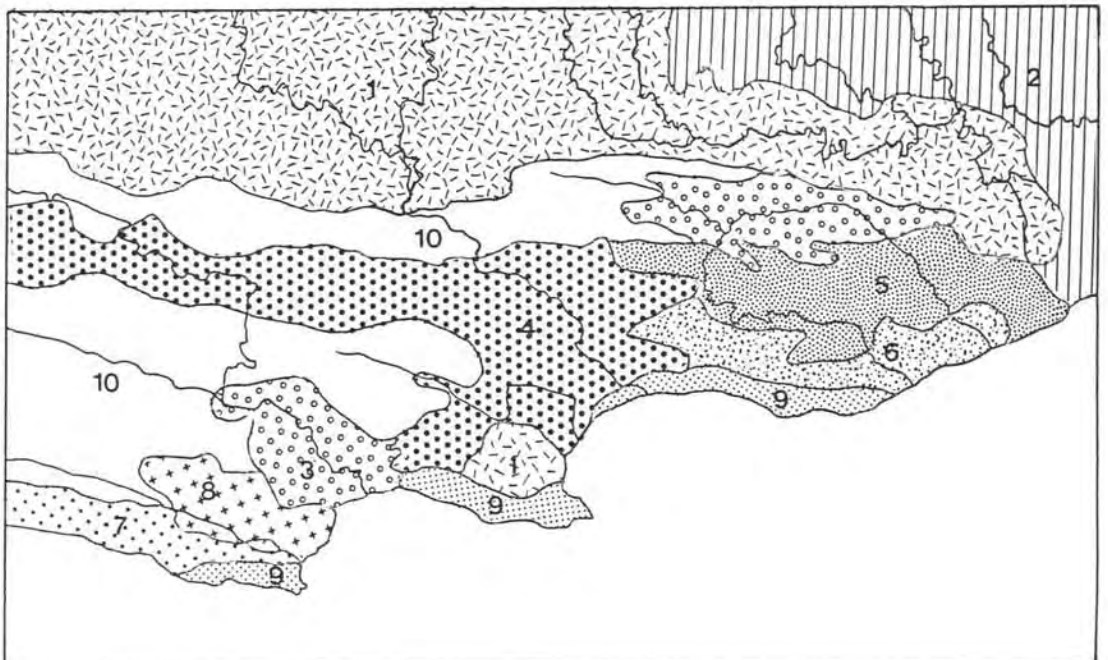
(VI) Unconsolidated soils and exposed rock

Unconsolidated soils, wherever they occur between the exposed rock of the upper mountains, are acid and dark due to an accumulation of organic material.

The predominating soil forms of the intermontane valleys north of the main crest of the coastal mountains are loams of intermediate fertility as defined by Cowling (1982) for the south-eastern Cape. Soil types of the Eastern Cape as classified by Hartmann (1986) are described below (Figure 2/4).

FIG.2/4: SOILS OF THE EASTERN CAPE (ex Everard 1986, after Hartmann, 1986)

1. Weakly developed lime rich soils.
2. Weakly developed and solonetzic soils interspersed with red clays.
3. Weakly developed soils with much rocky land.
4. Relatively deep, red, lime rich sandy clay loams.
5. Weakly developed soils interspersed with red sandy clays.
6. Red porous sandy clay loams and lithosols on lime.
7. Acid loamy sands.
8. Weakly developed stony soils.
9. Coastal sands and sandy soils.
10. Rock and lithosols.



The most important Eastern Cape soil types are described below:

(I) Weakly developed lime-rich soils

These soils predominate north of the Cape Fold Belt outliers. They are lime-rich and generally shallow, often associated with much rocky land.

(II) Weakly developed soils with much rocky land

The mostly shallow soils consist of a topsoil horizon overlying rock or partially weathered rock. They occur in the hilly areas around Grahamstown.

(III) Rock and lithosols

Shallow undifferentiated soils occur on the rocky and steep slopes of the Great Winterhoek, Suurberg and Tadjiesberg mountainous areas.

(IV) Relatively deep, red, lime-rich sandy clay loams

These soils are generally deep, well-drained sandy clay loams. The soil depth is variable on hillslope positions. They predominate in the Sundays River Valley area and extend inland in the intermontane valley between the Little and Great Winterhoek mountains.

(V) Weakly developed soils interspersed with red sandy clays

The typical composition of these soils is a dark grey topsoil overlying a lithocutanic subsoil. Most soils of the Bathurst and Albany districts belong to this type.

(VI) Red porous sandy clay loams

The middle hillslope and footslope positions typically have deep red porous sandy clay loams. They are shallower on the upper

hillslopes and subject to impeded drainage in the valley bottoms. The parent material of these soils are limestone-rich deposits of the Alexandria Formation. They are located mainly in the Alexandria district.

2.2.3.2 Soil fertility

Soil fertility is related to the geological parent material from which the particular soil type is derived and also the leaching regime to which it is subjected. The latter depends on the amount of rainfall, topographic position and soil texture.

Soil types derived from pre-Cape deposits (Cango and Kaaibans Groups, Gamtoos Formation), granite intrusions and recent alluvial, aeolian and marine deposits are usually fertile. Those derived from Bokkeveld and Witteberg shales and sediments of the Uitenhage Group have a variable but generally intermediate fertility status (Cowling 1984, Scriba 1984). In contrast, soils derived from the sandstones of the Table Mountain Group are typically nutrient-poor (Bond 1981, Cowling 1984, Scriba 1984, Van Daalen 1984). The latter predominate in the Southern Cape.

These soil fertility patterns are broadly related to the distribution of the major vegetation types. Fynbos and Afromontane forests occur on the nutrient poor soils, while thickets (e.g. Valley Bushveld) typically grow on nutrient rich soils. These interrelationships are however, not necessarily causally linked. Factors of soil water availability or impediment are probably of greater importance in shaping the distribution of the major vegetation types (cf Tinley 1982).

2.3 Climate

2.3.1 Climatic elements

2.3.1.1 Precipitation

Rainfall in the southern Cape varies considerably with topography, generally increasing with altitude from the coast to the crest of the coastal mountains. On the high peaks it may exceed 1 100 mm/annum,

dropping to 400 mm on the northslope foothills. Mean annual rainfall (R: mm) is linearly related to elevation: $R = 255,8 + 1,769 \text{ ALTITUDE}$ (in metres) ($r^2 = 0,84$; $P < 0,01$; Bond 1981). Rain shadow effects result in a rapid decline in rainfall from the high north slopes into the Langkloof (Bond 1981).

The rain is mostly cyclonic and orographic, with occasional thunderstorms. It normally falls in a soft drizzle. The rainfall is non-seasonal with spring and autumn peaks (Scriba 1984). Data from Goudveld State Forest (Table 2/2) illustrate these peaks as well as altitudinal effects.

| TABLE 2/2: MEAN MONTHLY RAINFALL (mm) AT GOUDVELD STATE FOREST | | |
|--|-----------------------------|----------------------------|
| | Sourflats (216 m a.s.l.) | Millwood (457 m a.s.l.) |
| JANUARY | 58,4 | 84,6 |
| FEBRUARY | 78,5 | 80,5 |
| MARCH | 74,9 | 111,0 |
| APRIL | 51,5 | 83,3 |
| MAY | 59,6 | 80,5 |
| JUNE | 42,9 | 55,4 |
| JULY | 48,8 | 55,1 |
| AUGUST | 66,1 | 73,2 |
| SEPTEMBER | 66,5 | 106,7 |
| OCTOBER | 64,4 | 107,6 |
| NOVEMBER | 75,1 | 102,4 |
| DECEMBER | 62,8 | 96,3 |
| ANNUAL MEANS | 749,5 | 1 036,6 |
| RECORDING PERIOD: 1901 - 1975 | | |
| Cameron, Pretorius and Reynell (1978) | | |

Mean annual rainfall and seasonal distribution patterns in the Eastern Cape are depicted in Figures 2/5 and 2/6.

According to Teague *et al.* (1981) the bulk of the rain comes in relatively few heavy downpours. Some low-intensity rain does however fall, usually lasting intermittently for 2-3 days.

FIG.2/5 SEASONAL DISTRIBUTION OF RAINFALL EASTERN CAPE
 (ex Everard 1985 and Köpke 1986)

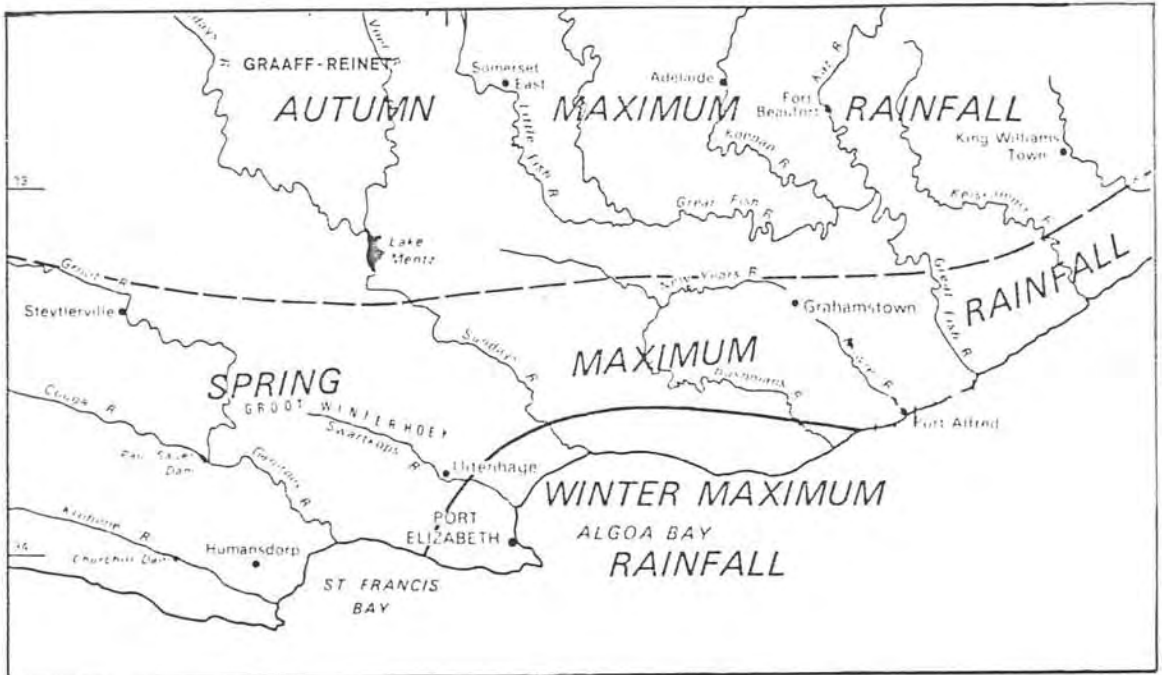
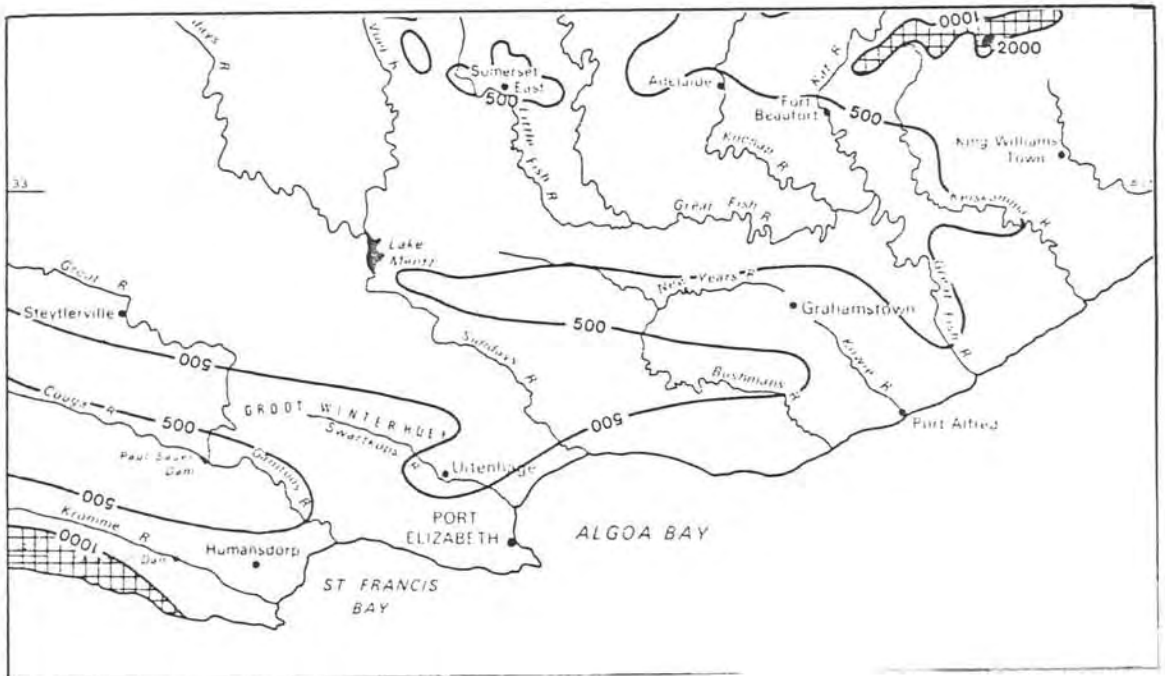


FIG. 2/6 AVERAGE ANNUAL RAINFALL EASTERN CAPE
 (500 and 1000 mm isohyets: ex Everard 1985 and Kopke 1986)



From west to east, rainfall increases from George (780 mm/a) to the Knysna area and Tsitsikamma (1 000 and 1 050 mm/a respectively). It is lower behind the coastal ranges (Langkloof) and along the Keurboomsriver Valley to the coast (± 520 mm/a) (Scriba 1984). The coastal forelands of the eastern Cape, generally receive 600–900 mm/a but the figure drops to below 500 mm/a in the interior and down the broad river valleys (Gamtoos, Sundays, Bushmans, Fish rivers). Regional rainfall characteristics are summarized by season and vegetation type in Tables 2/3 and 2/4.

| TABLE 2/3: RAINFALL MEANS AT SELECTED STATIONS (ex FUGGLE 1981) | | | | | | | | |
|---|----------|-----------|--------------|-------------|--------------|--------|--------|--------|
| | Latitude | Longitude | Altitude (m) | Annual (mm) | Monthly (mm) | | | |
| | | | | | Spring | Summer | Autumn | Winter |
| SOUTHERN CAPE | | | | | | | | |
| Oudtshoorn | 33°35' | 22°12' | 332 | 253 | 21,9 | 15,4 | 26,5 | 20,5 |
| George | 33°58' | 22°28' | 229 | 895 | 86,1 | 73,3 | 79,6 | 59,2 |
| Goudveld | 33°55' | 22°57' | 216 | 879 | 86,5 | 77,8 | 69,1 | 59,6 |
| Millwood | 33°53' | 22°59' | 457 | 1 082 | 100,4 | 96,6 | 87,7 | 76,0 |
| Harkerville | 34°03' | 23°14' | 213 | 976 | 87,9 | 71,1 | 83,7 | 82,5 |
| Plettenberg Bay | 34°03' | 23°22' | 73 | 655 | 59,0 | 38,7 | 58,2 | 62,4 |
| EASTERN CAPE | | | | | | | | |
| Jeffreys Bay | 34°03' | 24°41' | 6 | 510 | 46,8 | 29,8 | 46,0 | 47,4 |
| Uitenhage | 33°42' | 25°26' | 167 | 495 | 54,8 | 35,8 | 46,1 | 28,1 |
| Alexandria | 33°42' | 26°22' | 198 | 874 | 87,9 | 58,1 | 75,8 | 69,6 |
| Grahamstown | 33°18' | 26°32' | 539 | 622 | 61,4 | 52,8 | 57,6 | 35,7 |
| Bushmans River Mouth | 33°42' | 26°40' | 76 | 621 | 62,1 | 40,3 | 56,9 | 47,6 |
| Port Alfred | 33°34' | 26°50' | 61 | 652 | 65,9 | 45,6 | 60,7 | 45,1 |

Mists are important in the mountains where drizzle from S and SE winds can result in considerable precipitation (Cowling 1984). Snow occurs annually on the higher peaks of the Southern and Southeastern Cape coastal mountain ranges, but is more common and lies longer in the mountains of the interior (Bond 1981). Hailstorms are rare (Scriba 1984).

| TABLE 2/4: RAINFALL MEANS FOR VARIOUS VEGETATION TYPES <i>VIDE</i> SECTION 2.4 (ex FUGGLE 1981) | | | | | |
|---|-------------|--------------|--------|--------|--------|
| | ANNUAL (mm) | MONTHLY (mm) | | | |
| | | Spring | Summer | Autumn | Winter |
| FYNBOS | 587 | 55,3 | 43,5 | 55,3 | 41,3 |
| KNYSNA FOREST | 817 | 78,1 | 65,3 | 71,0 | 61,5 |
| ALEXANDRIA FOREST | 723 | 72,1 | 45,5 | 64,5 | 59,0 |
| VALLEY BUSHVELD | 570 | 53,1 | 41,3 | 48,5 | 29,4 |
| NOORSVELD | 229 | 20,3 | 19,2 | 25,8 | 11,5 |
| KARROID BROKEN VELD | 268 | 23,2 | 15,1 | 27,7 | 18,8 |

2.3.1.2 Temperature

Temperatures in the study area tend to increase with decreasing altitude and increasing longitude, i.e. warmer temperatures are experienced towards the Eastern Cape, in valley bottoms and in the Karroid interior (Tables 2/5 and 2/6). An environmental lapse rate of 0,6°C per 100 m has been measured in the Great-Winterhoek mountains near Uitenhage (Cowling 1984).

The temperature regime for the coastal plains and mountains tends to be equable, with greater diurnal and annual variations in the Eastern Cape river valleys. Mean monthly maximum and minimum temperatures at 4 localities are illustrated in Figure 2/7.

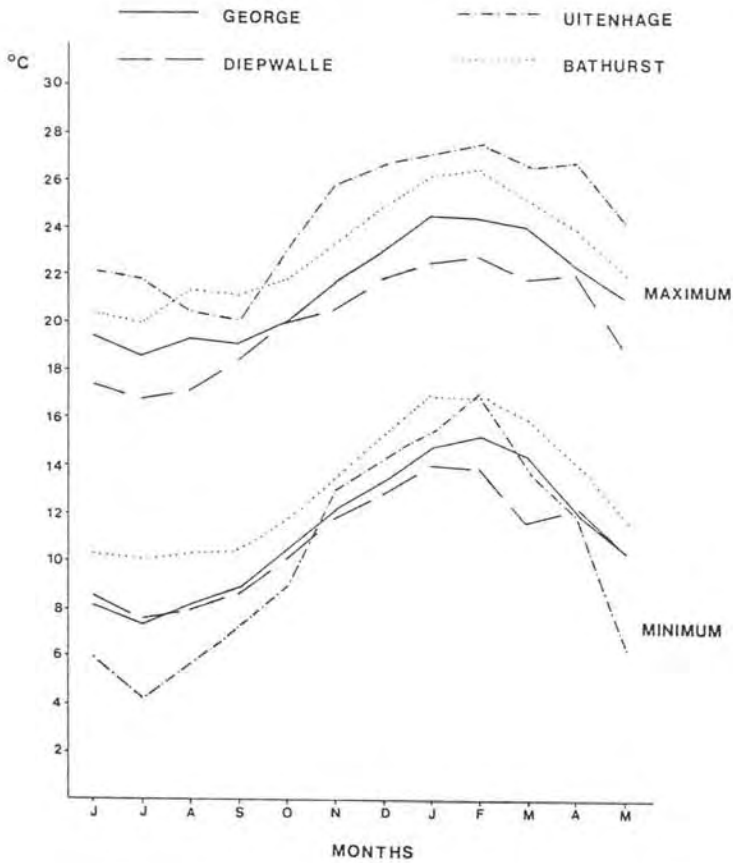
Cold snaps occur in winter associated with strongly developed cold fronts when followed by an anticyclone. Hot spells are correlated with persistent bergwinds (usually in spring) and with warm summer anti-cyclones (Cowling 1984). Frost is practically unknown in the coastal zone of the southern Cape (Bond 1981) and uncommon in the equivalent zone in the eastern Cape (Cowling 1984). It does occur during winter in the interior north of the Cape Fold Belt mountains.

| TABLE 2/5: TEMPERATURE CHARACTERISTICS AT SELECTED STATIONS (ex FUGGLE 1981) | | | | | | | | |
|---|----------|-----------|----------|-------------|---------------------------|--------|--------|--------|
| | Latitude | Longitude | Altitude | Annual (mm) | Mean daily temperature °C | | | |
| | | | | | Spring | Summer | Autumn | Winter |
| SOUTHERN CAPE | | | | | | | | |
| Oudtshoorn | 33°35' | 22°12' | 335 | 17,6 | 17,6 | 23,0 | 17,7 | 12,1 |
| George | 33°58' | 22°25' | 221 | 15,9 | 15,1 | 19,2 | 16,7 | 12,7 |
| Concordia | 34°00' | 23°03' | 259 | 16,4 | 15,4 | 19,3 | 17,2 | 13,7 |
| Diepwalle | 33°57' | 23°10' | 517 | 15,6 | 14,5 | 18,2 | 16,9 | 12,9 |
| Langkloof | 33°47' | 23°35' | 671 | 15,3 | 14,5 | 19,1 | 16,2 | 11,4 |
| Stormsriver | 33°58' | 23°53' | 243 | 15,3 | 14,8 | 18,3 | 16,0 | 12,1 |
| EASTERN CAPE | | | | | | | | |
| Uitenhage | 33°47' | 25°26' | 32 | 18,4 | 17,7 | 22,2 | 19,3 | 14,4 |
| Port Elizabeth | 33°59' | 25°36' | 60 | 17,7 | 16,8 | 21,1 | 18,4 | 14,3 |
| Grahamstown | 33°18' | 26°32' | 539 | 16,4 | 16,1 | 20,1 | 17,0 | 12,3 |
| Bathurst | 33°31' | 26°49' | 259 | 18,1 | 17,1 | 21,1 | 18,9 | 15,4 |

| TABLE 2/6: TEMPERATURE REGIMES FOR VARIOUS VEGETATION TYPES (ex FUGGLE 1981) | | | | | |
|---|----------------|---------------------------|--------|--------|--------|
| | ANNUAL (°C) | Mean daily temperature °C | | | |
| | | Spring | Summer | Autumn | Winter |
| FYNBOS | 16,8 | 16,0 | 20,3 | 17,2 | 12,7 |
| KNYSNA FOREST | 16,2 | 15,2 | 19,3 | 17,1 | 13,2 |
| ALEXANDRIA FOREST | 17,8 | 16,8 | 21,0 | 18,5 | 14,6 |
| EASTERN PROVINCE THORNVELD | 18,1 | 17,1 | 21,1 | 18,9 | 15,4 |
| VALLEY BUSHVELD | 18,3 | 17,7 | 21,6 | 18,8 | 14,6 |
| KARROID BROKEN VELD | 18,0 | 17,4 | 23,0 | 18,8 | 12,9 |

FIG.2/7 MONTHLY MEANS OF TEMPERATURES AT SELECTED STATIONS

Data ex Bond 1981, Cowling 1984 and Departmental Records: Environment Affairs

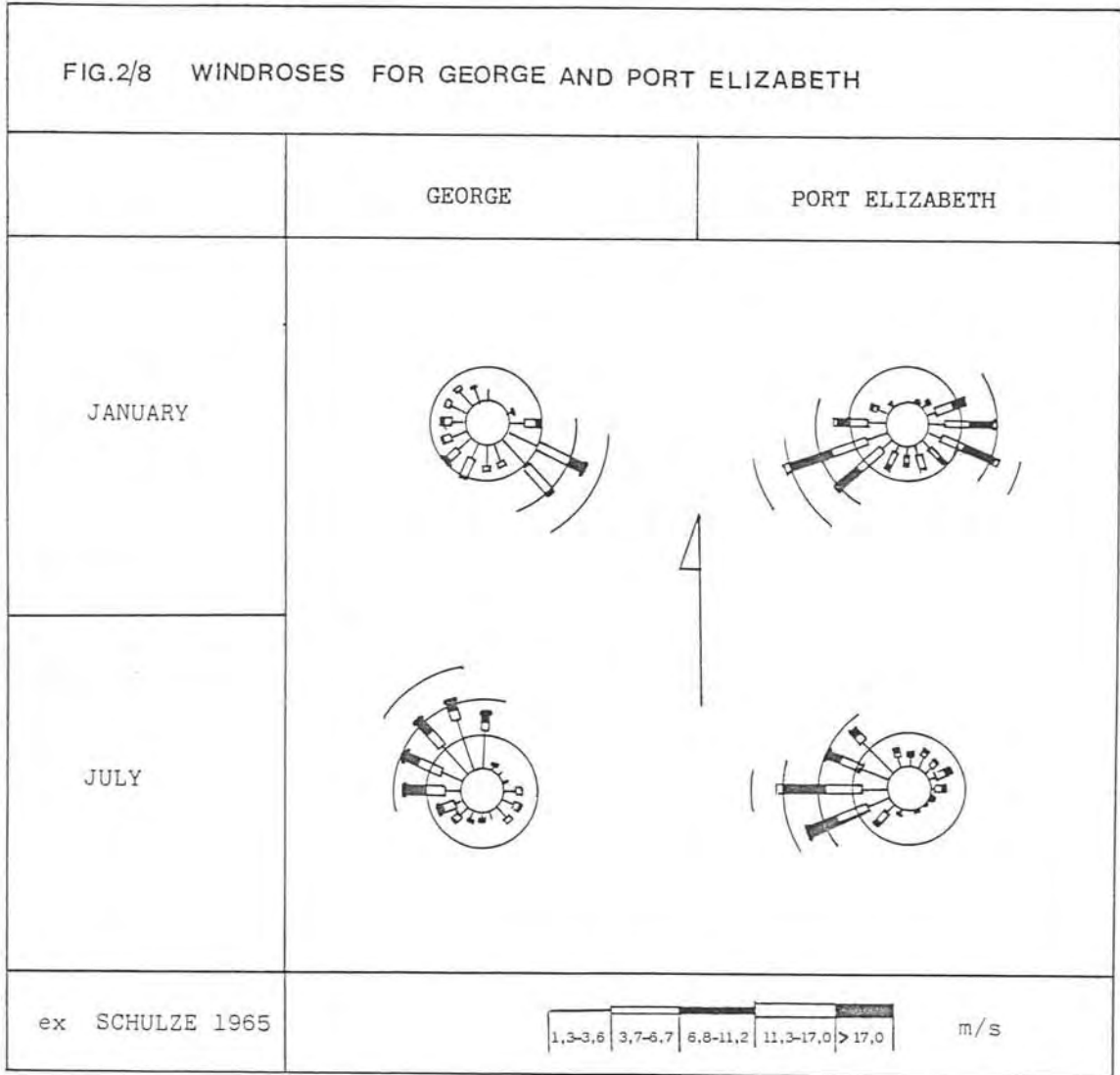


2.3.1.3 Wind

Winds in the Southern Cape coastal parts are mostly south to south-easterly in summer and northwesterly in winter. The main rain-bringing winds are south-westerly (Figure 2/8). No major directional tendencies are encountered in autumn and spring. In the eastern coastal parts of the region wind from the south-west and west pre-dominate throughout the year, although east and southeast winds are important during the summer months (Figure 2/8, McLachlan *et al.* 1982).

Hot, dry bergwinds occur periodically during the winter months. These are caused by dry subsiding air moving off the interior plateau in response to strong coastward pressure gradients (Bond 1981).

The wind regime in the mountains probably differs from that described (Everard 1985). In the interior, the winds are usually north-westerly (mainly in winter) and during thunderstorms strong and gusty south-westerly winds are a common feature (Schulze 1965).



2.3.2 Climatic synthesis

Combining the thermal regions of Poynton (1971) with Thornthwaite's moisture regions (cf Schulze and McGee 1978) the climate of the study area can be characterized as humid/subhumid (Southern Cape) to sub-humid/semi-arid (Eastern Cape) warmer temperate to subtropical.

According to a simplified Köppen classification (Schulze and McGee 1978) the following climatic types occur:

Cfb Southern and Eastern Cape coastal zone

BSk Southern Cape interior

BSh South-eastern and Eastern Cape interior extending down river valleys.

The components of the classification are defined in Table 2/7.

| Table 2/7: A simplified Köppen classification relevant to Southern Africa (after Köppen & Geiger 1936) | | |
|--|---|---|
| 1st letter | 2nd letter | 3rd letter |
| A, C, D Sufficient heat and precipitation for forest vegetation | | |
| A. Equatorial climates Mean temperature above 18°C for all months | f Sufficient precipitation during all months m Monsoon climate (forest vegetation despite dry season) w Winter dry season | |
| B. Arid zones | S Steppe climate W Desert climate temperature below 18°C | h dry-hot, mean annual temperature over 18°C k dry-hot, mean annual temperature below 18°C |
| C. Warm temperate climates Coldest month 18°C to 3°C | s Summer dry season w Winter dry season f sufficient precipitation during all months | a warmest month over 22°C b warmest month below 22°C but at least 4 months above 10°C |

Cowling (1982; 1984) distinguished three climatic types for the south-eastern Cape which can be extended to apply to the entire study area.

(I) Humid coastal mountain climate

The rainfall is under strong orographic influence and the highest precipitation is therefore recorded along the coast-facing slopes and foothills of the Cape Fold Belt mountain ranges (between 800 - 1200 mm). Temperatures are equable, but lower than of the surrounding lowlands. Light frosts and snow occasionally occur during the winter (Figures 2/9 and 2/10).

FIG.2/9 : GEORGE (221m) 16,4 860
e (73)

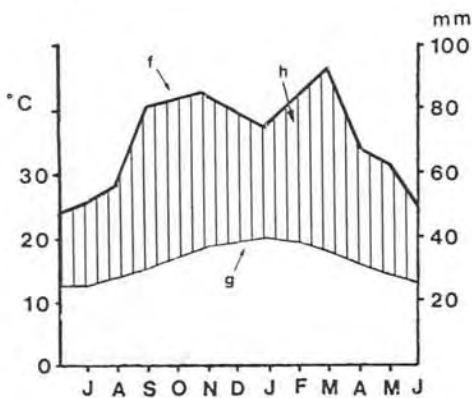
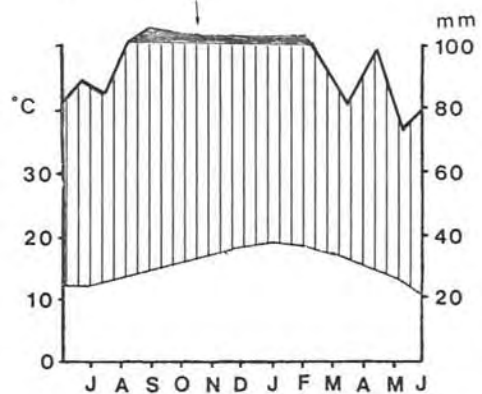


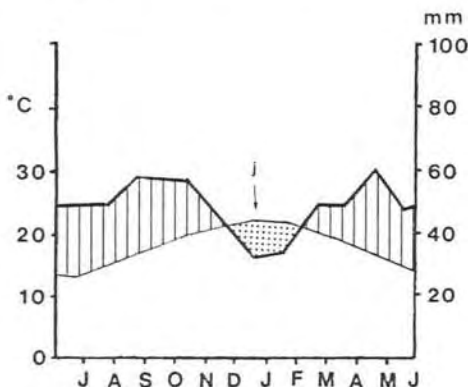
FIG.2/10 : DIEPWALLE (519m) 15,5 1214
(26)



(II) Coastal plain subhumid climate

The climate is mild with relatively low diurnal and annual temperature ranges. Average annual temperatures at various localities fall within the range of 15,5°C in the west to 18,0°C in the eastern parts. Annual rainfall means usually lie within 500-800 mm (Figure 2/11).

FIG.2/11 : PORT ELIZABETH (58m) 17,3 576
(84)



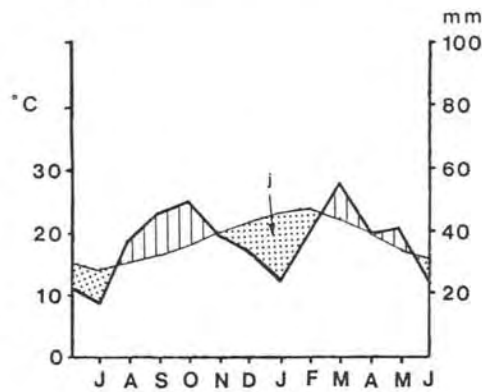
LEGEND

- a Station
- b Altitude
- c Mean annual temperature in °C
- d Mean annual precipitation in mm
- e Number of years of observation (the first stands for temperature, the second for precipitation)
- f Monthly means of precipitation (thick line) in mm
- g Monthly means of temperature (thin line) in °C
- h Humid period (hatched area)
- i Perhumid area (black area), mean monthly rainfall over 100 mm (scale reduced ten times)
- j Arid period (dotted area)

(III) Semi-arid valley climate

The river valleys of the South-eastern and Eastern Cape have a climate more similar to the Karroid interior in being warmer, drier and more variable than that of the adjacent mountains and interfluves. Temperature extremes are great and rainfall variability is high (Cowling 1984 *op. cit.* Louw 1976), generally below 500 mm per annum (Figure 2/12).

FIG.2/12 : HANKEY (122 m) 18,1 432
(52 - 24)



2.4 Vegetation

2.4.1 Vegetation classification

The vegetation classification used for the study area was adapted from that of Moll *et al.* (1984). This is focused on the fynbos biome and treats Cape Shrubland communities in detail, but lacks an adequate differentiation of the Subtropical Transitional Thicket communities. For the purposes of this study, their Cape Shrubland community classification has been simplified while the Subtropical Transitional Thicket communities have been subdivided following Acocks (1975), Cowling (1984) and Everard (1986).

The biogeographic affinities of vegetation communities are summarized in Table 2/8.

| TABLE 2/8: VEGETATION CATEGORIES IN THE STUDY AREA (SOUTHERN AND EASTERN CAPE) | | |
|---|--|---|
| Mapped vegetation category | Biogeographic affinities | Floral Kingdom Divisions |
| <u>Cape Fynbos Shrublands</u> Mountain Fynbos Grassy Fynbos | CAPE COMMUNITIES | CAPE FLORAL KINGDOM |
| <u>Mosaic of Cape Fynbos Shrubland and Subtropical elements</u> Dune Fynbos | CAPE/SUDANO-ZAMBEZIAN COMMUNITIES | CAPE - PALAEOTROPIC FLORAL KINGDOM TRANSITION |
| <u>Cape Transitional Small-Leafed Shrublands</u> Renosterveld | CAPE/KAROO-NAMIB COMMUNITIES | |
| <u>Subtropical Transitional Thicket</u> Kaffrarian Dune Thicket Alexandria Forest | TONGALAND-PONDOLAND/AFROMONTANE COMMUNITIES | PALAEOTROPIC FLORAL KINGDOM |
| Valley Bushveld Norsveld Spekboomveld | SUDANO-ZAMBEZIAN/TONGALAND PONDOLAND/KAROO-NAMIB COMMUNITIES | |
| <u>Subtropical Thicket-Grassland Mosaic</u> Bushclump Savanna | TONGALAND-PONDOLAND/SUDANO-ZAMBEZIAN COMMUNITIES | |
| <u>Afromontane Forest</u> Knysna Afromontane Forest Communities | AFROMONTANE COMMUNITIES | |
| <u>Karroid Shrublands</u> Karroid Communities | KAROO-NAMIB COMMUNITIES | |
| Adapted from Moll <i>et al.</i> (1984), Palmer 1980 and Cowling (pers. comm.) | | |

2.4.2 Vegetation description

The distribution of vegetation types is shown on Map 3. Distributional and environmental features are presented in Table 2/9 and each vegetation category is described below. Afromontane Forest and Valley Bushveld are the most important vegetation types as habitat for the

TABLE 2/9: SYNECOLOGICAL RELATIONSHIPS OF THE VEGETATION IN THE STUDY AREA (SOUTHERN + EASTERN CAPE)

| VEGETATION UNIT | DISTRIBUTION | PHYSIOGRAPHY | RAINFALL (mm/a) | SOIL |
|---------------------------|--|--|-----------------|--|
| Knysna Afromontane Forest | Between Mossel Bay and Uitenhage | On the coastal ranges of the Cape Folded Belt and in the Knysna region | > 800 | Acid, mostly deep organic-rich soils of good moisture status |
| Mountain Fynbos | Outeniqua, Tsitsikamma Kouga, Kammanassie, Baviaanskloof, Great Winterhoek, Elandsberg and Swartberg mountain ranges | Mainly from foothills up to and including upper mountain slopes. Upper south slopes in drier regions | > 750 | Acid, infertile, shallow to deep sandy loams, apedal subsoils often with eluviated horizon, drainage variable |
| Grassy Fynbos | Baviaanskloof, Eastern Kouga, Zuuranysberg, Elandsberg, Groot Winterhoek, Groot River Heights and Suurberg ranges. Tsitsikamma Humansdorp and Albany coastal forelands | North and lower south slopes of ranges, Tertiary planation surfaces and coastal forelands, mainly south slopes in the Suurberg | 400-750 | Acid, infertile, shallow to deep sandy loams to loamy sands, often of colluvial origin, some paleosols, drainage variable |
| Dune Fynbos | Intermittent stretches along the coast between Mossel Bay and Cape Recife | Coastal dunes | 300-800 | Mostly deep, neutral to alkaline calcareous sands, occasionally lithosols on calcrete, drainage variable |
| Renosterveld | Gouritz River to Port Elizabeth, with outliers near Grahamstown | Coastal forelands and intermontane valleys, pediments and lower slopes of Cape Fold Belt mountains in drier regions | 300-600 | Highly variable: duplex soils on coastal forelands and intermontane valleys, colluvial soils and lithosols on lower mountain slopes, more fertile and often heavier in texture than fynbos soils |
| Kaffrarian Dune Thicket | Stretches along coast from Jeffreys Bay eastwards | Littoral dune zone | 500-750 | Deep, calcareous coastal dune sands |
| Alexandria Forest | Coastal forelands of the Alexandria district | Substrate dissected by dry valleys forming an undulating terrain | 550-950 | Deep Quaternary sands overlying loosely consolidated Tertiary coastal limestone |
| Valley Bushveld | In valleys of the Gamtoos, Swartkops, Sundays, Bushmans, Kariega, Kowie and Great Fish rivers | Mainly river valleys with outliers in intermontane valleys | 350-500 | Soil depth variable, fertile and generally well-drained soils |
| Noorsveld | Eastern Cape interior north of Grootriver Heights and Suurberg, mainly Jansenville area | Wide, undulating middle part of the Sundays River valley | 250 (av) | Shallow, stony soils (but deeper than Karroo soils) |
| Spekboomveld | Arid slopes of the mountains in the Klein Karoo and Eastern Cape interior | Steep lower slopes of arid mountains of the interior | 250-300 | Variable, typically colluvial, rocky talus-type soils |
| Bushclump Savanna | Coastal forelands from Algoa Bay eastwards | On interfluves between river valleys | 500-750 | Mainly duplex soils, seasonally waterlogged |
| Karroid Shrublands | Arid interior of the Southern and Eastern Cape (Great and Little Karoo) | Predominantly flat terrain | 100-300 | On soils derived from shales and mudstones. More alkaline and sandier. Relatively infertile. |

Data from Acocks 1975, Cowling 1982, Marker and Russel 1984, Everard 1986 and Lubke *et al.* 1986

MAP 3

VEGETATION OF THE STUDY AREA

CAPE PROVINCE (SOUTH AFRICA)

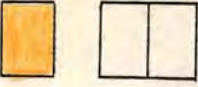
KNYSNA AFROMONTANE FOREST
 MOUNTAIN FYNBOS
 GRASSY FYNBOS
 DUNE FYNBOS



RENOSTERVELD
 KAFFRARIAN DUNE THICKET
 ALEXANDRIA FOREST
 VALLEY BUSHVELD



NOORSVELD
 SPEKBOOMVELD (not mapped)
 BUSHCLUMP SAVANNA
 KARROID SHRUBLANDS



DUNE FYNBOS/KAFFRARIAN DUNE THICKET MOSAIC
 RENOSTERVELD/AGRICULTURE MOSAIC

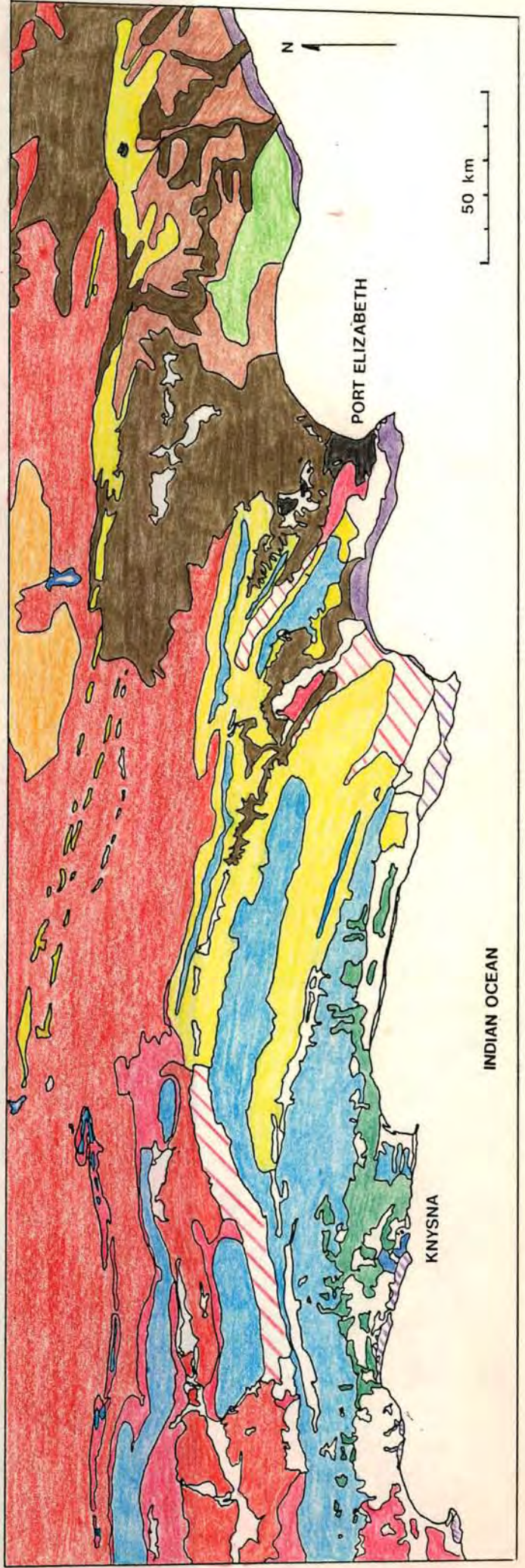


AREAS CLEARED OF NATURAL VEGETATION (eg. CULTIVATED LAND, PLANTATIONS)



CITIES AND TOWNS

DAMS



(adapted from Moll et al 1984 and Lubke et al 1986)

bushpig in the Southern and Eastern Cape respectively. These two types are accordingly described more exhaustively.

2.4.2.1 Afromontane Forest

Geldenhuis (1982, 1983) subdivided the Knysna forests into three major zones according to species composition: wet mountain, moist to medium moist plateau (Plate 5a), and dry valley slope or coastal forests. Although the Knysna forests as such are considered Afromontane (White 1978), only the wet mountain forests are typically so. The dry coastal forest or scrub forest is very rich in species, many of them shared with the Indian Ocean Coastal Belt forests (Moll and White 1978). The most common species of the plateau forests, *Olea capensis* ssp. *macrocarpa* is equally abundant in the Afromontane and Indian Ocean Coastal Belt forests.

Based on Phillips (1931), Laughton (1937) and Von Breitenbach (1974), six forest types are presently recognized. The forest type classification follows a soil moisture availability gradient as reflected in the structure and composition of the vegetation. Soil moisture availability increases with altitude (orographic effect), soil depth and impeded drainage and is modified by varying solar radiation on different aspects.

Very dry scrub forest (vdSF)

Very dry scrub forest is found on sites with reduced moisture availability (lower plateau, western and northern aspects, ridges). It consists of a dense mixture of tall shrubs (3-6 m) and stunted, bushy trees (6-12 m).

Abundantly represented as small trees or shrubs are *Cassine aethiopica* and *C. peragua*. Others include *Allophyllus decipiens*, *Apodytes dimidiata*, *Buddleia saligna*, *Psydrax obovata* ssp. *obovata*, *Canthium ventosum*, *Cassine papillosa*, *Diospyros dichrophylla*, *Euclea schimperi* var. *schimperi*, *Xanthoxylon davyi*, *Maytenus acuminata*, *Pterocelastrus tricuspidatus*, *Rhus chirindensis*, *R. lucida*, *Sideroxylon inerme* and

PLATE 5

- a. Knysna Forest (Goudveld)
- b. Commercial *Pinus radiata* stand (Goudveld)
- c. Fynbos (Goudveld)

PLATE 5

a



b



c



Tarchonanthus camphoratus. The common shrubs are *Buddleia salviifolia*, *Carissa bispinosa*, *Dovyalis rhamnoides*, *Euclea racemosa*, *Gonioma kamassi*, *Maytenus heterophylla* and *Rhus tomentosa*.

The forest floor is usually covered with dry leaf litter and practically devoid of an herbaceous ground layer. Groups of low ferns and herbs are confined to more open patches.

Dry high forest (dHF)

On sites with a moderately dry climate and edaphic factors reducing soil moisture availability, such as excessively drained deep sandy soils, deep clay soils, or shallow soils drying out in summer, dry high forest is normally encountered.

This is a fairly dense type of forest consisting of small to medium tall trees forming an irregular canopy (8-10 m), and an open undershrub layer with a rich ground flora.

The main canopy-forming trees are: *Pterocelastrus tricuspidatus* (most frequent), *Apodytes dimidiata*, *Psydrax obovata* ssp. *obovata*, *Cassine papillosa*, *Curtisia dentata*, *Lachnostylis hirta*, *Olea capensis* ssp. *macrocarpa*, *Olinia ventosa*, *Podocarpus falcatus*, *P. latifolius* and *Rapanea melanophloeos*. In the lower storey *Gonioma kamassi*, *Canthium mundianum*, *Cassine peragua*, *Diospyros dichrophylla* and *Maytenus acuminata* predominate. The low and rather open layer of undershrubs consists mainly of thorny species such as *Cassine haematocarpa*, *Dovyalis rhamnoides*, *Maytenus heterophylla* and *Scutia myrtina*.

The ground layer is well developed and is formed by ferns, grasses and herbs (e.g. *Thelypteris bergiana*, *Pellaea viridis*, *Oplismenus hirtellus*). The strangling climber *Pyrenacantha scandens* and *Rhoicissus tomentosa* are often conspicuous.

Medium-moist high forest (mmHF)

Medium-moist high forests typically occur on the plateau with its temperate and humid climate and fairly moist, moderately deep soils.

The forest consists of two fairly dense tree strata above a very dense undershrub layer and a generally scanty ground flora. This forest type covers approximately a third of the forest area.

The upper main canopy (12-22 m) is formed by *Olea capensis* ssp. *macrocarpa*, *Podocarpus latifolius* (the two most abundant species), *Apodytes dimidiata*, *Olinia ventosa*, *Pterocelastrus tricuspidatus* and *Rapanea melanophloeos*. Specimens of *Podocarpus falcatus* are generally scattered and often emerging above the general canopy. Common co-dominants include *Canthium obovatum*, *Curtisia dentata* and *Nuxia floribunda*. *Ocotea bullata* and *Maytenus peduncularis* less frequently so. Common understorey species are *Gonioma kamassi*, *Burchellia bubalina*, *Canthium mundianum*, *C. ventosum*, *Diospyros whyteana*, *Halleria lucida*, *Maytenus heterophylla* and *Trimeria grandifolia*.

The undershrub layer is about 3-6 m high and usually consists of a dense continuous thicket of *Trichocladus crinitus*. The ground flora of small ferns, low grasses and herbs is sparse under the dense undershrub, but becomes richer in small openings.

Moist high forest (mHF)

This forest type is found on sites which are moist throughout the year, such as eastern and southern slopes and level portions of the upper plateau with restricted drainage.

The forest consists of three ill-defined mid-dense to broken tree strata, a varying dense to open undershrub layer and a luxuriant ground flora. The upper canopy of 20-30 m height is often overtowered by very tall *Podocarpus falcatus* and *Olea capensis*. Other canopy-forming species include *Apodytes dimidiata*, *Nuxia floribunda*, *Ocotea bullata*, *Podocarpus latifolius*, *Rapanea melanophloeos* and more occasionally *Ilex mitis*, *Kiggelaria africana* and *Maytenus peduncularis*. In the intermediate storey *Psydrax obovata* ssp. *obovata*, *Cassine papillosa*, *Curtisia dentata*, *Platylophus trifoliatus* and *Pterocelastrus tricuspidatus* are frequently occurring. *Gonioma kamassi* is again the most common understorey species.

The undershrub layer is of variable distribution, height and density. *Trichocladus crinitus* groups are generally scattered and more open. *Cyathea capensis* (a tree fern) is typically found in wet depressions and along streamlets. The rich ground flora is dominated by ferns: *Blechnum* spp, *Rumohra adianthiformis* and *Pteris buchananii*. A typical feature is the frequent occurrence of several-stemmed *Ocotea bullata* and *Platylophus trifoliatus*, arising from large old stumps.

Wet high forest (WHF)

Wet high forests are associated with cool, wet climatic conditions and badly drained to waterlogged soils on southern and eastern slopes, mountain foothills and upper plateau sites.

A medium-dense two-storeyed stocking of narrow-crowned trees forms a 12-20 m high canopy over a tree fern storey or luxuriant, shrub interspersed ground vegetation. The irregular broken canopy is usually formed by *Ocotea bullata*, *Cunonia capensis* and *Podocarpus latifolius*. *Gonioma kamassi* and *Nuxia floribunda* are common dominants. In the lower tree storey *Curtisia dentata*, *Halleria lucida* and *Olea capensis* spp. *capensis* are numerous.

On the very badly drained sites a dense jungle of *Cyathea capensis* occurs. On more open, less badly drained sites tree ferns are replaced by scattered *Sparrmannia africana* and dense communities of *Blechnum* ferns.

Very wet scrub forest (vwsf)

On very cool and wet climatic sites or very shallow peaty loam soils, very wet scrub forest occurs. It consists of an open mixture (6-10 m) of stunted and bushy trees and shrubs over a dense ground layer.

Trees forming the canopy include *Cunonia capensis*, *Ocotea bullata*, *Halleria lucida*, *Platylophus trifoliatus*, *Podocarpus latifolius*, *Rapanea melanophloeos* and *Virgilia divaricata*. Common shrubs are *Cyathea capensis*, *Cassine parvifolia*, *Diospyros glabra*, *Laurophyllus capensis*

and *Sparrmannia africana*. The luxuriant ground layer consists mainly of *Blechnum attenuatum*, *B. capense*, *B. tabulare*, *Gleichenia polypodioides* and *Todea barbara*.

2.4.2.2 Cape Fynbos Shrublands

The shrublands and heathlands of this category predominate on acid, infertile sandy substrates of the Cape Fold Belt mountains and coastal plains. Cape Fynbos Shrublands have the structural characteristics of the "heathland syndrome", including small, long-lived leaves, sclerophylly and evergreen hemicryptophytes (cyperoids and restioids) (Specht 1979 ex Cowling 1984). Typical differentiating families include the *Proteaceae*, *Ericaceae* and *Restionaceae*.

(a) Mountain Fynbos

Moll *et al.* (1984) recognize three main subdivisions based on a moisture gradient from wet to dry sites, and corresponding physiognomic characteristics of the vegetation. Wet mountain fynbos consists largely of closed, mid-high to tall ericoid or proteoid shrublands on annually or perennially waterlogged sites (Plate 5c). Mesic mountain fynbos comprises open to closed plant communities of restioid, ericoid and proteoid mixtures on seasonally waterlogged mesic sites. Dry mountain fynbos communities are generally more open and consist of tall restioids with the predominance of low shrubs. These communities are found on xeric sites, usually on northern slopes.

These subdivisions of Mountain Fynbos are structurally heterogenous and should rather be seen as landscape units with a certain specified set of communities which are detailed for the study area in Tables 2/10 and 2/11.

(b) Grassy Fynbos

This unit includes the fynbos communities of the lower north slopes and planed forelands of the Cape Fold Belt in the southeastern Cape (Cowling 1984). Structurally, grassy fynbos is similar to the mountain fynbos

TABLE 2/10: Fynbos plant communities of the coastal mountain ranges (Outeniqua and Tsitsikamma Mountains)

| Communities | Habitat | Diagnostic features |
|---|---|--|
| Heathlands | | |
| Wet heathlands; southern slopes | Wet south slopes. 600m to mountain crests | Dense, small-leaved shrubland; 0,5-1,0m high. Restioid cover more than 50%. Mid-dense, small-leaved ericoid-restioid shrubland. Scattered broad-leaved shrubs. Height 0,5 to 1,0m. |
| northern slopes | Wet north slopes. 700m to mountain crests | |
| Graminoid heathlands | Steep, rocky north aspects 380 - 1 060m | Tall open canopy of <i>Simoneilus multiflorus viridescens</i> |
| Proteoid shrublands | | |
| Proteoid shrublands with a heath understorey. Medium-tall mid-dense <i>Leucadendron eucalyptifolium</i> / <i>Protea mundii</i> / <i>P. neriifolia</i> shrubland | Mesic south aspects: 400-1 160m | Closed canopy formed by these species. Dense understorey of restioids, graminoids and small-leaved shrubs |
| Tall sparse to mid-dense <i>Leucadendron uliginosum</i> shrubland with a closed to open heath understorey | Gravelly soils on N and NE aspects at higher elevations; 370-1 240m | <i>L. uliginosum</i> visually dominant in the canopy. Understorey varies from a closed to an open heath |
| Tall mid-dense <i>L. eucalyptifolium</i> / <i>Berzelia intermedia</i> shrubland | Steep mesic south aspects; 300-1 230m | Dense canopy of broad sclerophyll proteoid leaves; 1,5-2,0m overlies a small-leaved ericoid understorey |
| Medium tall mid-dense <i>P. neriifolia</i> / <i>P. coronata</i> shrubland | Low to mid-altitude southern slopes; 350-880m | Fairly open canopy of proteoid leaves. Ericoid understorey |
| Tall dense <i>P. aurea</i> shrubland | Lower elevations, south and north aspects; 420-1 000m | May form woodlands with a dense canopy; sparse cyperoid understorey |
| Proteoid shrublands with a mixed ericaceous/graminoid understorey | | |
| Medium-tall dense, <i>P. neriifolia</i> / <i>P. mundii</i> shrubland | Moderately steep, mesic northerly aspects | Canopy a proteoid layer 1-2m tall. Understorey dominated by shrubs and graminoids |
| Medium-tall, dense <i>P. repens</i> shrubland | Valley bottoms, northern slopes; 550-625m | Proteoid canopy 1-2m, dominated by <i>P. repens</i> |
| Restioid shrublands | | |
| Medium-tall, mid-dense <i>Elegia galpinii</i> shrubland with emergent proteoids | North aspects, shallow rocky soils; 610-1 210m | Tall coarse-stemmed restios with broad tussocks. Proteoids are generally present |
| Medium-tall mid-dense restioid shrublands | Mesic colluvial soils; north slope valley bottoms; 640-890m | Restio tussocks 1-2m tall emergent proteoids |
| Dry shrublands | | |
| Waboomveld (medium-tall to low mid-dense to open <i>P. nitida</i> shrubland) | Mid and lower elevations 600-900m on northern talus slopes | Very variable. <i>P. nitida</i> always present. Rich in C4 grasses |
| Arid fynbos | Lower northern foothills 300-600m. Shallow stony soils | Low, open or sparse shrublands dominated by shrubs. Restios seldom important (Southwood 1982) |

TABLE 2/11: Fynbos plant communities of the inland mountain ranges (Southern Cape and Tsitsikamma Forest Regions)

| Communities | Habitat | Diagnostic features |
|--|---|--|
| Heathlands | | |
| Mountain crest heathlands | Rocky crests and steep slopes above ± 1 700m | Dense, small-leaved ericoid shrubs with scattered ground proteas |
| Plateau heathlands | High altitude plateau on northern slopes of Swartberg East | Low, closed ericoid/graminoid heathland |
| Tall, <i>Erica demissa</i> grassy heathlands | Steep, cool, southern aspects (Baviaans-koof) | Dense canopy of <i>Erica demissa</i> with a grassy understorey |
| Proteoid shrublands | | |
| Medium-tall, mid-dense <i>Protea punctata</i> shrubland | Cool, mesic upper slopes | Dominated by <i>Protea punctata</i> , with Ericaceae ground-layer |
| Medium-tall, mid-dense <i>Protea repens</i> shrubland | Mid to lower slopes with southern aspects predominating | Dominated by <i>Protea repens</i> , with a restioid ground-layer |
| Medium-tall, mid-dense <i>Protea lorifolia</i> shrubland | Mid to lower slopes with northerly aspects predominating | Dominated by <i>Protea lorifolia</i> , with a restioid ground-layer |
| Scattered <i>Protea</i> /restioid shrubland | Mid altitudinal crest plateaux in Klein Swartberg and Anysberg | Variably scattered <i>Protea</i> spp. with a visually dominating restioid ground-layer |
| Tall, mid-dense <i>Protea mundii</i> / <i>Leucadendron loeriense</i> shrubland | Mesic, steep southern aspects of upper elevations (eastern mountain ranges) | Canopy layer numerically dominated by <i>L. loeriense</i> with patchy occurrence of <i>Protea mundii</i> / <i>L. eucalyptifolium</i> , with a dense ericaceous or restioid understorey |
| Tall, mid-dense <i>Protea neriifolia</i> shrubland | Mesic southerly mid to upper slopes | <i>Protea neriifolia</i> and <i>Leucadendron eucalyptifolium</i> dominate the proteoid layer; ericoid-restioid understorey |
| Scattered <i>Leucadendron salignum</i> shrubland | Lower slopes or remnants of tertiary plateaux | With strong graminoid component and visually characterised by conspicuous, usually scattered <i>Leucadendron salignum</i> |
| Dry shrublands | | |
| Waboomveld | Typically talus slopes of lower foothills zone, also easterly or westerly slopes of incising drainage lines | Structurally and floristically heterogeneous, but <i>Protea nitida</i> always present |
| Arid fynbos | Xeric mid to lower mountain slopes | Fine-leaved shrubs predominate the mid-dense to open canopy overlying a relatively dense grassy understorey. Incidence of restios increases with altitude |

(Seydack 1986)

types, except for the prominence of grasses in the understorey at the expense of restioids. C₄ grass genera like *Themeda*, *Trachypogon*, *Heteropogon*, *Brachiaria* and *Eragrostis* are characteristically represented. Grassy fynbos furthermore differs from mountain fynbos by a greater proportion of nonproteoid nanophylls and forbs. Grassy fynbos communities can be classified as either mesic or dry (Moll et al. 1984), occurring on seasonally waterlogged mesic and xeric sites (northern slopes, arid mountain tops) respectively.

Community dominating species include (cf Cowling 1982): *Erica demissa*, *E. pectinifolia*, *E. diaphana*, *Trachypogon spicatus*, *Themeda triandra*, *Heteropogon contortus*, *Elionurus mutica*, *Tristachya leucothrix*, *Restio triticeus*, *R. cuspidatus*, *Thamnochortus glaber*, *T. fruticosus*, *Tetraria compressa*, *Leucadendron salignum*, *Leucospermum cuneiforme*, *Protea neriifolia*, *Passerina pendula* and *Clutia alaternoides*.

2.4.2.3 Dune Fynbos

Dune fynbos consists of mid-dense to closed mid-high shrublands occurring on relatively deep, calcareous or acid sands. It differs structurally from other fynbos types by a strong component of large-leaved shrubs and the lack of proteoid shrubs. Although the grass cover can be high, restioids and small-leaved shrubs dominate in the herb and shrub layers respectively.

Diagnostic species are *Euclea racemosa* ssp. *racemosa*, *Restio eleocharis*, *R. leptoclados* and *Agathosma apiculata* (Cowling 1984). Dune fynbos is further characterized by a strong component of non-fynbos shrubs and trees which link it to the Tongaland/Pondoland dune thicket: *Rhus crenata*, *Olea exasperata*, *Maytenus procumbens*, *Rhoicissus tridentata* and *Sideroxylon inerme* (Cowling 1984).

2.4.2.4 Renosterveld

Structurally this vegetation type is a small leaved shrubland dominated by *Asteraceae*. It is restricted to fine-grained soils derived from Bokkeveld, Witteberg and Cango shales. Restioid and proteoid growth

forms are secondary or absent. Deciduous geophytes are well represented.

The dominant shrub is *Elytropappus rhinocerotis*. Grasses and geophytes are conspicuous in the understorey. Other dominant genera are *Eriocephalus*, *Anthospermum*, *Passerina*, *Relhania*, *Aspalathus*, *Helichrysum*, *Pteronia*, *Selago*, *Felicia* and *Herrmannia*. *Rhus* spp., *Acacia karroo*, *Euclea undulata* and *Aloe ferox* may be present as scattered emergents (Cowling 1982).

2.4.2.5 Subtropical Transitional Thickets

Structurally the thicket communities are dominated by broadleaved, evergreen, sclerophyllous shrubs and low to mid-high trees, many of which are stem spinescent. Succulents of Karroid affinity are conspicuous in dry areas and vines are scattered throughout. Ecologically the communities are restricted to relatively deep, well-drained, fertile soils (Cowling 1984).

Subtropical thicket is a vegetation type with a closed canopy composed mostly of shade-intolerant species, hence the tendency of these thickets to be unistratal with no canopy seedlings in the shade zone. It is composed predominantly of trees and shrubs dispersed by animals (chiefly birds). Typical genera are *Euclea*, *Diospyros*, *Sideroxylon*, *Rhus*, *Maytenus*, *Cassine*, *Olea*, *Crassula*, *Aloe* and *Euphorbia* (Lubke et al. 1986).

Five subtropical thicket types are differentiated for the study area: Kaffrarian Dune Thicket, Alexandria Forest, Valley Bushveld, Noorsveld and Spekboomveld.

(a) Kaffrarian Dune Thicket

This thicket is a closed shrubland to low forest dominated by evergreen, sclerophyllous trees and shrubs with a high cover of stem spines and vines (Cowling 1984). It consists of a single stratum at 3-5 meter, straddled by woody and herbaceous climbers. There is a poorly developed

understorey and a well developed ground layer with 60% cover of herbs and grass. Succulents are unimportant (Mc Lachlan et al. 1982).

Dune thickets occur on fairly mesic sites at low altitudes (<300 m) on deep calcareous, well-drained coastal dune sands.

Diagnostic and dominating species are: *Cassine aethiopica*, *Sideroxylon inerme*, *Cussonia thyrsoflora*, *Schotia afra* var. *afra* and *Euclea undulata*. Typical shrub and tree genera include *Euclea*, *Diospyros*, *Sideroxylon*, *Rhus* and *Cassine* (Cowling 1984, McLachlan et al. 1982). Undisturbed slip faces not ascended by tree dune thicket have a somewhat different complement of species. The most important are *Rhus crenata*, *Rhynchosia caribaea*, *Imperata cylindrica*, *Myrica cordifolia*, *Azima tetraacantha* and *Brachylaena discolor*. Numerically most abundant on dune slacks are *Sporobolus virginianus* (sand grass), *Gazania rigens*, *Mariscus congestus*, *Arctotheca populifolium*, *Juncus krausii*, *Psorelea repens* and *Helichrysum* spp.

For more detailed reference to dune ecology on a national scale refer to Tinley (1985).

(b) Alexandria Forest

This generally short, very dense forest on the coastal forelands of the Alexandria district grows on stable, deep sandy soils overlying loosely consolidated coastal limestone. An altitudinal range of 100-350 m applies, with an annual rainfall of between 550 to 950 mm (Marker and Russel 1984).

The forest has a variable physiognomy, ranging from tall (ca 15 m) to shorter types verging on thicket. Marker and Russel (1984) recognize 3 forest types, each with its characteristic species:

- (I) Short scrub forest on northerly aspects with an average canopy height of 5 m. Emergents are rare. Typical species: *Fagara capense*, *Allophyllus decipiens*, *Apodytes dimidiata*, *Canthium spinosum*, *Diospyros dichrophylla*, *D. villosa*, *Grewia occidentalis* and *Acacia karoo*.

- (II) Medium high forest of the southern and easterly aspects and plateaux. Average canopy height is 6 m, but interspersed with emergents. A second subtype is formed whenever the emergents occur at sufficient densities to form a more or less continuous canopy. Common species found include *Brachylaena discolor*, *Schotia latifolia*, *Ehretia rigida*, *Dovyalis rhamnoides*, *Acokanthera oppositifolia*, *Euclea schimperi*, *Carissa bispinosa*, *Azima tetracantha* and *Teclea natalensis*.
- (III) Tall forest of the valley floors. The canopy height averages 10 m, with emergents exceeding 15 m. A well developed understory is present. Characteristic species: *Cordia caffra*, *Strychnos decussata*, *Celtis africana*, *Behnia reticulata*, *Podocarpus falcatus*, *Ekebergia capensis*, *Ficus capensis* and *Gardenia thunbergiana*.

(c) Valley Bushveld

The Valley Bushveld is a mid-high to tall, closed, large-leaved succulent shrubland (Cowling 1984). It consists of an impenetrable tangle of spinescent shrubs, low trees and vines (Plate 6 b and c). Structurally the communities are dominated by evergreen sclerophyllous shrubs and succulents (Everard 1986). The grass component is subordinate, with a low basal cover (Aucamp 1979). Prominent succulent genera are *Euphorbia*, *Crassula*, *Aloe* and *Delosperma* (Lubke et al. 1986).

A great diversity of growth forms are found: leaf and stem succulent shrubs, low trees and vines, arborescent rosette succulents, succulent herbs, large and small-leaved sclerophyllous and orthophyllous shrubs, grasses, forbs, annuals and geophytes (Cowling 1984). The relative presence of these growth forms is related to rainfall gradients of quantity and seasonal distribution. Rainfall quantity increases towards the east and from inland to the coast. The proportion of summer rainfall also increases towards the east. Accordingly, succulence is favoured towards the interior and the grass component increases towards the east.

Ecologically the Valley Bushveld is restricted to deepish, well-drained, fertile soils, derived from shales and conglomerates (Cowling 1984).

PLATE 6

- a. Planted pastures, rooted over by bushpigs (Farm Vrede, Knysna district).
- b. Valley Bushveld: Waters Meeting Nature Reserve, Bathurst.
- c. Valley Bushveld: Waters Meeting Nature Reserve, Bathurst.

PLATE 6

a



b



c



Its communities are found in the hot and arid valleys of the Eastern Cape draining into the Indian Ocean. These valleys receive less rain than the intervening ridges where Bushclump Savanna often occurs. Average annual rainfall is below 500 mm and highly variable. Temperature extremes are typical, but winter temperatures are high enough for growth whenever sufficient moisture is available (Aucamp 1979). Valley Bushveld can be broadly subdivided into an inland and coastal form (cf Everard 1986). The southern variation of Valley Bushveld proper and the Fish River Scrub (Acocks 1975) largely resemble the inland form. A resemblance to the coastal form and also to the Alexandria forest (Acocks 1975) is evident for the Addo Bush and Sundays River Scrub.

Typical succulent genera are *Euphorbia*, *Crassula*, *Aloe* and *Delosperma* (Lubke et al. 1986). Characteristic and common species include i.a. *Euclea undulata*, *Schotia afra* var. *afra*, *Portulacaria afra*, *Grewia occidentalis*, *Pappea capensis*, *Scutia myrtina*, *Plumbago capensis*, *Putterlickia pyracantha*, *Rhoicissus tridentata/digitata* (vines), *Rhigozum obovatum*, *Brachylaena ilicifolia*, *Phyllanthus verrucosus*, *Ehretia rigida*, *Capparis citrifolia*, *Azima tetraacantha* and *Panicum maximum* (grass) (Acocks 1975, Aucamp 1979, Everard 1986).

Inland Valley Bushveld

Occurs in the Fish and upper Sundays River valleys. It is a low, relatively sparse thicket with a large number of succulents (Everard 1986). Thorny plants (often scramblers) are also important, with few veld grasses, although shade grasses may be plentiful (Acocks 1975). This form is largely equivalent to Acock's (1975) Southern Variation of Valley Bushveld and his Fish River Scrub.

Numerically dominant species are *Scutia myrtina*, *Capparis citrifolia*, *Rhoicissus digitata* (Southern Variation) and *Portulacaria afra*, *Grewia robusta*, *Euphorbia bothae*, *Asparagus striatus* and again *Rhoicissus digitata* for the Fish River Scrub (Acocks 1975).

Coastal Valley Bushveld

The coastal form is subdivided into a western and an eastern type, corresponding with the Sundays River Scrub of the lower Sundays River valley (including the Addo Bush) and the coastal Kaffrarian thicket of the Kariega, Bushmans and Kowie River valleys respectively.

Western Type

This is a low (2,5 m) exceptionally dense, impenetrable thicket characterized by a high proportion of spinescent shrubs and woody creepers, with a fair proportion of succulents (Everard 1986). Dominant species are *Euclea undulata*, *Schotia afra* var. *afra*, *Schotia latifolia*, *Sideroxylon inerme*, *Cassine* spp. *Rhus longispina*, *Azima tetracantha*, *Cussonia spicata*, *Portulacaria afra* and the climber *Rhoicissus tridentata*. Tall *Aloe* spp. are conspicuous and *Panicum maximum* is a characteristic grass species of the margins (Acocks 1975, Taylor and Morris 1981).

Eastern Type

This eastern type occurs in the river valleys receiving relatively more rain than the western, succulent form. Structurally the thicket is a closed shrubland to low forest dominated by evergreen, sclerophyllous trees and shrubs with a high cover of stem spines and vines. Succulents form a small proportion of the flora with most species being woody (Everard 1986). This type is visually dominated by two aborescent *Euphorbia* spp. (*Euphorbia triangularis*/*E. grandidens*). Associated with these are spinescent shrubs (*Scutia myrtina*, *Azima tetracantha*, *Carissa bispinosa*, *Capparis sepiaria*), arborescent *Aloe* spp. and succulents (*Portulacaria afra*, *Cotyledon* and *Crassula* spp.). *Pelargonium peltatum* and *Sarcostemma viminale* are conspicuous scramblers.

(d) Noorsveld

Noorsveld occupies the wide, undulating middle part of the Sundays River valley, north of the Grootriver Heights and Zuurberg, centred in the Jansenville area. It is a uniform, 1-2 m high scrub dominated by

Euphorbia coerulescens (Noors) and interspersed with occasional small trees. It occurs at altitudes between 300–600 m.a.s.l. with an average annual rainfall somewhat below 250 mm. Other common species include *Rhigosum obovatum*, *Euclea undulata*, *Pappea capensis*, *Nymannia capensis*, *Lycium austrinum*, *Aloe ferox* and *Portulacaria afra* (Acocks 1975).

(e) Spekboomveld

This veld type, also known as Succulent Mountain Scrub, occurs on steep sandstone, quartzite and shale mountain slopes of the Eastern and Southern Cape. It is a dense thicket dominated by *Portulacaria afra* (Spekboom) and receives 250–300 mm of rainfall per annum. Other important trees and shrubs are *Crassula portulacaeae*, *Lycium austrinum*, *Pappea capensis*, *Euclea undulata*, *Rhigosum obovatum* and species of *Grewia*, *Rhus* and *Schotia* (Acocks 1975).

2.4.2.6 Bushclump Savanna

Bushclump Savanna broadly coincides with what Acocks (1975) called Eastern Province Thornveld and the Acacia Savanna of Lubke *et al.* (1986). It consists of a mosaic of grassland and subtropical thicket clumps interspersed with or without thickly sprinkled *Acacia karroo*. It occupies the ridges between the deep broad valleys draining southeastwards towards the Indian Ocean. Rainfall ranges from under 500 to 900 mm, mainly 600–750 mm per annum (Acocks 1975).

The grassland is favoured by shallow duplex soils which are seasonally waterlogged. The grassveld is sourish with fynbos elements. Grasses such as *Themeda triandra*, *Tristachya hispida*, *Heteropogon contortus*, *Elionurus argenteus*, *Eragrostis capensis*, *Sporobolus africanus*, *Digitaria* and *Cymbopogon* spp., *Pentaschistis angustifolia*, *Karoochloa curva*, *Ehrharta calycina*, *Setaria perennis* and *Merxmuellera disticha* are found intermingled with fynbos elements. The latter are represented by sedges (*Schoenoxylum*, *Ficinia*, *Tetraria*) and shrubs (*Passerina*, *Agathosma*, *Aspalathus*, *Bobartia*, *Leucospermum*, *Metalasia*, *Erica*, *Struthiola* and *Restio*) (Acocks 1975).

2.4.2.7 Karroid Shrublands

These shrublands are found predominantly on shales and mudstones in hot, arid areas (<150-300 mm/annum). The veld types primarily involved *sensu* Acocks (1975) are Succulent Karoo in the Southern Cape interior and (False) Karroid Broken Veld in the interior of both Eastern and Western Cape. No cartographic differentiation of the Karroid shrublands was undertaken since the distribution of bushpig does not extend into them. They are therefore considered to be outside the actual study area.

The Karroid Broken Veld of the Little Karoo has a dominant succulent component, dwarf trees - notably *Euclea undulata* - and shrubs are numerous while grasses are relatively scarce. Succulent Karoo is also dominated by succulents, mainly mesembs, with few trees or large shrubs (Acocks 1975).

2.4.3 Vegetation of the intensive study area

The intensive study area comprises the three state forests Goudveld, Gouna and Diepwalle (Map 2). Most of the research activities were centred on Goudveld (Plate 4). The main vegetation types are those typical for the foothills of the Outeniqua mountains and the upper coastal plateau as described in section 2.4.2. (Table 2/12, Plate 5a, b, c and Plate 6a).

| State Forest | Vegetation type | FOREST (2.4.2.1) | FYNBOS (2.4.2.2) | PLANTATION |
|--------------|-----------------|------------------|------------------|------------|
| | GOUDVELD | 4 697 | 4 204 | 2 654 |
| | GOUNA | 3 556 | 791 | 1 903 |
| | DIEPWALLE | 3 083 | 1 208 | 534 |
| | | 11 336 | 6 203 | 5 091 |
| TOTAL | | 22 630 | | |

Pinus radiata, *P. pinaster* and *P. elliottii* are the main plantation species. The vegetation to the south of the state forests, originally

consisting of fynbos on the flats and indigenous forests in the river valleys, has largely been transformed for agricultural purposes.

2.5 Fauna

The biotic zones of Africa and their associated faunas were reviewed by Bigalke (1978a, b), Werger (1978) and Rautenbach (1978). Three of the six recognised by Rautenbach (1978) impinge on the study area: the South West Cape, Forest and Southern Savanna Woodland zones. In the western part, the Forest zone predominates, bordering on the South West Cape. The eastern portion falls into the Southern Savanna Woodland zone (3.1: Fig. 3/1).

Most mammal species of the Forest and South West Cape zones have survived in the study area. Their ranges have however been limited by changes in land use. The Southern Savanna Woodland zone is phytochorologically heterogeneous and is characterized by the co-existence of a diversity of vegetation types. The grass component is prominent. The mammal fauna is diverse and dominated by cursorial species. Herbivores are primarily grazers (Bigalke 1978a). At least 20 medium and large mammal species have been lost or reduced to remnant populations in sanctuaries (Skead 1980, 1986). Notable examples are the lion (*Panthera leo*), serval (*Leptailurus serval*), blue antelope (*Hippotragus leucophaeus*), red hartebeest (*Alcelaphus buselaphus*), black wildebeest (*Connochaetes gnou*), buffalo (*Syncerus caffer*), quagga (*Equus quagga*) and Cape Mountain zebra (*Equus zebra*).

The Forest biotic zone is faunistically quite distinct. It has little in common with the South West Cape zone, but is faunistically relatively closely related to the Southern Savanna Woodland (Rautenbach 1978). This relationship, expressed by the number of shared species, results from the presence of forest-related vegetation types within the Southern Savanna Woodland zone. The distribution of the bushpig within the study area is centred around Afromontane forest and Valley Bushveld. It extends into ecotonal areas and transitional vegetation types and enters fynbos and Karroid shrublands as an agri- and silvicultural follower. The Valley Bushveld, although part of the Southern Savanna Woodland zone, is more closely related to forest as a habitat type for

terrestrial mammals. The Afromontane forest/Valley Bushveld habitat complex share the same dominant ungulate assemblage of bushpig, bushbuck (*Tragelaphus scriptus*) and blue duiker (*Cephalophus monticola*). More widely distributed species which also occur in the study area, include leopard (*Panthera pardus*), ratel (*Mellivora capensis*), large-spotted genet (*Genetta tigrina*), porcupine (*Hystrix africae-australis*) and baboon (*Papio ursinus*). The incidence of vervet monkeys (*Cercopithecus pygerythrus*) increases progressively from the west to the east and they are joined by the tree hyrax (*Dendrohyrax arboreus*) in suitable habitat in the eastern part. Habitat specialists such as the Cape clawless otter (*Aonyx capensis*) and marsh mongoose (*Atilax paludinosus*) are also found in the study area.

2.6 Land-use and management

2.6.1 Southern Cape

Forestry, agriculture and tourism are the dominant forms of land-use in this region. Of the ca 60 000 ha indigenous forest approximately 75% is in public ownership. The forests are managed by the Forestry Branch of the Department of Environment Affairs, according to the principles outlined by Seydack, Grewar and Van Dijk (1982), Seydack (1982) and Seydack *et al.* 1990. Nature conservation, timber utilization and recreation are the important land uses requiring multipurpose management. Over 500 000 ha of fynbos in the mountains are similarly managed for water conservation, nature conservation and recreation (Seydack 1986).

Commercial timber plantations have been established with exotic species, primarily *Pinus*, on 76 040 ha (Environment Affairs 1985). The main product from publicly owned plantations (57 400 ha) is softwood sawlogs for construction purposes.

Agriculturally the study area can be subdivided into two regions: the coastal plateau of the Mossel Bay, George, Knysna and Humansdorp districts and the more arid interior of the Little Karoo/Langkloof just north of the coastal mountain ranges.

The main crops of the coastal plateau are wheat (>50 000 ha), maize (4 700 ha) and vegetables, such as potatoes, peas, brassicas and green beans. The most important cultivated pasture species include rye grass (*Lolium spp.*), lucerne (*Medicago sativa*) and clovers (*Trifolium spp.*), as well as *Pennisetum clandestinum*, *Panicum spp.*, *Chloris gayana* and *Digitaria smutsii*. Animal husbandary in the region is based on over 45 000 head of meat and dairy cattle and sheep for wool (>100 000 small stock units). Agricultural development has basically reached the limit of its possibilities for horizontal extension (Agriculture and Water Affairs 1985a, Weitz pers. comm.). In the arid interior north of the coastal mountain ranges, known as Langkloof, the two main agricultural pursuits are fruit production under irrigation and a combination of dry land wheat with small stock grazing. From approximately 6 300 ha of irrigated fruit orchards apples, pears, apricots, peaches and prunes are produced (Agriculture and Water Affairs 1985b).

2.6.2 Eastern Cape

Apart from the industries in Port Elizabeth and surroundings, agriculture predominates in this region. The Department of Environment Affairs, Forestry Branch, manages 19 764 ha of indigenous forests under multiple use principles and 88 % of the timber plantations of the region, mainly exotic *Pinus spp.* amounting to 22 908 ha (Environment Affairs 1985).

Four agricultural zones may conveniently be distinguished, the first three denoted by the predominant natural vegetation:

- (I) Bushclump Savanna/Alexandria forest zone of the Alexandria, Bathurst and Albany districts;
- (II) Valley Bushveld zone (principal districts: Uitenhage, Kirkwood, Albany);
- (III) Fynbos zone (western and higher lying portions of the Eastern Cape);
- (IV) Irrigation zone in the Gamtoos and Sunday River valleys.

The statistics provided below (Table 2/13) were extracted from the agricultural development plan for the Eastern Cape region (Agriculture and Water Affairs 1981).

| Table 2/13: Summarized characterization of Eastern Cape AGRICULTURE | |
|---|---|
| ZONE | INTENSITY AND TYPE OF AGRICULTURE |
| I | Semi-intensive to intensive Crops: Pineapple (22% of regional production) Chicory Grains (mainly maize, wheat, oats) Stock: Cattle: dairy and meat production Boer goats: for meat |
| II | Extensive Small stock farming with Boer and Angora goats for mohair (30% of national Angora goat population in this region) Some dryland wheat |
| III | Semi-extensive to extensive Sheep and Angora goats for wool Grain crops (wheat) and potatoes |
| IV | Intensive (under irrigation) Citrus fruit ($\pm 7\ 000$ ha), tobacco, potatoes, vegetables, lucern, cotton. |

Clearing of natural vegetation for crops and the establishment of planted pastures in zones I, III and IV has locally reduced the availability of suitable habitat for bushpig, but increased the availability of food. Wheat fields dispersed within the Valley Bushveld and the introduction of prickly pear (*Opuntia* sp.) in zone II have also augmented food supplies for these animals.

3. THE GENUS POTAMOCHOERUS: A REVIEW OF ITS TAXONOMY AND PHYLOGENY

3.1 Distribution

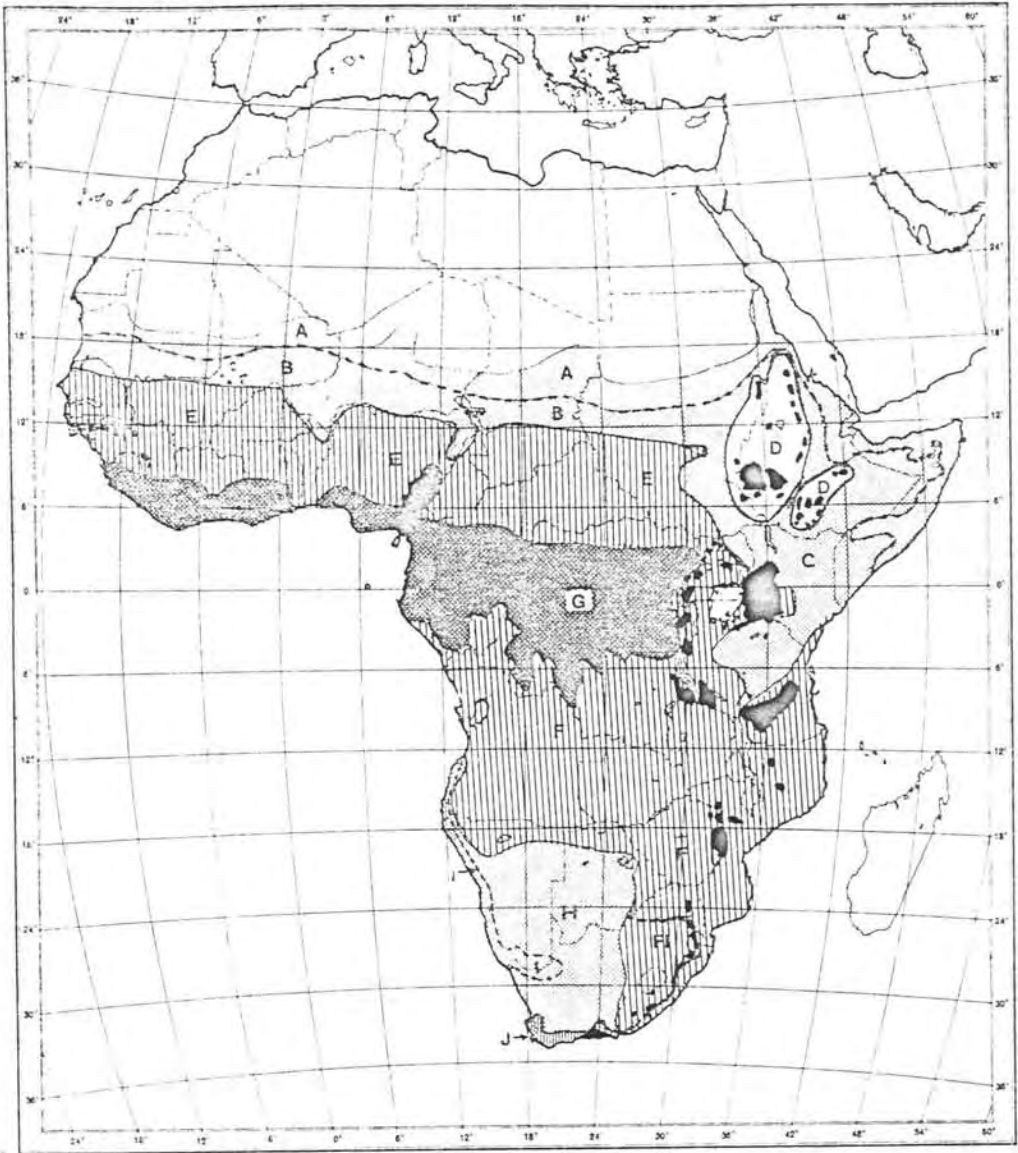
The distribution of the bushpig is confined to Africa south of the Sahara and some islands off the east coast of the continent (Haltenorth and Diller 1980). It occurs wherever there is suitable habitat (typically with sufficient cover). All forest types, bush thickets and vegetation associated with water courses or marshes (reed beds) may thus be inhabited by bushpigs.

Figure 3/1 shows the biotic zones of Africa according to Smithers (1983: after Rosevear 1953, Davis 1962 and Rautenbach 1978).

Following Ansell (1971), Haltenorth and Diller (1980) and Smithers (1983), the distribution of the bushpig is summarized below (Fig. 3/2a).

- (I) In West Africa: in and on the fringes of the Forest region (Lowland forest, rain forest) in Senegal, Sierra Leone, Liberia, Ghana, Nigeria and south-eastwards to Cameroun, Gabon and the Congo Republic. In Lowland and Afromontane Forest zones of central and south-eastern Africa in Zaire, Uganda, Kenya, Tanzania, Zimbabwe and the Ethiopian Highlands.
- (II) Somali Arid and Northern Savanna zones: of limited local occurrence in association with suitable habitat conditions.
- (III) Widely distributed in the Southern Savanna Woodland zone in association with rain forest patches and riverine habitats: Southern Zaire, Angola, Zambia, Zimbabwe, Moçambique, eastern Caprivi (Namibia) and northern Botswana (Okavango swamps and adjacent river systems).
- (IV) In South Africa: in the Southern Savanna Woodland, Southern Savanna Grassland and South West Cape zones in association with Afromontane or Subtropical forest patches and thickets.
- (V) Islands off the east coast of Africa: Madagascar, Mayotte, Zanzibar and Mafia.

FIG.3/1: BIOTIC ZONES OF AFRICA(ex SMITHERS 1983)



Main biotic zones south of the Sahara :

(after Rosevear 1953, Davis 1962 and Rautenbach 1978)






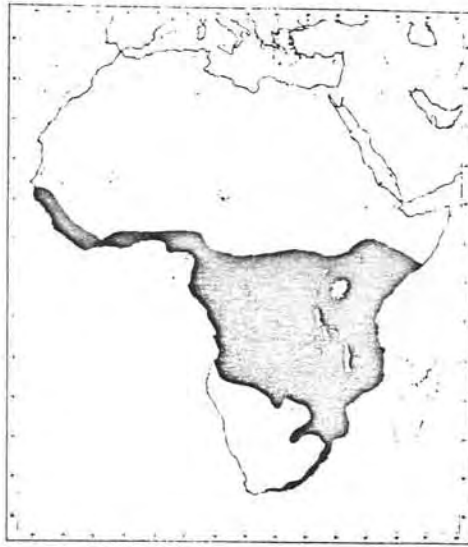
| | | |
|---|------------------------------|--|
|  | ARID ZONES | A : Sudanese Arid B : Sahelian C : Somali Arid H : South West Arid I : Namib Desert |
|  | SAVANNA ZONES | E : Northern Savanna F : Southern Savanna Woodland Fl : Southern Savanna Grassland |
|  | FOREST ZONES | G : Lowland Tropical Forest  Isolated montane or evergreen forest patches. |
|  | SOUTH WEST CAPE ZONE(fynbos) | |

FIG.3/2: GEOGRAPHIC DISTRIBUTION OF POTAMOCHOERUS

a. AFRICA

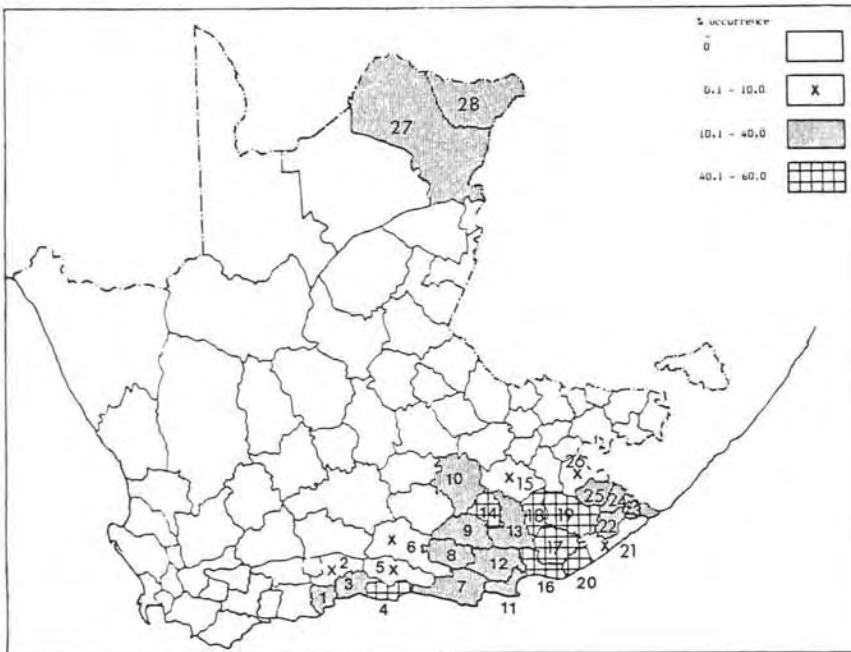


(ex Smithers 1983; distribution on Madagascar not indicated)

b. CAPE PROVINCE (SOUTH AFRICA)

(Adapted from Lloyd and Millar 1983)

DIVISIONAL COUNCIL DISTRICTS



- 1 Mossel Bay
- 2 Oudtshoorn
- 3 George
- 4 Knysna
- 5 Uniondale
- 6 Willowmore
- 7 Humansdorp
- 8 Steytlerville
- 9 Jansenville
- 10 Graaff-Reinet
- 11 Port Elizabeth
- 12 Uitenhage
- 13 Somerset-East
- 14 Pearston
- 15 Cradock
- 16 Alexandria
- 17 Albany
- 18 Bedford
- 19 Fort Beaufort
- 20 Bathurst
- 21 East London
- 22 King William's Town
- 23 Komga
- 24 Stutterheim
- 25 Cathcart
- 26 Queenstown
- 27 Vryburg
- 28 Mafeking

In South Africa the species is known to occur in the western, northern and eastern parts of Transvaal, it occurs widely in parts of central and eastern Natal and southwards along the coastal parts of the eastern and southern Cape Province (Smithers 1983).

The distribution in the Cape Province extends north-eastwards along the coast from as far west as 21°40' longitude (more or less coinciding with the southern extension of the Afromontane forest/fynbos mosaic). They occur on the coastal plateau and mountains (Outeniqua and Tsitsikamma mountains) extending northwards into the Karoo/fynbos transition of the intermontane valley north of these mountains (Langkloof). Further east the species occurs from the coast to the Baviaanskloof/Great Winterhoek Mountains and the eastern outliers of the Cape Fold Belt Mountains (e.g. Zuurberg). The distributional range extends north of these mountains where Subtropical thicket vegetation stretches into the interior (Fig. 3/2b).

Judging from the historical record (Du Plessis 1969, Skead 1986), the distribution of bushpig in Southern Africa has not altered to any great extent, although they may in parts have been locally exterminated or driven back by human developments (Smithers 1983). An authentic specimen from Swellendam was mentioned by Roberts (1951) and the only area from which the bushpig seems to have disappeared is along the coastal belt from Swellendam to Mossel Bay (Stuart 1985).

3.2 Taxonomy

3.2.1 Classification

The classification of the species is as follows (Haltenorth 1963, Ansell 1971):

| | |
|-------------|----------------------------------|
| Class: | Mammalia |
| Order: | Artiodactyla |
| Suborder: | Nonruminantia (Suiformes) |
| Infraorder: | Suina |
| Superfamily | Suioidea |
| Family | Suidae (Gray 1821) |
| Subfamily: | Suinae |
| Genus: | <i>Potamochoerus</i> (Gray 1854) |
| Species: | <i>porcus</i> (Linnaeus 1758) |

The bushpig is the least specialized of the African suids (Cooke and Wilkinson 1978). Adult mass may range between 45 and 120 kg: head/body lengths 100-150 cm and shoulder heights 55-80 cm (Haltenorth and Diller 1980).

In the Southern Cape, average adult weights were determined as 72 and 69 kg for males and females respectively (Seydack 1983). There appear to be no significant differences in body mass between the sexes. The morphology of the head differs between the sexes and the slightly heavier male body mass is related to these differences. Males develop three pairs of wart-like facial structures: over the canine root flanges on the snout (preocular); on the malar eminences (infraocular) and on the jaw angles (gonial). The infraocular and gonial structures consist entirely of cartilaginous tissue, whereas the preocular snout knobs are formed by cartilaginous tissue above the canine flange crests. The development of these structures is variable, as is the facial coat colour patterning (3.2.2). Whitish whiskers (cheek beards) and ears tufted with terminal tassels of hairs are typical for the species.

The coat consists of relatively long, bristly hairs, with a long dorsal, whitish crest, but no undercoat. The general colour is variable within and between subspecies (3.2.2) and changes with ontogenetic development. The neonatal coat of pale, yellowish buff stripes on a brown ground colour is replaced by a rufous brown, gradually changing to the mature colour. The adult body colour is red-brown, grey-brown to dark brown/black. The tail has sagittally aligned (feathered) black terminal hairs. Female bushpig have 3 pairs of mammae.

The elongate, fairly narrow skull has a typically straight dorsoventral profile. Suid skull characteristics are compared in Table 3/1 (from Cooke and Wilkinson 1978). In males there are maxillary flanges around the roots of the upper canines. On these flanges are elevated lateral crests, the upper parts of the crests being rugose. The nasals widen above the canine flanges and in males there is an expanded rugose area on the nasals and the adjoining part of the maxillae. These rugose flange crests are covered with cartilaginous tissue to form the preocular snout tuberosities.

| Table 3/1: Summary of characters in living suid skulls (ex Cooke and Wilkinson 1978) | | | | |
|--|---|--|---|---|
| Character | <i>Sus</i> | <i>Potamochoerus</i> | <i>Hylchoerus</i> | <i>Phacochoerus</i> |
| Lateral profile | Almost straight, slight change of slope at nasal/frontal suture | As in <i>Sus</i> | Parietals elevated above nasal plane; slope change at nasal/frontal suture | Profile concave near nasal/frontal suture; convex at parietals |
| Orbits | Well below fronto-parietal surface face | As in <i>Sus</i> | Below fronto-parietal surface | Elevated above fronto-parietal surface |
| Frontal and parietal area | Gently arched | As in <i>Sus</i> | Parietal area flat or concave | Gently arched; frontals flat wide |
| Parietal constriction | Narrow but much wider than snout | Narrow, about equals snout width | Very broad | Narrow, about equals nasal breadth |
| Braincase below parietal crest | Sides almost vertical | Bulges outward | Parietal crest overhangs braincase | Bulges slightly outward |
| Occiput | Narrow; no marked median ridge | Broader than <i>Sus</i> but similar | Broad; strong median ridge | Much like <i>Potamochoerus</i> |
| Angle of auditory canal | Steeper than 45° from horizontal | Less than 45° (c. 35°-40°) | Low, close to 20° | Close to 45° |
| Nasals and muzzle shape | Nasals parallel-sided or narrowed in middle; gently rounded, curved into near-vertical side walls | Nasals widen posteriorly, expanded in middle in males; flat and project over vertical or hollowed side walls | Nasals wide in middle, taper slightly towards back; well rounded; muzzle broad, widely arched above canine area | Nasals expanded above canine, narrowed in middle; well rounded; muzzle slightly wider above canine area |
| Premaxilla/nasal opening | Premaxilla upper border almost straight; nasals not downcurved at tips | As in <i>Sus</i> | Premaxilla border strongly concave; tips of nasals strongly downcurved | Premaxilla border moderately concave; nasals droop towards tips |
| Back of premaxilla | Almost to position above p ⁴ | Ends above C-p ² diastema | Ends above C | Ends above C-p ³ diastema |
| Position of infraorbital foramen | Above p ⁴ | Above M ² | Above M ¹ | Above front of M ² |

Table 3/1 (continued): Summary of characters in living suid skulls (ex Cooke and Wilkinson 1978)

| Character | <i>Sus</i> | <i>Potamochoerus</i> | <i>Hylochoerus</i> | <i>Phacochoerus</i> |
|----------------------------|---|---|---|---|
| Canine flanges | Small | Small in female; high crest in male | Broad with low lateral crest | Large and tubular |
| Canine form | Small, curve laterally | Small, curve laterally | Large, curve laterally | Large, curve laterally and upward |
| Zygoma structure | Root curves at 45° to axis of skull; then smooth sweep to lateral border; parallel to skull axis; lateral walls nearly vertical | Root curves sharply so that anterior border approximately perpendicular to skull axis; lateral walls parallel to skull axis, flare slightly (10°) downwards | Root curves at 45° to skull axis; smooth sweep in female but curve sharply to perpendicular in males; lateral walls flared and thickened in older males | Root sweeps gently back from just behind infraorbital foramen, continuing at 30° in female 45° in male; lateral walls broad below orbits, flared outwards |
| Lower border of zygoma | Parallel to occiusal plane | Slopes down towards back | Slopes markedly down | Parallel to palate but elevated |
| Origin of levator rostri | High, deeply scooped | Not very high, moderate scooping | Small and shallow | Elongate, triangular shallow |
| Ridge below levator rostri | Strong, sharp | Moderate, blunt | Small, weak | Strong |
| Origin of depressor rostri | Weak, shallow | Deeply scooped | Weak, shallow | Moderate |
| Incisors | 6 upper incisors | 6 upper incisors | 2 upper incisors in adult, often shed | 2 upper incisors, retained in adult |
| Premolars | p ¹ retained, but sometimes shed | p ¹ absent | p ¹ absent, p ² shed early | p ¹ absent, p ² and p ³ shed early |
| Upper canine structure | Flattened oval cross-section; strong medium dorsal groove, weak ventral enamel band; ribbed; inset dorso-median and dorso-lateral enamel strips | Rounded quadrilateral cross-section; weak dorsal median groove; strong median groove weaker lateral groove, both high up sides; enamel bands as in <i>Sus</i> | Sub-rectangular cross-section, higher than wide strong dorsal and median grooves, weaker lateral groove; enamel bands as in <i>Sus</i> | Sub-rectangular cross-section, long axis diagonally upward; strong, broad, dorsal and ventral grooves, weaker anterior grooves; no enamel except at tips in juveniles |

The bushpig has a nearly complete and relatively unspecialized dentition (Kingdon 1979). The dental formula of the permanent dentition of the adult is 3/3.1/1.4/3.3/3 = 42. Some individuals may have 40 or 44 teeth depending on the absence or presence of the upper and lower first premolars (Seydack 1983). The molars are brachyodont (low-crowned) and bunodont (blunt-rounded crowns), a typically omnivore dentition.

There are numerous similarities between the bushpig and pigs of the genus *Sus*, especially the wild boar (*Sus scrofa*). Many cranial characteristics (Table 3/1), dentition and the coat marking of piglets are similar in *Potamochoerus* and *Sus*. Milstein (1971) goes as far as to suggest that the monotypic genus *Potamochoerus* should probably be more realistically incorporated in *Sus*. According to reports, bushpig X *Sus scrofa* interbreeding is possible (Simoons 1953, Milstein 1971). Since continued breeding of hybrid stock is not reported, hybrids are presumably sterile (cf Milstein 1971).

3.2.2 Species and subspecies differentiation

Over a century ago Gray (1868) differentiated between two species of *Potamochoerus*; namely *Potamochoerus africanus*, the bushpig, and *P. porcus*, the red river hog. This differentiation already reflected the two major groupings of *Potamochoerus* inhabiting southern and eastern as against central western Africa respectively. These two forms were described as follows (Gray 1868):

P. africanus: "Ears densely hairy; internally white, with black edge and tuft. Fur black. Head and back whitish or yellowish; forehead and back black-varied; large spot beneath the eyes black.

Skull: male. The lateral tubercular ridge prominent, and elevated above the upper surface of the nose; lateral process on the base of the sheath of the upper canine broad, compressed, reaching to the level of the upper surface of the nose. Female with transverse ridge at the base of the sheath of the upper canine."

P. porcus: "Ears densely hairy; edges of ears and pencil white. Fur red-brown, beneath greyish white. Head and ears black; whiskers on the cheek, streak over and below the eyes, and dorsal mane white.

Skull: Male, the prominence of the canine flat-topped and not raised above the surface of the nose; the lateral process of the sheath of the upper canine narrow at the base, dilated above, short, not reaching

to the level of the upper surface of the nose. Female with only a ridge across the base of the sheath of canine."

Proceeding from the subgeneric classification of *Potamochoerus* by Major (1897 *op. cit.* Lönnberg 1910), Lönnberg (1910) comes to recognize 5 species with 11 subspecies. His update was based on cranial dimensions and coat characteristics from museum specimens. Two main groups, each with species status and subspecific subdivisions, were again recognized:

(I) *Potamochoerus choeropotamus*-group: southern and eastern African distribution and

(II) *P. porcus*-group: western African distribution.

| TABLE 3/2: DISTINGUISHING EXTERNAL CHARACTERISTICS OF <i>POTAMOCHOERUS CHOEROPOTAMUS</i> VS <i>P. PORCUS</i> GROUPS | |
|---|---|
| <i>Potamochoerus choeropotamus</i> -group | <i>Potamochoerus porcus</i> -group |
| 1. Hair all over body consisting of long, partly very long bristles, often not very dense. In adults skin may be seen between bristles. | 1. Body covered with shorter hair, but appears denser. Skin as a rule concealed. |
| 2. General coat colour variable with shades of brown to black, but darker shades generally predominating. | 2. General coat colour reddish brown or rufous. |
| 3. Dorsal mane or crest strongly developed and often begins already on the nape between the ears. Long mane bristles dark, blackish or dark brown, with more or less strongly developed whitish tips, which sometimes may be dominating in colour although bristles are dark at base. | 3. Dorsal crest conspicuously white. Hair extends very little above general hairy covering. |
| 4. Ears externally black with black margins, black fringe and tuft. | 4. Ears are black, with more or less of the upper margin towards the tip and part of the tuft whitish. |
| 5. Forehead between ears and eyes as a rule pale; greyish to white in colour; sometimes mixed with dark brown. | 5. Forehead between ears and eyes: well marked black area contrasting with red body (in adults) or variably face-patterned. |
| cf Lönnberg (1910) | |

In addition to the two species mentioned, Lönnberg (1910) distinguished *P. larvatus*, *P. hassama* and *P. intermedius* as separate taxa with species status. *P. larvatus*, the Madagascar bushpig, occurs in two forms: a red brown smaller subspecies occupying the western, drier and more open part of Madagascar (*P.l. larvatus*) and a darker, larger subspecies in the eastern moist tropical forest of the island (*P.l. nova*). *P. hassama*

from Ethiopia outwardly resembles the *P. choeropotamus*-group, but is more closely related to the *P. porcus*-group when based on skull characteristics. *P. intermedius*, inhabiting western Uganda, with its white face, well-developed dorsal crest and long bristly coat (*P. choeropotamus*-group features) and pale rufous back and sides (*P. porcus*-group features) is truly intermediate in characteristics and occurs in the contact zone between these two groups.

Lönnbergs (1910) taxonomic update is summarized below.

Potamochoerus choeropotamus (Desmoulins)

P. ch. choeropotamus

P. ch. mashona

P. ch. johnstoni

P. ch. nyasae

P. ch. daemonis

Potamochoerus porcus (Linnaeus)

P. p. porcus

P. p. pictus

P. p. albifrons

P. p. ubangensis

Potamochoerus larvatus (F. Cuvier)

P. l. larvatus

P. l. hova

Potamochoerus hassama (Heuglin)

Potamochoerus intermedius (n.sp.).

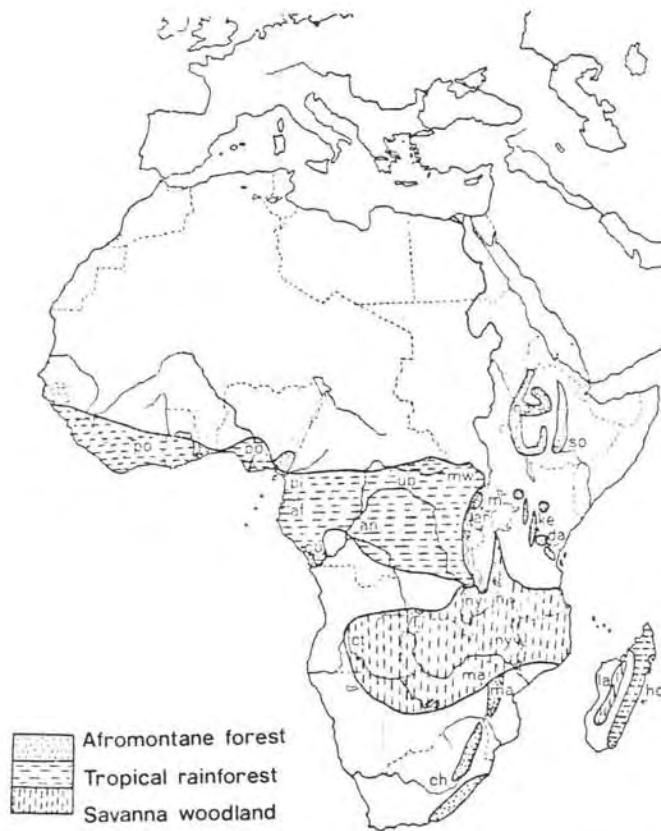
In his review of the distributional ecology of the African suids Von Boetticher (1933) recognized 20 subspecies, all considered to belong to a single species, *Potamochoerus porcus*, Linnaeus. Five groupings were distinguished apparently based on geographic affinity (Table 3/3, Fig. 3/3). Overall, the association of coat colour and distribution over biomes is specially noteworthy. The *Potamochoerus porcus*-group in the lowland tropical forest, having a red-brown coat, the darker brown to black coats of Afromontane forest forms and the more yellowish brown to dirty reddish coat colours of savanna forms (Copley 1949), both of the *P. choeropotamus* group, form a pattern similar to

TABLE 3/3: POTAMOCHOERUS SUBSPECIES DISTRIBUTION AND DISTINGUISHING FEATURES

| Subspecies | Occurrence* | Distinguishing features |
|---|--|---|
| <u>Potamochoerus choeropotamus</u> -group | | |
| <i>P.p. choeropotamus</i> | South Africa | Group-typical: grey/whitish forehead, black ears and tufts, dark dorsal crest and body; with long bristles. |
| <i>P.p. maschona</i> | Moçambique, Zimbabwe | Relatively narrow-headed compared to <i>P.p. choeropotamus</i> . |
| <i>P.p. cottoni</i> | Angola | Resembling <i>P.p. choeropotamus</i> , coat colour variable (Hill and Carter 1941). |
| <i>P.p. daemonis</i> | Kilimanjaro Mountains | Small-sized, very dark coat with long hair. |
| <i>P.p. nyasae</i> | Northern Zambia, Malawi | Skull relatively narrow parietal region. General body colour resembles <i>P.p. choeropotamus</i> , but more rufous/dirty red on back and sides. |
| <i>P.p. johnstoni</i> | Northern western Malawi, North eastern Zambia, Southern Tanzania | Resembles <i>P.p. choeropotamus</i> , but coat colour more yellowish brown to dirty red. |
| <i>P.p. keniae</i> | Forests around Nairobi (Kenya) | Unrecorded (?) |
| <u>Potamochoerus hassama</u> - group | | |
| <i>P.p. hassama</i> | Montane forests of Ethiopia | Coat characteristics as <i>P. choeropotamus</i> - group. Cranial features somewhat resemble those of <i>P. porcus</i> - group. |
| <i>P.p. somaliensis</i> | Ethiopian savannas | Smaller than <i>P. hassama</i> (Colour of pelage?) |
| <u>Potamochoerus larvatus</u> - group | | |
| <i>P.p. larvatus</i> | Western and south western Madagascar | Skull with comparatively narrow parietal. |
| <i>P.p. hova</i> | Eastern and north eastern Madagascar | Dark coat; larger-sized. |
| <u>Potamochoerus intermedius</u> - group | | |
| <i>P.p. intermedius</i> | Ruwenzori Mountains, Western Uganda | Basis for subspecific subdivision uncertain. |
| <i>P.p. arrhenii</i> | Rwanda, Burundi (Lake Kivu) | Cranial features and type of coat as <i>P. choeropotamus</i> - group (long bristles not dense). Coat colour of body as <i>P. porcus</i> - group, but dorsal crest dark as for <i>P. choeropotamus</i> - group. While <i>P.p. arrhenii</i> tends more to <i>P. choeropotamus</i> - group characteristics, <i>P.p. mawambicus</i> relates closer to the <i>P. porcus</i> - group. |
| <i>P.p. mawambicus</i> | North eastern Zaire (Ituri-area) | |
| <u>Potamochoerus porcus</u> - group | | |
| <i>P.p. porcus</i> | Guinea, Sierra Leone, Ivory Coast, Ghana, Southern Nigeria | Group-typical: forehead black, ears black with upper edge and part of tuft white. Otherwise rufous-red coat of short dense hairs with dark legs and feet. Dorsal crest white. |
| <i>P.p. pictus</i> | Lower Niger River to southern Cameroun | Differentiated from group by cranial dimensions and smaller size. |
| <i>P.p. ubangensis</i> | Northern Zaire | Snout below eyes whitish. Smaller than other spp. of <i>P. porcus</i> - group. |
| <i>P.p. albifrons</i> | Gabon | Head with much white, but snout black. |
| <i>P.p. albinuchalis</i> | Western Zaire | White nape. |
| <i>P.p. congicus</i> | Lower Congo River adjacent Northern Angola | Differentiated from group by cranial characteristics. |
| * Incomplete and uncertain in many cases | | |
| from Lönnberg 1910, Von Boetticher 1933 and Haltenorth 1963 | | |

variations in bushbuck (*Tragelaphus scriptus*) and the African buffalo (*Syncerus caffer*) (Grubb 1972 and 1978).

FIG.3/3 :BUSHPIG SUBSPECIES DISTRIBUTION ex LÖNNBERG(1910)



Potamochoerus porcus (L.): po P.p. porcus, pi P.p. pictus, ub P.p. ubangensis,
 af P.p. albifrons, co P.p. congicus, an P.p. albinuchalis, mw P.p. mawambicus,
 im P.p. intermedius, ar P.p. arrhenii, ha P.p. hassama, so P.p. somaliensis,
 ke P.p. keniae, dae P.p. daemonis, ny P.p. nyasae, jh P.p. johnstoni,
 ma P.p. maschona, ct P.p. cottoni, ch P.p. choeropotamus, la P.p. larvatus,
 ho P.p. howa

In the taxonomic revision by Haltenorth (1963) only 13 subspecies were retained; belonging to a single species. Ansell (1971) adhered to this, forming the presently accepted subdivision of the genus (Table 3/4).

As noted by Ansell (1971), some of the subspecies are however named on inadequate material, while some of the merging of subspecies by Haltenorth (1963) may not be consistent; similarly as a result of inadequate material. The genus is undoubtedly in need of further taxonomic revision.

| Table 3/4: Taxonomic subdivision of <i>Potamochoerus</i> Gray, 1854 ex Ansell (1971) |
|---|
| <i>P.p. porcus</i> (Linn., 1758). Senegal and Gambia east to the lower Niger. (Including <i>penicillata</i> Schinz, 1848) |
| <i>P.p. pictus</i> (Gray, 1852). Lower Niger to southern Cameroun. |
| <i>P.p. albifrons</i> (Du Chaillu, 1860). Gabon; Congo (Br.). |
| <i>P.p. congicus</i> (Lönningberg, 1910). Lower Congo (K.); and probably extreme northern Angola. |
| <i>P.p. ubangensis</i> (Lönningberg, 1910). Central African Republic. Central and northern Congo (K). (Including <i>mawambicus</i> Lorenz, 1923). |
| <i>P.p. albinuchalis</i> (Lönningberg, 1919). West Congo (K.), south to the Kasai District. (Regarded by Schouteden, 1945 as a synonym of <i>ubangensis</i>). |
| <i>P.p. nyasae</i> (Forsyth Major, 1897). Angola; northern Botswana; south-eastern Congo (K.); Zambia; the Caprivi; southern Tanzania; Moçambique; and Rhodesia. (Including <i>johnstoni</i> Forsyth Major, 1897; <i>maschona</i> Lönningberg, 1910; and <i>cottoni</i> Pinfold, 1928). |
| <i>P.p. koiropotamus</i> (Desmoulins, 1831). South Africa. (Including <i>africanus</i> Schreber, 1791 and <i>capensis</i> Gray, 1868). |
| <i>P.p. daemonis</i> (Forsyth Major, 1897). Northern Tanzania; Zanzibar and Mafia Islands; southern Kenya; Uganda, Ruanda-Urundi. (Including <i>intermedius</i> Lönningberg, 1910; <i>keniae</i> Lönningberg, 1912; and <i>arrheni</i> Lönningberg, 1917). |
| <i>P.p. hassama</i> (Heuglin, 1863). Abyssinia. |
| <i>P.p. somaliensis</i> (de Beaux, 1924). Southern Somalia. |
| <i>P.p. larvatus</i> (F. Cuvier, 1822). Western and south-western Madagascar. (Including <i>madagascariensis</i> Grandidier, 1867; and <i>edwardsi</i> Grandidier, 1867). |
| <i>P.p. hova</i> (Lönningberg, 1910). Eastern and north eastern Madagascar. |

3.3 Evolutionary aspects

3.3.1 Phylogeny of the African suids

Recent reviews of the phylogeny of Suidae are those by Thenius (1970) and Cooke and Wilkinson (1978). The latter authors focus on the African suids and this section is primarily based on their interpretation of available phylogenetic evidence.

Suid fossil remains are not yet known from the African Oligocene, but were found in a number of lower to middle Miocene deposits. Suidae fossil remains are fairly plentiful in Pleistocene deposits and also occur in those of the Pliocene. This leaves a gap in our knowledge of the later Miocene, making it difficult to firmly reconstruct the precise nature of the interlinking relationships between the early and the later groups (Cooke and Wilkinson 1978). Many "species" or taxa erected by various authors were derived from inadequate material, eg. solely from dental remnants or based on cranial expressions of sexual dimorphism, dental variability and wear stages (Thenius 1972). To further complicate interpretation, organs of social evolution (e.g. those pertaining to display) are not necessarily concordant with environmental evolution, and functional morphological convergence makes the unravelling of phylogenetic relations difficult (Thenius 1970). Furthermore, there appears to be a tendency for conservative ancestral stocks to give rise to more progressive species, and to continue to exist alongside the daughter species after the presumably allopatric speciation event (White and Harris 1977).

The fossil ancestors of the true pigs (Suidae) and the peccaries (Tayassuidae) first appear in the Oligocene (Cooke and Wilkinson 1978). At that stage the two families were already segregated, although a common Eocene ancestral group is assumed (Thenius 1972). Some peccary-like fossils occur in Eurasia, but in general the Neogene forms belonging to the Suidae and the Tayassuidae are restricted to the New World (Cooke and Wilkinson 1978). The diagnostic features of the Tayassuidae are: molarization of premolars, vertical alignment of the upper canines, proximal fusion of the medial metatarsals, complex digestive tract and dorsal glands (Thenius 1972).

The suiform ungulates are derived from the Dichobunidae, but the geologically oldest suid is *Propalaeochoerus* from the middle Oligocene (Thenius 1972). *Propalaeochoerus* is thus considered the ancestral taxon of the true pigs, the Suidae. The earliest forms were, *inter alia*, characterized by 5-digit front legs, orbitae in mid-cranium, and rooted and vertically-socketed canines. Subsequent evolutionary changes primarily involved the cranium and dentition. Some of the main adaptational trends and specializations included increased snout elongation, orbital elevation, maxillary deepening, from rooted, vertically-socketed to outwardly-turning rootless canines, extension of the zygomatic arches, tooth reductions and molar hypsodonty (Thenius and Hofer 1960, Thenius 1970, 1972, White and Harris 1977, Cooke and Wilkinson 1978).

Five subfamilies were identified within the Suidae (cf Colbert 1935 and Simpson 1945: both *op. cit.* Cooke and Wilkinson 1978) and their characteristics and phylogenetic relations are briefly reviewed below. The five subfamilies are Hyotheriinae, Listriodontinae, Tetraconodontinae, Sanitheriinae and Suinae. Geological time scales are placed in perspective in Figure 3/4 (after Eysinga 1978 ex Smithers 1983).

Subfamily *Hyotheriinae*

(a) *Propalaeochoerus*

This genus from the upper Oligocene of Europe is considered by Cooke and Wilkinson (1978) to form the basal stock for the two major and divergent lines of suid evolution:

(I) *Hyotherium*-lineage, involving *Hyotherium*, Listriodontinae, Tetraconodontinae and Suinae, and the

(II) *Xenchoerus*-lineage (Sanitheriinae).

(b) *Hyotherium*

The earlier Hyotherinii (= *Palaeochoerus*; Oligo-Miocene) were small, with a primitive cranium: preorbital skull length equal to postorbital length, large orbitae, without extended zygomatic arches, and no *cristae*

alveolaris. They had a simple and complete dentition, with brachyodont and bunodont molars and vertically-aligned, rooted canines (Thenius 1970).

FIG.3/4 :GEOLOGICAL TIME TABLE
(after Eysinga 1978 ex Smithers 1983)

| T | ERA | PERIOD | EPOCH |
|------|-----------|------------|----------|
| 0.01 | CAINOZOIC | QUATERNARY | HOLOCENE |
| 0.2 | | | TERTIARY |
| 0.4 | | NEOGENE | |
| 0.6 | | | |
| 0.8 | | PALAEOGENE | |
| 1.0 | | | |
| 1.2 | | EOCENE | |
| 1.4 | | | |
| 1.5 | | | |
| 1.8 | | | |
| 3 | | | |
| 4 | | | |
| 5 | | | |
| 10 | | | |
| 15 | | | |
| 20 | | | |
| 22.5 | | | |
| 30 | | | |
| 35 | | | |
| 40 | | | |
| 45 | | | |
| 50 | | | |
| 55 | | | |
| 60 | | | |
| 65 | | | |

T : GEOLOGICAL TIME IN MILLIONS OF YEARS

Figure 3/6 (page 103) relates suid evolution to this time table.

Hyotherium of the Mio-Pliocene were of larger size, had somewhat more elongated snouts, broadening of the zygomatic arches, development of *incisura infra-orbitalis* and well-developed *cristae alveolaris* (Thenius 1970). *Hyotherium, sensu strictu*, shows a marked sexual dimorphism in that the male lower canine is hypsodont and open-rooted; whereas the male upper and both upper and lower canines in the female have closed roots (Cooke and Wilkinson 1978).

Hyotherium fossil remains are recorded from Miocene deposits in Africa (Cooke and Wilkinson 1978). Separation of Listriodontinae and Tetraconodontinae from the Hyotheriini had already taken place in the Oligocene (Thenius 1970).

Subfamily *Listriodontinae*

This subfamily forms a major branch of suid evolution that split off early from the Hyotheriini. Following Cooke and Wilkinson (1978) three genera are involved pertaining to the African continent: *Listriodon*, *Kubanochoerus* and *Lopholistriodon*. The listriodonts retain a molar structure closely analogous to *Hyotherium*, but show an evolutionary trend toward great size in one direction (*Kubanochoerus*) and marked lophodonty in another (*Lopholistriodon*).

Kubanochoerus (= *Bunolistriodon*)

This genus was widely distributed in Africa and Eurasia during the Miocene. Diagnostic features include a complete dentition, more or less continuous, with massive stocky canines; broad spatulate incisors, brachyodont, bunodont and simple molars; simple premolars; a cranium with the preorbital region very elongated and narrow; reduced postorbital region and strongly developed zygomatic arches. A tendency towards massive size is exhibited (Cooke and Wilkinson 1978).

Lopholistriodon

The skull is primitive, close to *Hyotherium*, but the dentition is specialized: extreme development of the transverse crests in the molars

and fourth premolar and suppression of accessory cusps; premolars possess enlarged cingular platforms. Members of the genus are generally of small size, having crania with narrow nasal ridges (Cooke and Wilkinson 1978).

Subfamily Tetraconodontinae

Members of this subfamily are typified by enlarged third and fourth premolars. The ancestral genus of this subfamily *Conohyus*, which first appeared in the late Oligocene of central Asia, differs little from *Hyotherium* except for the characteristic premolar enlargement. Further development then resulted in giant forms in the Plio-Pleistocene (*Sivachoerus*, *Tetraconodon*) (Thenius 1970).

From late Miocene-Pleistocene African deposits, large extinct suids have been referred to the genera *Nyanzachoerus* and *Notochoerus*. In both genera the tympanic bullae are relatively slender and forwardly directed, recalling the condition in the Hyotheriinae. The enlarged premolars were taken to suggest an affinity with Tetraconodontinae, which in turn is closely related to the Hyotheriinae (Cooke and Wilkinson 1978). In contrast, *Bunolistriodon massai*, from the common Miocene genus, is considered the probable ancestor of *Nyanzachoerus* by Harris and White (1979). The same authors discuss evidence suggesting *Nyanzachoerus jaegeri* to be ancestral to the genus *Notochoerus*. *Nyanzachoerus/Notochoerus* predominate in the African Pliocene, but are supplanted by the *Kolpochoerus* and *Metridiochoerus* lineages in early Pleistocene (White and Harris 1977).

Subfamily *Sanitheriinae*

According to the original classification this subfamily contains a single genus (*Sanitherium*), but Cooke and Wilkinson (1978) propose to expand the subfamily by including the genus *Xenochoerus* (= *Diamantohys*) and also the genera *Hyosus*, *Sivahyus* and *Hippohyus* (formerly classified under Suinae).

Xenochoerus has a widespread distribution in deposits of central Europe, Asia and Africa. Its diagnostic features are small size; upper molars

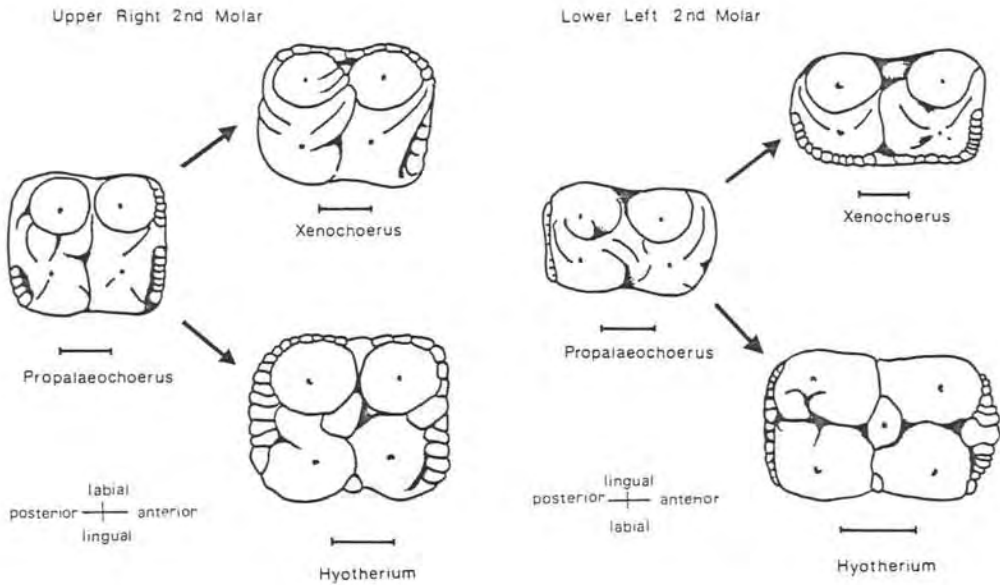
with high isolated bunodont labial cusps and low crescentic lingual cusps (opposite in the lower molars) and strongly developed labial cingulum. The upper premolars show incipient molarization (Cooke and Wilkinson 1978). These authors also demonstrate great similarity, especially regarding the dentition, and a close relationship to *Sanitherium*.

Hyosus is taken as the direct linear ancestor of *Hippohyus* (Pilgrim 1926 *op. cit.* Cooke and Wilkinson 1978) and the resemblance of both to *Sanitherium* is noted. The only substantial difference between *Sanitherium* and *Hyosus* is the absence of the labial cingulum in the latter. Cooke and Wilkinson (1978) conclude that *Sanitherium* is apparently a highly evolved side branch of the *Xenochoerus-Hippohyus* line and reflects many of its features. They demonstrated that *Xenochoerus-Sanitherium-Hippohyus* form a distinct lineage and constitute one of the two major branches of early suid evolution (discussed below).

The earliest suid ancestors apparently had a bunoselenodont dentition, of which there still remained some evidence in *Propalaeochoerus* (Thenius and Hofer 1960). The bunodont condition found in *Hyotherium* and many later suids was considered secondary, derived from a primitive selenodont condition. The term "neobunodonty" was proposed for this secondary bunodont condition (Stehlin 1899 *op. cit.* Cooke and Wilkinson 1978). By the early Miocene the *Hyotherium* and *Xenochoerus* lines were fully differentiated. The subfamily Hyotheriinae is characterized by a trend toward increased size; development from the transverse ridges of *Propalaeochoerus* to rounded, isolated, and tall tubercles of sub-equal height; a multiplication of these accessory elements; reduction or disappearance of the labial cingulum on the lower molars; the retention of relatively simple, trenchant, bladed premolars in the upper and lower jaws; precocious development of hypsodont lower canines. The subfamily Sanitheriinae, represented at that stage by *Xenochoerus* and *Sanitherium*, shows a retention of a primitive selenodont molar structure and subsequently its elaboration and perfection; development of a prominent labial cingulum on upper and lower molars with a marked inclination to preferential wear on the lingual cusps of the upper and labial cusps of the lower molars; molarization of the premolars and, in later forms,

achievement of marked hypsodonty in the molars (Cooke and Wilkinson 1978).

**FIG.3/5 :NEOBUNODONT versus SANITHERINE DICHOTOMY
IN EARLY SUID MOLAR EVOLUTION**
(ex Cooke and Wilkinson 1978)



Diagrammatic representation of suid molars to show the dichotomy of *Propalaeochoerus* into two divergent lines of evolution: the "neobunodont" condition (*Hyotherium*) and the "sanitherine" condition (*Xenochoerus*).

Cooke and Wilkinson (1978) summarize the proposed evolution of the neobunodont and sanitherine conditions from the *Propalaeochoerus* stock (Fig. 3/5): "In the neobunodont pigs there are four subequal cusps that are elaborated by the regular insertion of furrows and secondary furrows. These tend to cut off secondary tubercles, which become rounded and isolated. In the sanitherine pigs the cusps are unequal, with those on one side forming fore and aft ridges. Elaboration of these teeth also takes place by the insertion of furrows and secondary furrows, but in this case the ridges are retained and elongated. The furrows become deeply incised but do not cut off isolated tubercles; rather the lobes are produced, become elongated lengthwise and remain contiguous for the greater part of their length. The secondary furrows are very irregular and produce a variety of complications on the basic pattern".

During the Oligocene the Dichobunidae, the probable ancestral stock of the Suidae, are most abundant in Europe. It is also in Europe that *Propalaeochoerus*, the first true pig, was common. The molars of *Propalaeochoerus* have a structure amenable to interpretation as the linear ancestor of either *Hyotherium* or *Xenochoerus*. *Propalaeochoerus* may thus be the common ancestor of both of these divergent genera. Cooke and Wilkinson (1978) further propose that from the Oligocene *Propalaeochoerus* the Suidae split into two branches: *Hyotherium*, which contained the progenitor of modern pigs and *Xenochoerus*, which ultimately led to the highly evolved *Hyosus-Hippohyus* group in the Pliocene and Pleistocene of Asia.

By early Miocene, both *Hyotherium* and *Xenochoerus* were widespread in Europe, Asia and Africa. In addition, Africa had a highly evolved and differentiated assemblage of bunolistriodonts and intermediate listriodonts. Although Europe and Asia also had conservative equivalents of these animals, the center of this assemblage had shifted from Europe to Africa (Cooke and Wilkinson 1978). During middle and late Miocene, movement of suids between Eurasia and Africa presumably occurred in both directions, whereas by late Miocene the centre of radiation had moved to Asia. In Asia a second burst of adaptive radiation apparently took place, mainly concerning the subfamilies Tetraconodontinae and Sanitheriinae. Africa remained relatively impoverished until the late Pliocene-early Pleistocene (Cooke and Wilkinson 1978).

The subfamily Suinae presumably arose in Asia from a dicoryphochoerid stock, although probably via a bunolistriodont ultimately of African origin. By middle Pliocene-Pleistocene the suids, mainly represented by members of the Suinae, had repenetrated Africa. There then followed a third burst of adaptive radiation that gave rise to a great variety of types and also contained the immediate ancestors of the modern African suid genera (Cooke and Wilkinson 1978).

Subfamily *Suinae*

Typical features of the subfamily involve elongation of the skull, complication of the cheek teeth and various developments of the canine

tusks. The Suinae made their appearance in the late Miocene (Thenius 1970) and are clearly on the neobunodont line of descent (Cooke and Wilkinson 1978). The genera of the subfamily include *Dicoryphochoerus*, *Microstonyx*, *Sus* and the Plio-Pleistocene - Recent genera of Africa: *Kolpochoerus*, *Potamochoeroides*, *Metridiochoerus*, *Hylochoerus*, *Potamochoerus* and *Phacochoerus*.

The primitive *Dicoryphochoerus* are considered ancestral to *Sus* and other suine genera. Cooke and Wilkinson (1978) reason that the early members of *Dicoryphochoerus* may be synonymous or at least derived from a small bunolistriodont. Both show

- (I) simple bunodont molars with few accessory elements;
- (II) the lower P4 with a bifid central conical cusp and a large tubercle on the talonid,
- (III) the remaining lower premolars with pointed blades and short talonids;
- (IV) the upper P4 with two cusps, a labial and lingual, both compressed laterally and tuberculated; and
- (V) the remaining upper premolars with a single flattened bladelike cusp and broad posteriolingual talons.

Microstonyx, which is closely related to *Dicoryphochoerus*, is so far only reported from Europe and Asia of the upper Miocene to lower Pleistocene (Cooke and Wilkinson 1978).

Members of *Sus* are characterized by elongate skulls, with zygomatic arches not inflated; the upper canines small to moderate in size and surrounded by small canine flanges, tips truncated by wear against lower canines; the premolars, except upper P4, elongate and relatively narrow with cutting edges and high cingulum in lower PM and brachyodont and bunodont molars, with enamel of moderate thickness (Cooke and Wilkinson 1978). Species of the *Sus* lineage are recorded since the Pliocene: *Sus minor*, via *Sus strozzi* (early Pleistocene) leading on to *Sus verrucosus/Sus scrofa* (Thenius 1970).

The extant suine genera can be traced, either via *Dicoryphochoerus* or directly, back to the sub-family Listriodontinae, rather than having an independent origin from the Hyotheriinae (Cooke and Wilkinson 1978). The Plio-Pleistocene to extant African genera are discussed under two divergent evolutionary groupings, the "potamochoerine" and "phacochoerine" groups respectively.

The potamochoerines

Kolpochoerus (= *Mesochoerus*)

Kolpochoerus is widely distributed in the later Pliocene and Pleistocene, ranging from southern to northern Africa. Early *Kolpochoerus* forms had a skull architecture resembling that of *Potamochoerus* but with zygomatic arches laterally expanded and drooping. Male canines resemble those of *Hylochoerus* in structure and cross-section, but are relatively shorter and stouter. Female canines are much smaller than those of the male. The cheek teeth resemble those of *Sus* or *Potamochoerus* in general structure. The molars are higher crowned and have lateral columns that are distinct and well separated. Premolars are more *Sus*-like than *Potamochoerus*-like (Cooke and Wilkinson 1978).

The earliest known *Kolpochoerus*, *K. afarensis*, which was a small suid contemporaneous with the large *Nyanzachoerus pattersoni* and *Notochoerus euilus* according to deposits from Ethiopia, had affinities to the later species of the genus, but was also basically similar to the bushpig in skull structure and to the wild boar in some dental features. The zygomatic arches jut out abruptly as in *Potamochoerus porcus*. The incisors are like those of the bushpig, but the small canines and associated flanges are *Sus*-like. The premolars are intermediate in form between those of the bushpig and wild boar (Cooke and Wilkinson 1978). While the early *Kolpochoerus* have many similar ties with *Potamochoerus* and *Sus*, the later specimens share a number of features with *Hylochoerus*: broad zygomatic arches, broad forehead region, relatively long and pointed nasal alia, broad and flat symphyses and the position of the mandibular joint (Thenius 1981). Unlike *K. afarensis*, from mid-

Pliocene, the later species have elongated and hypsodont M3 (Thenius 1981).

Although the affinities of *Kolpochoerus afarensis* place it closest to *Kolpochoerus limnetes* as a probable ancestor of that lineage, it is also basically similar to *Potamochoerus* in cranial structure and to *Sus scrofa* in some dental features. This suggests that both *Kolpochoerus* and *Potamochoerus* probably were derived from a common ancestor that possessed basic *Sus*-like features.

Hylochoerus

The giant forest hog, *Hylochoerus meinertzhageni*, is the largest of the extant wild pigs with a limited range in forested Equatorial Africa. Diagnostic features of the skull, apart from its larger size, are the wide dorsally flattened parietal area, concave between the orbits instead of domed, expanded zygomatic arches, robust and outflaring canines, especially in males and surrounded by long, low flanges. The upper incisors and premolars are reduced. The elongated molars are laterally constricted and are strengthened by abundant cement. The third molars normally have three pairs of laterals. The lower jaw is typically with a wide symphysis. (Cooke and Wilkinson 1978, Thenius 1981). The molar structure of *Hylochoerus* can easily be derived from *Kolpochoerus limnetes* and some *Kolpochoerus* are regarded as the probable ancestral stock of the giant forest hog. (White and Harris 1977, Cooke and Wilkinson 1981). Ewer (1958b) had previously shown that *Hylochoerus* is phylogenetically not intermediate between *Potamochoerus* and *Phacochoerus*, but rather a strongly evolved "potamochoerine".

According to Thenius (1981), *Kolpochoerus limnetes* is somewhat too specialized as an ancestor of *Hylochoerus* and consequently he considered the latter to be derived from pre-*K. limnetes* *Kolpochoerus* in the late Pliocene. The ancestral stock of *Hylochoerus* was savanna-adapted, which explains corresponding adaptive and ethological features of the present-day giant forest hog: I) tendency towards hypsodonty of M3; II) lateral elongation and constriction of the molars as incipient columnarization, III) phacochoerine reduction of frontal dentition and IV) diurnality. Thenius (1981) concluded that recurrent changes of

vegetation in tropical Africa during and since the Pleistocene resulted in the secondary adoption of forest life by the giant forest hog.

Potamochoerus

The bushpig is the least specialized of the African suids, retaining a simple brachyodont dentition and a long, narrow skull. Following Cooke and Wilkinson (1978) the diagnostic features of *Potamochoerus* are:

- skull resembling that of *Sus*
- strong canine flanges in the male
- abrupt sweep of zygomatic arches
- stout premolars
- posterior cingulum not as high as in *Sus*
- molars more columnar, slightly higher crowned, enamel relatively thin and folding more apparent than in *Sus*.

Fossil remains of *Potamochoerus* are relatively rare. The first African fossil records are from the late Pliocene. Except for minor size and cranial differences the Pliocene representatives are virtually indistinguishable from extant examples. Since there is currently no evidence to support derivation from African stock, and since the genus is unknown from Europe, an Asian origin is assumed (White and Harris 1977).

It is generally assumed that *Potamochoerus porcus* was descended from an immigrant Asiatic *Propotamochoerus* (e.g. Thenius 1950; but contradicted by Azzaroli 1975). The earliest small suine, *Kolpochoerus afarensis* (from northeast Africa) is in some respects *Potamochoerus*-like, but also has features of the dentition that resemble *Sus*. *K. afarensis* could not be derived from a *Propotamochoerus* ancestor in which they were not present and Cooke and Wilkinson (1978) thus deem it more probable that the ancestor was more *Sus*-like or came from a stock closer to *Dicoryphochoerus*.

The suines *Kolpochoerus*, *Hylochoerus* and *Potamochoerus* share upper canines that are essentially *Sus*-like in the possession of a strong ventral band of ribbed enamel, as well as two thin inset enamel strips

on the lateral surfaces. The premolars are also *Sus*-like, although the lower P4 of *Kolpochoerus* is more like that of *Potamochoerus*. This group thus presumably has a common *Sus*-like ancestor, perhaps with closer affinities to *Sus verrucosus* than to *S. scrofa* (Cooke and Wilkinson 1978).

The phacochoerines

Potamochoeroides

The genus is represented by only a single species, *Potamochoeroides shawi*. The general structure of the teeth and skull resemble that of *Potamochoerus*, but differs particularly with respect to the third molars which are I) longer and more hypsodont; II) the enamel of the lateral pillars is more deeply infolded and III) a cement covering may be present. The lower M3 has a clear resemblance to that of *Metridiochoerus jacksoni*. The premolars are retained in contrast to their reduction in *M. jacksoni*. Rather, the premolars have *Sus* or *Potamochoerus* features. The upper canines of *Metridiochoerus* are more or less phacochoerine, whereas those of *P. shawi* are stout, short tusks; strongly curved and with a wide ventral band of ribbed enamel, as well as two thin inset upper enamel bands typical of *Sus*, *Potamochoerus* and *Hylochoerus*. The canine flanges are small and *Sus*-like. The lower canines are verrucose and rise much as in the bushpig. The orbitae are more elevated than in bushpig, giving a warthog profile, but the snout is short and does not droop much below the palatal plane. The zygoma are deep below the orbits, somewhat resembling those of *Phacochoerus*, with their maxillary roots much like that of *Sus verrucosus*. The mandibular symphysis is shorter and there is little constriction of the mandibles and palate in the region of the canines (Cooke and Wilkinson 1978).

There are substantial and noteworthy resemblances to *Metridiochoerus jacksoni*, suggesting some kind of relationship, but the retention of the premolars, the suine canines, narrow parietal constriction and short snout are considered to warrant generic separation. This genus is considered to provide a clue as to the *Sus*-like ancestry of the metridiochoere/phacochoere lineage (Cooke and Wilkinson 1978).

Metridiochoerus

The members of this late Pliocene/Pleistocene genus are of moderate to large size with broad parietal and occipital areas; elevated orbits, but less so than in the warthog, accompanied by an elevation of the maxillary root of the zygoma. The lower jaw resembles that of the giant forest hog in general form, but symphysis and corpus are without marked inflation. The premolars are greatly reduced. The third molars are moderately hypsodont to hypsodont with complex talon or talonid. The pillars tend to unite to produce complex enamel islands and areas of dentine with scattered islands of enamel. The upper canines have thin or no enamel and lower canines verrucose (Cooke and Wilkinson 1978).

A number of fossil suids share the common features of premolar reduction and a tendency toward a characteristic pattern in well-worn molars. Cooke and Wilkinson (1978) consider it probable that these share a common heritage from an as yet unknown ancestor. The fossil suids involved are considered to belong to a group, the *Metridiochoerus*-complex, including the genera *Metridiochoerus*, *Stylochoerus* and possibly *Potamochoeroides*. Harris and White (1979) consider *Stylochoerus* and *Potamochoeroides* as synonymous with *Metridiochoerus*.

Metridiochoerus underwent a substantial adaptive radiation during the early Pleistocene and at one point four metridiochoere species existed contemporaneously (White and Harris 1977). *Metridiochoerus andrewsi* has clear phacochoerine cranial features (elevated orbitae and occipital condyles) and mandibles (short, broad symphysis). The broad forehead is more hylochoerine (Thenius 1981). *Metridiochoerus* is important here in the context of the ancestry of *Phacochoerus* and the possible ancestral relationship with the other living African suid species.

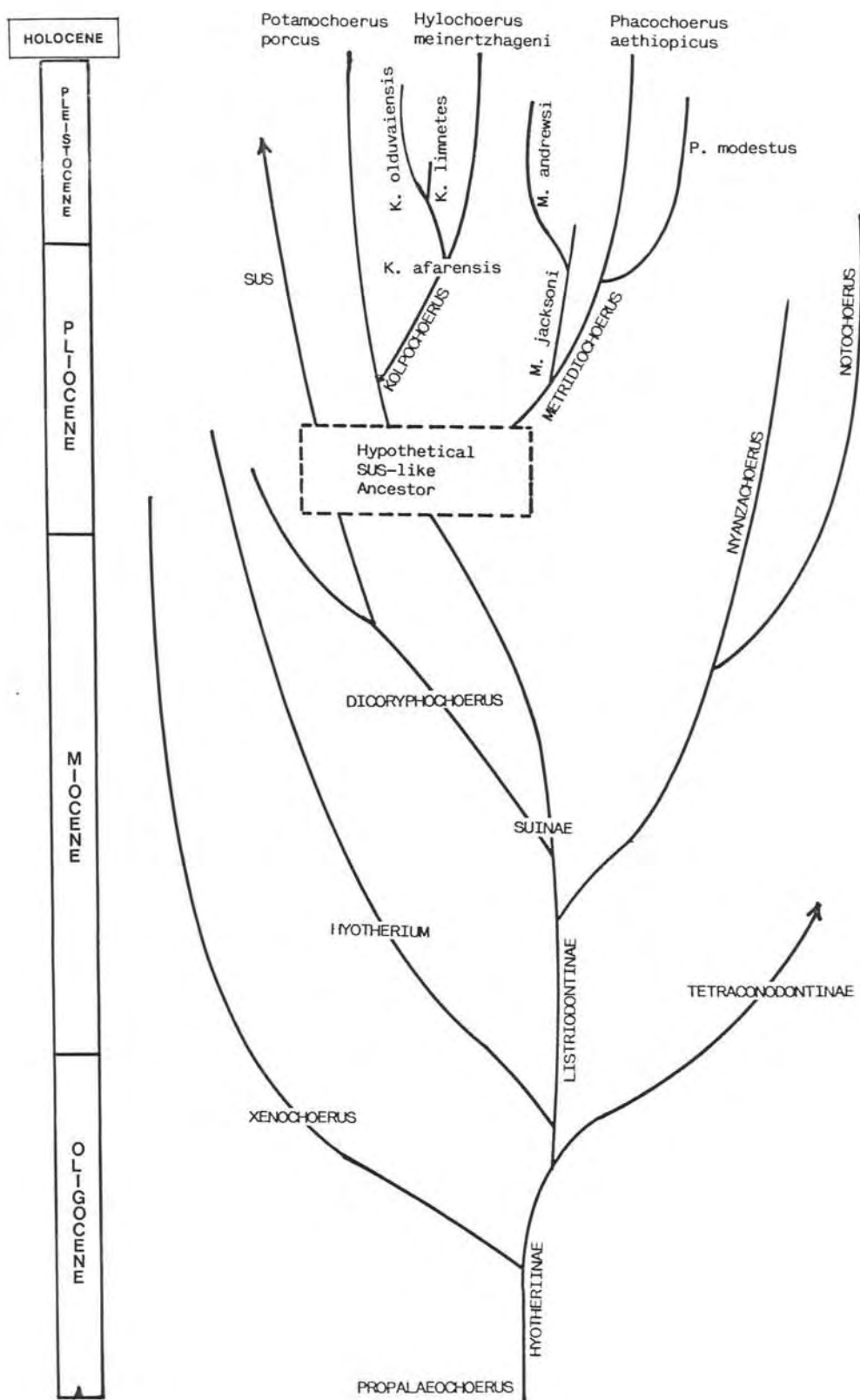
Phacochoerus

The orbits are set back and greatly elevated, the cranial region is more anteroposteriorly compressed, the zygomatic arches are broad and thickened and there are enlarged bony bosses around the sockets of the upper canines. The upper canines are large, outflaring and free of enamel, except at the tips; the lower canines verrucose. Incisors and premolars are reduced; the latter commonly shed in the adult. The molars and especially the third molars, are hypsodont and formed of closely packed little-folded oval to subtriangular columnar elements; well cemented. M3 talons are considerably elongated (Cooke and Wilkinson 1978).

The extant *Phacochoerus aethiopicus* (warthog) is derived from the *Metridiochoerus*-lineage (Thenius 1970, White and Harris 1977, Cooke and Wilkinson 1978). The genus is taken to be of African origin as indicated by its widespread occurrence in the early Pleistocene of Africa and the absence of ancestral forms in Eurasia (Thenius 1970). *Phacochoerus* is highly specialized towards life in the savannas: adaptations and reductions of incisors and premolars facilitate selective grass plucking; molar hypsodonty, columnarization and M3 elongation facilitate effective mastication of abrasive grasses, as do other cranial adaptations which improve the grinding actions of the jaw; and the elevated position of the orbitae allow a constant look-out during feeding by day in the open (Ewer 1958a).

The presumed phylogenetic relationships leading up to the extant African genera are diagrammatically presented in Figure 3/6 (cf Thenius 1970, White and Harris 1977, Cooke and Wilkinson 1978, Thenius 1981). As an outcome of this interpretation, *Hylochoerus* and *Phacochoerus* are seen as offshoots of the *Kolpochoerus* lineage and *Metridiochoerus*-complex respectively. *Potamochoerus* has close affinities with the early *Kolpochoerus* stock. The more primitive members of both the *Kolpochoerus* and *Metridiochoerus* lineages have some *Sus*-like features and a relatively conservative dentition not far removed from a simple bunodont ancestral stock. Also, the similarity in karyotype suggests a close phylogenetic relationship between the genera *Phacochoerus* and *Sus* (Bosma 1978). Cooke and Wilkinson (1978) consequently speculate that the same

FIG.3/6:DIAGRAMMATIC CONJECTURE OF AFRICAN SUID PHILOGENY



After Cooke and Wilkinson (1978), Harris and White (1979) and Thenius (1981).

stock may have provided the ancestors for both the *Kolpochoerus* line and for the members of the *Metridiochoerus*-complex, the former remaining fairly conservative, while the latter differentiated more dynamically.

3.3.2 Palaeoecology

Phenotypic change during the course of evolution may broadly follow one of two main patterns: a pattern of continuous gradual evolutionary change, with the rate of change independent of speciation, is termed "phyletic gradualism". Alternatively, a pattern of phenotypic conservatism within species and of association of most phenotypic change with speciation, results in "punctuated equilibria" (Vrba 1985a). Speciation, *sensu* Vrba (1985a), now refers only to multiplication of species, i.e. lineage splitting in distinction to phyletic evolution within unbranching lineages.

Vrba (1985a) proposed the turnover-pulse hypothesis according to which speciation, as well as extinction and most migratory events, does not occur unless forced by changes in the physical environment. Accordingly, most lineage turnover in the history of life has occurred in pulses, nearly synchronous across diverse groups of organisms and in predictable synchrony with changes in the physical environment. The underlying argument is briefly that species are habitat specific and normally conservative in their evolution. They thus respond by tracking environmental oscillations with their geographic distributions, rather than by evolving. If, in response to environmental change, the resources required by a species persist, the species and its distribution remain unchanged. If not, the species' distribution becomes fragmented, i.e. vicariance occurs, either with or without evolutionary change. Possible evolutionary changes include extinction, phenotypic evolution within the same species and speciation (Vrba 1985a). However, only rarely are the environmental stimuli strong enough that not only the contraction of range, but also speciation or extinction results (Vrba 1985a).

Two main predictions follow from the preceding reasoning:

- (I) evolutionary events are a direct function of environmental change
- and (II) speciations and extinctions across diverse lineages often occur

as concerted pulses in predictable synchrony with changes in the physical environment (Vrba 1985b). The Miocene-Recent African record of Bovidae supports these predictions. Synchronous evolutionary events among taxa presumed to be species are concentrated near the Miocene-Pliocene boundary, in the late Pliocene 2,5 million years ago and in the mid-Pleistocene (Vrba 1985c). Prior to this there was an explosive evolution of open-country large mammals including species of Felidae, Hyaenidae, Giraffidae and Bovidae in North Africa, Central Asia and in the Sub-parathyan province (Bernor 1985).

Global temperature progressively declined from the Paleocene until the end of the Miocene (Brain 1985, Tyson 1986). In eastern Africa rainfall had diminished by the early Miocene and aridity was especially aggravated during cold periods. The tropical lowland rainforest of the Congo basin however, apparently did not experience any major changes (Van Zinderen Bakker 1986). A seasonal dry climate was well established in East Africa at least 20 M years ago and in western Kenya a change toward arid conditions is suggested to have occurred around the Middle Miocene (Bonnefille 1985, cf Bernor 1985). The temperature plunge between 6,5 and 5,0 M years ago (Terminal Miocene Event) resulted in a rapid and dramatic sea-level drop of over 100 m worldwide (Brain 1985, Tyson 1986). There is evidence that the origin of the extensive savanna dates to the end of the Miocene (Axelrod 1985, Vrba 1985b). Many of the typical monophyletic groups of savanna mammals are first recorded near the Miocene/Pliocene boundary (Vrba 1985b, Tyson 1986).

The early Pliocene in general had a stable modern type of climate and open vegetation in East Africa was replaced by woodland and forest (Van Zinderen Bakker 1986). A cold episode marked the beginning of the late Pliocene, after 3M years ago (Brain 1985, Bonnefille 1985, Tyson 1986, Van Zinderen Bakker 1986). Following thereon, during the Pleistocene, the earths' temperature has oscillated between glacial and interglacial conditions on at least 17 occasions (Brain 1985). Three main episodes of grassland extension are recorded between 2,4 and 1,7 M years ago (Bonnefille 1985). This is in accord with the suggestion that for any one given area a change to more open habitat correlates with reduced temperature and less certainly also with reduced rainfall (Vrba 1985b). About 2,5 M years ago a particularly marked and widespread environmental

change occurred in Africa, involving an increase once more in open grasslands at the expense of woodland and tree cover (Vrba 1985b). This environmental change is reflected in bovid biostratigraphy and phylogeny around this period (Vrba 1985b and c).

While palaeoenvironmental change and mammalian community evolution are closely tied, Bernor (1985) stresses other factors which strongly influence provincial evolution, especially those permitting episodic faunal exchange. Overall, the course of global palaeoclimatic change was in a direction resulting in tropical forest communities giving way to cooler and more seasonal open-country ones. In contrast to the emphasis placed on the punctuated equilibria pattern by many authors (e.g. Vrba 1985a), Bernor (1985) maintains that Neogene evolution of the savanna-mosaic chrono-faunas should be seen as long-term evolutionary radiations; often gradual rather than pulsed in nature, provincially distinct and subject to repeated evolutionary convergence.

After the appearance of *Nyanzachoerus jaegeri* and *N. kanamensis* at ca 5 M years ago, African suid evolution shows conservatism until about 3 M years (White 1985). At the 3 M year mark *Metridiochoerus* appears, possibly either through immigration from Asia or punctuation from *Kolpochoerus*. Simultaneously, the rapidly phyletically evolving lineage of *Kolpochoerus limnetes* to *K. olduvaiensis* derives from the formerly stable *K. afarensis*. At the same time, the new phyletically evolving lineage *Notochoerus capensis* to *N. scotti* derives from *Notochoerus euilus* (White 1985). The African fossil suid record indicates a steadily increasing diversity, reaching its maximum in the latest Pliocene/early Pleistocene. A major part of African suid evolution appears to follow a pattern of phyletic gradualism. However, the break at 3 M years during mid-Pliocene appears to be a real one (White 1985). This break may be in synchrony with the lineage turnover pulse established for bovids around 2,5 M years by Vrba (1985c), but White (1985) cautions against the automatic acceptance of a causal linkage with the associated environmental changes.

The palaeoenvironmental change from predominantly tropical forest to more open vegetation types from mid-Miocene through the Pleistocene, resulted in new browsing/grazing and grazing niches. The three major

African suid radiations, namely the *Nyanzachoerus/Notochoerus* (Mio/Pliocene), *Kolpochoerus* and *Metriodiochoerus* (Plio-Pleistocene) lineages, were the consequence of adaptations in occupying such niches. In all three lineages convergence is exhibited in respect of dental and cranial characters, as well as a tendency towards increasing size and sexual dimorphism, from the primitive to the more progressive members within each lineage. The most important trend in the dentition has been the elaboration of the molars, particularly of the third molar, from low-crowned bunodont to high-crowned, cement-covered multicusped teeth. Along with this elaboration of the molars goes a reduction in the premolars and incisors (Ewer 1958a, Cooke and Wilkinson 1978, Harris and White 1979). Strong multilinear convergence is also exhibited in cranial features such as elevation of the orbits, deepening of the maxilla and reduction of the role of the temporal muscle (Harris and White 1979). These dental and skeletal features are all presumed to be adaptively significant for the mastication of a more fibrous diet (Harris and White 1979). The larger the herbivore, the more fibrous the diet it can select (cf Janis 1976) and the progressive size increase is presumably also related to the handling of increasingly fibrous browse and grass diets.

The most progressive members of all three lineages became extinct, the extant *Hylochoerus* and *Phacochoerus* being derived from more primitive members of the *Kolpochoerus* and *Metriodiochoerus* lineages respectively. A combination of environmental change, and therewith the nature of the available food resources, and interspecific competition, particularly with the ruminant artiodactyls, may have caused these extinctions. Ruminants are at an advantage where the quantity of food, of given equal quality, is limiting, since they need to take in smaller amounts per unit body weight than non-ruminants (cf Janis 1976). The detoxification of plant defensive compounds is also an important advantage of the ruminant digestive system, which is of particular significance in the context of browsing (Freeland and Janzen 1974, Janis 1976, Rhoades 1979). It is suggested that environmental change or competition with ruminants, or both, probably resulted in insufficient quantities of food being economically obtainable by the large-sized terminal members of the three suid lineages. Also Vrba (1985b) notes that once an ancestral species of a clade is established as, for example, an open grassland

grazer, its descendent species are highly unlikely to switch to a browsing, predominantly woodland existence. Constraints on switching basic vegetational habitats appear to be generally applicable for diverse mammalian groups (Vrba 1985b).

In concluding this chapter it is appropriate to take a brief look at how the three extant African suid species cope, i.e. how they are adapted to successfully occupy their respective niches. The warthog (*Phacochoerus*) is essentially a grazer which has retained some rooting capability. The species is well-adapted to feed on grasses containing abrasive silicates with their multicusped, hypsodont third molars (Herring 1980). The small inwardly pointed incisors are used like a pair of tweezers to pluck out the selected food and reject the unwanted material (selective grass plucking)(Ewer 1958a). The grinding is orthal in direction, unlike the bushpig where simple chopping movements of the jaw are employed. The elevated orbits follow as a consequence of the high position of the glenoid fossa which results in increased power for grinding. Elevated orbits also facilitate vigilance while feeding in an open environment (Ewer 1958a). Of the suid species *Phacochoerus* also has the largest relative surface area of the occipital region of the brain, which is associated with improved visual performance (Kruska 1970). Unlike *Hylochoerus*, the warthog retained the ability to root as well as graze. The grazing, non-ruminant warthog is thus able to supplement its diet whenever surface feeding becomes (seasonally) difficult (Kingdon 1979). Cumming (1975) considers the grazing/rooting combination as the key to the successful competition of the warthog with ruminants in particularly the more arid savanna regions.

In *Hylochoerus* the molar cusps are arranged in lophs, resulting in sharp hills and valleys. The third molars are somewhat elongated, but all three molars are used simultaneously in a more chopping rather than a grinding action, although some sideways jaw movement occurs. According to these features the giant forest hog is considered a browser (Ewer 1958a and 1970, Herring 1980).

Both premolars and incisors are reduced, suggesting a pure vegetarian diet and selective feeding respectively (Ewer 1958a). The grinding adaptations of the posterior part of the skull are absent: the glenoid

is not raised; the paroccipital processes are relatively short and the conformation of the posterior part of the skull and mandible is potamochoeroid (Ewer 1958a). All these features are in line with the known diet of the species, consisting primarily of soft herbaceous material, including young grass. The animals apparently do not root for subterranean food items (Ewer 1958a). A browse/grass diet is comparatively fibre-rich and increased body size increases the tolerance for such diets through the effect of scaling on metabolic requirements and storage capacity (cf Janis 1976). The quantity of food available places limits on size increases and an optimal body size results for the prevailing quality/quantity constraints (cf Illius and Gordon 1987). Non-ruminant herbivores compensate for a relatively low digestive efficiency in the forestomach with a higher turnover in digesta, resulting in a larger optimal body size for any given dietary fibre level, compared to ruminants (cf Janis 1976). Thus, given its size, the giant forest hog requires comparatively larger quantities of food of relatively low fibre and plant toxin levels. This combination of food quantity and quality is apparently only available in highly productive tropical environments with both browse and grass in close proximity. The restricted occurrence of the giant forest hog in tropical forest/savanna ecotone habitat (Kingdon 1979) could possibly be explained along these lines. Similarly, the more widespread occurrence of *Hylochoerus* during the Pleistocene (cf Thenius 1981) may be attributed to the presumed higher incidence of favourable habitat, as outlined. This ties in with evidence pointing toward greater habitat diversity and more finely grained habitat mosaics during the Pleistocene in many regions of the world (Graham and Lundelius 1984).

Following Janis (1976), and others cited in this section, the Eocene climate was largely humid and tropical and with the start of the Oligocene a trend towards a cooler, drier climate commenced which continued throughout the Tertiary. In the tropical forest environment of the Eocene, herbivores would have been able to select a largely cellulose-free diet of reproductive structures and young growth stages all the year round (Janis 1976). The small-sized, early hyotherine pigs, with their simple bunodont molars and short snout, i.e. no digging specialization, presumably subsisted on such a diet. As the climate became cooler and more arid, growth would have become more seasonal and

herbivores would have been faced with a diet that was more fibrous during certain parts of the year (Janis 1976). As discussed above, the ruminant digestive system is also superior in dealing with toxic secondary compounds. The ruminant strategy with forestomach fermentation was thus presumably a superior way of trying to cope with both these problems encountered by herbivores (Janis 1976).

Faced with the postulated increasing bottlenecks in food quality, ancestral suid species apparently responded by *i.a.* either dental specializations (bunodonty to lophodonty for browsing and brachyodonty to hypsodonty for grazing), coupled with body size increases, or circumvented the bottlenecks by specializing in the utilization of alternate food sources (rooting specialization). The large suid browsing or grazing specialists have died out. This may have been due to changing environments and ruminant competition, resulting in a reduction in food of acceptable quality.

The extant *Sus scrofa* and *Potamochoerus porcus* represent suid taxa which have adopted a strategy of rooting specialization. Their presumed ancestral stock were small bunolistriodonts with brachyodont, bunodont, simple molars, suggesting an unspecialized omnivore diet. They had a wide geographical distribution during the tropical conditions of the early Miocene and the very elongated preorbital region (Cooke and Wilkinson 1978) indicates that rooting was then already of decisive importance.

For the bushpig, digging with the snout for subterranean food items constitutes an essential element in foraging. The rhinarium is the most important digging organ (Ewer 1958a, Herring 1972). The importance of rhinarium digging is reflected in the elongated and vertical-sided snout. The mandible and palate are constricted behind the canines and the symphysis is elongated. These characters are all related to the digging functions of the snout (Ewer 1958a): I). The rectangular section allows the snout muscles to run straight from their origins to their insertions on the rhinarium for maximal efficiency; II) the elongated symphysis strengthens the snout region and III) the constriction separates off the digging rhinarium from the masticatory

cheek teeth, such separation being commonly found where functions other than eating are performed by the front of the mouth.

4. SOCIAL ORGANIZATION

4.1 The sociobiological setting

Leuthold (1977) defines social organization as "the result of all social interactions and spatial relations among members of a single-species population". Social organization may thus be viewed as consisting of three major interlinked components: group structure (size, composition), spatial organization (e.g. territoriality or overlapping ranges) and mating/rearing system (e.g. monogamy or polygamy).

These three components of social organization provide the frame within which individuals strive for survival, maintenance and reproduction (Gosling and Petrie 1981):

Survival and maintenance:

- securing a food supply
- minimizing energy loss
- avoiding injury and disease
- avoiding predation

Reproduction:

- finding and competing for a mate
- producing offspring
- rearing offspring

Success is largely influenced or determined by group membership and the role which the individual plays within the group. Dispersal and alloparental care are important sociological phenomena providing different options to individuals of particular age and sex classes. In addition to the three main components of social organization, dispersal and alloparental care will also be briefly discussed in this section.

The behavioural adaptations maximizing an individuals reproductive success, survival and the survival of offspring to maturity are described as "strategies" by Crook, Ellis and Goss-Custard (1976). The combination of strategies adopted by individuals in pursuit of vital functions related to mating, rearing, resource exploitation and predator avoidance form complex socio-ecological systems which are controlled by the interactions of numerous internal constraints and external environmental factors. Crook, Ellis and Goss-Custard (1976) present a model describing these systems functionally and at the same time providing a classification for mammalian societies (Table 4/1). This classification serves as a descriptive frame for further discussion and comparisons.

In Table 4/2 a set of postulated interdependencies between external environmental forces and species parameters interacting to mold social structures are presented (Crook, Ellis and Goss-Custard 1976).

| TABLE 4/2: MATRIX OF SOME IMPORTANT EXTERNAL ENVIRONMENTAL VARIABLES (EEV) SPECIES PARAMETERS (SP) AND PRINCIPAL SOCIAL SYSTEM VARIABLES (PSSV) | | | |
|---|--|--|--|
| | Resource-exploitation and predation avoidance sub-systems | Mating sub-system | Rearing sub-system |
| EEV | Resource density, resource distribution, density of predators | Resource distribution | Resource seasonality |
| SP | Mobility potential, susceptibility to predation | Role of male in rearing | Role of male in rearing, maturation rate of young |
| PSSV | Group size and stability, cover utilization, range exclusivity | Duration of male-female bond, no. females mated/male | Duration of the female bond, duration of the female-offspring bond |
| Crook <i>et al.</i> (1976) | | | |

Table 4/1: COMPONENTS OF SOCIAL SYSTEMS (after Crook, Ellis and Goss-Custard 1976)

| SOCIAL SUBSYSTEMS | STRATEGIES |
|--|--|
| <p>1. <u>MATING SUBSYSTEM</u></p> <p>(a) Number of females with which each male consorts during a breeding season</p> <p>(b) Duration of male/female bond</p> | <p>(a) Monogamous pair</p> <p>(b) Monogamous mating/brief pairing</p> <p>(c) Serial polygamy/sequential short term bonds</p> |
| <p>2. <u>REARING SUBSYSTEM</u></p> <p>(a) Duration of male/female bond (i.e. including lactational period)</p> <p>(b) Duration of female/young bond (i.e. bonding past weaning)</p> | <p>(a) No male assistance, young leave at weaning</p> <p>(b) No male assistance, young remain until subsequent young are born.</p> <p>(c) No male assistance, young remain with mother until after birth of subsequent young</p> <p>(d) Male assistance, young leave family at weaning</p> <p>(e) Male assistance, young leave prior to birth of subsequent offspring</p> <p>(f) Male assistance, young remain with pairbonded parents long past weaning, dependence usually decreasing slowly with age after birth of subsequent offspring.</p> |
| <p>3. <u>RESOURCE EXPLOITATION SUBSYSTEM</u></p> <p>(a) Group size</p> <p>(b) Group stability</p> <p>(c) Refuge or cover utilization</p> <p>(d) Range exclusivity</p> <p>a - c may also express predator avoidance strategy</p> | |

Numerous studies have shown or implied the adaptive value of a species' social structure particularly with regard to resource exploitation and predator avoidance (Eisenberg *et al.* 1972, Barash 1974, Clutton-Brock 1974, Jarmann 1974, Geist 1974, Clutton-Brock and Harvey 1977 and 1978, Van Schaik and Van Hooff 1983).

The sociobio-ecological interrelationships, mainly applicable to African bovids, are depicted in Figure 4/1 (Leuthold 1977).

FIG.4/1 INTERRELATIONSHIPS BETWEEN MORPHOLOGY/PHYSIOLOGY, ECOLOGY AND SOCIAL ORGANIZATION IN AFRICAN BOVIDS (Leuthold 1977)

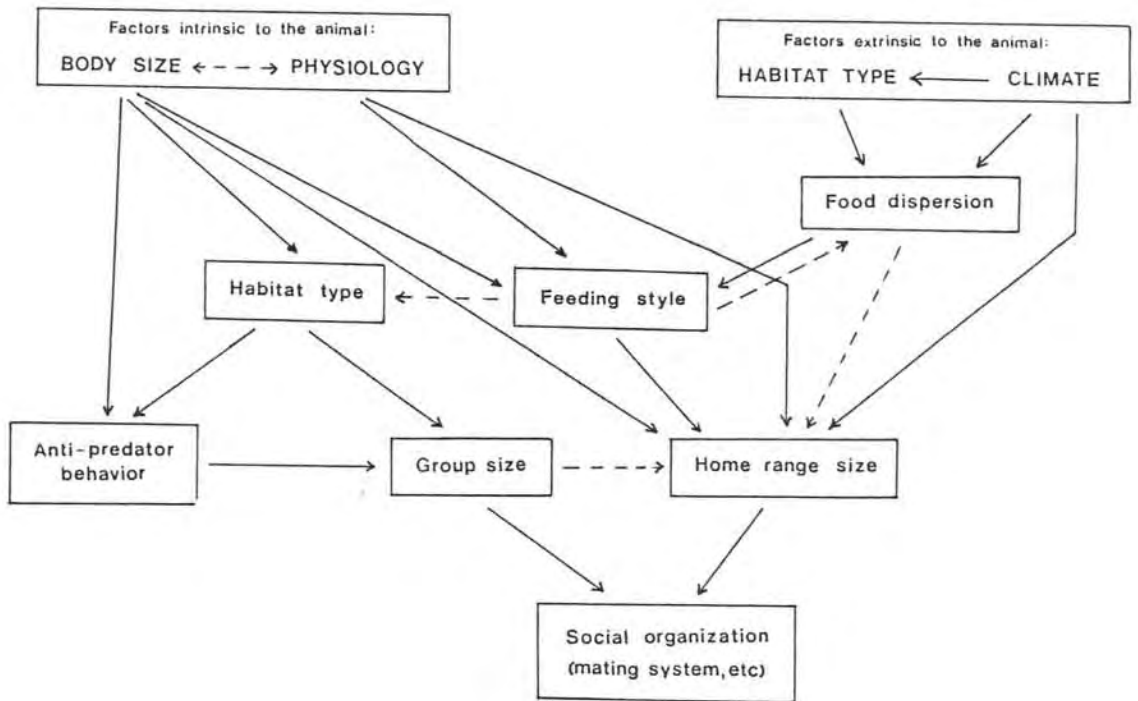


Figure 4/1 illustrates the basic thesis that variation in distribution, density and quality of food supplies is largely responsible for population dispersion patterns (density, group size, spatial relations), that differences in population dispersion play an important part in determining differences in breeding systems and that these affect a wide

variety of morphological and physiological traits (cf Clutton-Brock and Harvey 1978).

Cause-effect relationships between morphology, ecology and social organization should not however, be generally inferred. It is quite probable that the different traits influenced each other mutually during the course of evolution. Correlation in itself is not adequate. The mode of operation must be demonstrated in order to substantiate cause-effect relationships (Altmann 1974). Neither should the plasticity in a species' social organization be ignored. It is becoming increasingly clear that a species is seldom typified by an unique social structure (e.g. MacDonald 1979, Messier and Barrette 1982). While variation in social systems often confirms basic predictions of socio-ecology, it contradicts the premise that a species' social system is a fixed product of natural selection. What has more likely been selected for is a social predisposition. The outcome may be more than one social system, depending on the individual history and current circumstances (Lott 1984).

As pointed out by Geist (1978a) the social system of a species is not only a product of its adaptive resource exploitation strategies governed by environmental factors such as resource distribution, abundance, seasonality or cover type, but also a consequence of ancestral adaptations (see also Clutton-Brock 1974).

4.1.1 Group structure

The continuum of association with conspecifics ranges from solitary individuals to social groups of variable composition and size to aggregations of social units. The degree of gregariousness is largely species-specific, but may exhibit considerable variation under different environmental conditions. It is important to differentiate between groupings which constitute coherent social entities and loose associations or aggregations. The latter simply constitute any number of animals being together in one place in response to some external factor, whereas a social unit is defined as the smallest cohesive group of conspecifics, including single animals where applicable (Leuthold 1977).

Population structure depends on group composition, in terms of sex and age, and group size. Whereas group composition is functionally related to breeding strategy (mating, rearing), group size largely reflects factors of food resource exploitation and antipredator behaviour. Mammalian group sizes appear to be adaptations to two major classes of selective forces: the distribution and density of essential resources and patterns of predation and antipredator behaviour (Alexander 1974, Altmann 1974, Jarman 1974, Clutton-Brock and Harvey 1977 and Krebs and Davies 1981).

Numerous empirical studies tend to support the idea that larger groups are better at detecting predators (Van Schaik *et al.* 1983). Predation pressure thus tends to increase gregariousness. With respect to food procurement there are two main possibilities (Van Schaik *et al.* 1983).

- (a) Feeding in a group may enhance an individual's feeding success, because of
 - (i) better detection and exploitation of food with a patchy and unpredictable distribution;
 - (ii) cooperative defence of food resources, particularly in the case of predators (cf Lamprecht 1978)
 - (iii) optimization of return times to patches depleted at earlier visits and
 - (iv) reduced time required per individual for anti-predator vigilance.
- (b) Feeding efficiency is lowered with increasing group size due to competition among group members.

Decreased feeding efficiency appears to occur generally, either through mutual interference at food sources or through indirect competition for food supplies (Clutton-Brock and Harvey 1977). Feeding interference is expected to be most pronounced where individuals consume or defend whole food sources, forcing latecomers to search elsewhere, and where the distance between food items is large. Conversely, it should be least important where individuals only take a proportion of the food available

at each source and where the distance between food items is small, as in many grazing situations (Clutton-Brock and Harvey 1978, Gosling and Petrie 1981).

4.1.2 Sociospatial organization

Sociospatial organization is seen here as an expression of spatially related dominance, i.e. dealing with the degree and nature of spatial exclusivity (territoriality). Dominance may be characterized as an attribute that provides its holder with access to certain resources in precedence over other individuals, without actual contest.

Leyhausen (1965 and 1971) was the first to differentiate between two major forms of dominance:

(i) Absolute dominance

Absolute dominance is a fixed attribute of an individual, effective wherever it goes within its society and regardless of external circumstances. The resultant social structure is an absolute hierarchy.

(ii) Relative dominance (Territoriality)

If the dominance of an individual is tied to some external condition, such as space, relative dominance is applicable. An individual may then be dominant over another in one place, but not in another. This characterizes a relative social hierarchy. Spatially localized dominance (territoriality) is the most important variety of relative dominance.

Absolute and relative dominance may occur simultaneously in different social segments of the same population: relative dominance among territorial males and rank dominance among females and/or "bachelor" males.

Territoriality is a widespread phenomenon. Its existence has been reported for species of every vertebrate class (Brown and Orians 1977).

The original and most widely followed definition of territoriality is due to Noble (1939 ex Owen-Smith 1977): a territory is any defended area. Territoriality is here defined to apply whenever an individual defends an area, directly or indirectly, resulting in spatial exclusivity in relation to other members of the same sex and similar dominance status. The presence of subordinates in the area may be tolerated by the territory holder(s) depending on intensity of competition and type of resource (access to food or mates).

Competition for food is thought to determine the distribution favoured by females, which in turn determines the competitive strategies of males. The interaction of these two factors then yields the distribution of males and females observable in nature (Van Schaik and Van Hooff 1983). Two main types of territoriality are encountered: territoriality as a male mating strategy, i.e. a spatially related way of intermale competition for access to females (most African bovids: Leuthold 1977), and resource territoriality, relating to the defense of an area to ensure priority access to its food resources. Both sexes may be involved in the defense of resource territories and the female often plays a prominent role. It should be noted that mating access territoriality most often also has consequences in terms of access to food resources and vice versa. Lek territories are an example of an exception.

Territorial defence varies among species from immediate aggressive exclusion of intruders to an increasingly greater use of indirect methods, like vocal advertisements, visual displays and olfactory marking in combination with periodic aggressive encounters. Since the costs of defending a territory increase continuously with increasing size, there should be strong selective advantages for more indirect forms of territory defence, such as olfactory marking, which still function in the absence of the territory holder. Such olfactory "intimidation mechanisms" should reduce ambiguity about territory occupancy and limits and the cost of such ambiguity in competition for dominance in disputed areas (Geist 1966 and 1978a, Gosling and Petrie 1981).

The extent of territory "overlap" tends to be roughly related to territory size (Clutton-Brock and Harvey 1977: for primate species). In association with surveillance and territory overlap the aspect of economic defendability of the relevant resource(s) such as females, food or shelter becomes important. If the resource is superabundant, unpredictable in time or space or widely dispersed, i.e. costly to defend, territoriality may either be absent or take on special forms (e.g. leks).

The defensibility of a feeding area will be high if the patch richness of the food source tends to be high in terms of energy concentration; the relative patch density is low to moderate, coupled with temporal stability of the resource, and the species is highly mobile (Eisenberg 1983). Conversely, for species using ubiquitous food resources which have a low energy content (leaves, grass) and exhibit temporal variation in distribution, defense of feeding areas is poorly developed. Resource defendability is dependent on the distribution of the resource in space and time and on the density of the competitors (Horn 1968, Wiens 1976, Geist 1978 a and b, Lott 1984). Resource territoriality is thus found mainly under conditions of resource stability, predictability and moderate productivity, as in subtropical and tropical plant communities (Geist 1974 and 1978a). Territorial defence is suggested to be most advantageous where intraspecific competition is most intense (stable environments: Geist 1974) and the costs of feeding competition correspondingly high (Clutton-Brock and Harvey 1977).

In many cases territory size varies with changes in population density, since the costs of defence are influenced by changes in intensity of competition. When the overall population density increases and competition builds up, the territory contracts, and vice versa ("elastic disc" concept of Julian Huxley, 1934; ex Wilson 1975). This relationship holds true only for a certain range of population densities. There is a limit beyond which the animal cannot be pushed. It then stands and fights, or else the territorial system begins to disintegrate. With decreasing population density the territory expands up to a certain limit. At low densities, territories may either be non-contiguous or their boundaries ill-defined (Wilson 1975).

Numerous studies have demonstrated that territory size can depend on short-term resource levels, i.e. contraction of the territory in the face of increased resource availability (Hixon 1980, Stamps and Tollestrup 1984). Such behaviour was termed the "just-sufficient" strategy by Von Schantz (1981). However, often territorial behaviour or size is not related to short-term fluctuations in resource levels (e.g. Von Schantz 1981). This lack of correspondence between immediate resources and territory size is ascribed to territory holders ignoring short-term fluctuations in resource levels because their defence depends on both the present and expected future value of the resources in the territory (prospective resource defense: Stamps and Tollestrup 1984, "obstinate strategists": Von Schantz 1981). With resource increases a territory holder may unilaterally contract his territory, but re-expansion may be costly when the need arises. For this reason a territory owner should maintain a territory of a fixed size, making no attempt to alter its size to track random variation in the environment (provided that means and variances remain unchanged). For energy or profit maximizers the optimal territory size would thus be that fixed area minimizing the probability of starvation (Lima 1984).

Apart from resource level fluctuations discussed above, territory size tends to vary inversely with average food density or productivity (Lima 1984). According to the "sufficient resource" hypothesis, territory owners would defend an area just providing access to sufficient resources for maintenance and reproduction. Smaller territories would accordingly be required and maintained in relatively productive areas. As an alternate option applying in certain cases Verner (1977) proposed the "super-territory" hypothesis. According to this hypothesis an area maximizer would defend a disproportionately large territory, thereby inhibiting the reproductive performance of other animals by preventing them from utilizing the spare food within its "super-territory", thus increasing the territory owners' relative fitness (territoriality as a form of interference competition). This is in line with the contention of Geist (1978a) that individuals ought not only to maximize their reproductive fitness by competition for resources or efficiency in resource use, but that they should also reduce the reproductive fitness of other individuals directly. Not the absolute number, but the proportion of offspring in the following generation is what counts.

Super-territory size is expected to decrease wherever food production and competitor density increase concurrently, but should not be affected by changes in food production alone (Verner 1977).

4.1.3 Mating systems and rearing

Following Ralls (1977) and Krebs and Davies (1981) four categories of mating systems may be recognized:

- monogamy : one female has a bond with one male
- polyandry : one female has bonds with several males
- polygyny : several females have bonds with one male
- promiscuous: mating bonds between sexes only

These categories are not clearly separable in all cases, and alternate mating patterns may apply to the same species, largely depending on the nature of resource distribution (cf Lott 1984).

Polygamy is often used as a general term for when an individual of either sex has more than one mate (Krebs and Davies 1981). Taking the female as reference, polygamy is here defined as a mating system where several females mate with one or several males, whereas monogamy (*sensu lato*) describes the mating systems where one female bonds and mates with one or several males. With such definitions all mammalian mating systems should be covered by the polygamy/monogamy (*s.l.*) dichotomy.

Emlen and Oring (1977) propose that certain environmental factors determine the degree to which mates can be monopolized. The greater the potential to monopolise a number of mates, the greater should be the intensity of sexual selection and the tendency for polygamy. Accordingly two preconditions hold for the evolution of polygamy (Emlen and Oring 1977):

- (I) Multiple mates, or resources sufficient to attract multiple mates, must be energetically defensible by individuals. Primary among the environmental factors affecting the potential for such control are the spatial and temporal patterns of resource dispersion.

- (II) The ability of animals to utilize the environmental potential for polygamy. This depends in a large part on the degree of parental care required for the successful rearing of the young, i.e. the importance of paternal rearing investment.

Reproductive effort may be defined as the total resources in time and energy used by an animal for reproduction. Reproductive effort can be partitioned into parental effort (rearing) and mating effort (acquiring mates). In polygamous species males tend to invest relatively more into the mating effort than females. For monogamous species a relatively greater proportion of the reproductive effort of the male is put into rearing. Monogamous females invest relatively more energy in the mating effort compared to females mated polygamously (Krebs and Davies 1981).

A prolonged association between one female and a male is an essential feature of monogamy (cf Wittenberger and Tilson 1980). It must be assumed that some fitness benefits accrue from this association extending beyond actual mating for it to be maintained (cf Trivers 1972). Paternal care is closely associated with monogamy among mammals (Ralls 1977, Clutton-Brock and Harvey 1978). The greatest degree of paternal investment occurs in those species in which sexual maturity may be delayed and the older off-spring remain with the family group (Type II monogamy: Kleiman 1977).

Suggested ways of male parental investment include the following:

- (I) Defence of territory (i.e. food resources for female and offspring) (Kleiman 1977, Clutton-Brock and Harvey 1978)
- (II) Defence of young (Kleiman 1977)
- (III) Infant carrying (primates: Clutton-Brock and Harvey 1977)
- (IV) Food provisioning (canids: e.g. Moehlman 1983).

It is difficult to assess whether paternal investment in rearing is causally related to monogamy or a consequence thereof (Clutton-Brock and Harvey 1978); it could be either (cf Van Schaik and Van Hooff 1983).

Monogamy is relatively rare among mammals (Kleiman 1977, Eisenberg 1983) and its socio-ecological basis as opposed to the conditions favouring polygamous mating patterns, of revealing significance. Monogamy seems to be favoured when environmental resources are inadequate to support more than one breeding female i.e. when the carrying capacity of the habitat is insufficient to permit another female simultaneously to raise a litter in the same home range (Kleiman 1977, Eltringham 1979). This would imply a low food resource density which is relatively uniform in space and time (absence of productivity spurts or gradients: Geist 1974) and energetically costly to collect (Bekoff, Daniels and Gittleman 1984).

It appears that the socio-ecological interactions favouring monogamy and food resource territoriality are similar (cf Emlen and Oring 1977) and monogamous animals are generally found to be highly territorial (Crook, Ellis and Goss-Custard 1976, Kleiman 1977, also cf Clutton-Brock and Harvey 1977).

In addition to a relatively high paternal rearing investment, monogamy in mammals is associated with a number of sociobiological features together forming what is here termed the "monogamy syndrome". Sexual dimorphism in body size is reduced or absent (Ralls 1976 and 1977, Kleiman 1977, Geist 1978a, Eisenberg 1983 and Jarman 1983). When retained in the group, subadults exhibit breeding deferment and "helping" behaviour, i.e. alloparental care (Kleiman 1977, Eltringham 1979, Eisenberg 1983) of the usually altricial young (Zaveloff and Boyce 1980). High levels of intrasexual aggression between females is characteristic (Burley 1977, Kleiman 1977, Wittenberger and Tilson 1980, Van Schaik and Van Hooff 1983).

For the association of group territoriality, male parental care, helping behaviour and low fecundity, the reader is also referred to Brown (1982).

4.1.4 Alloparental care

Individuals may compete not only alone, but also supported by those who share common goals (Geist 1978a). In an abstract sense individuals may

be perceived to work for their genotypes and may therefore cooperate with closely related individuals in spreading their genes. Cooperation and even altruism may arise as a consequence (Hamilton 1964, Wilson 1975). Alloparental care is an expression of such cooperation. Although kin selection may be useful for explaining some examples of helping, there are many exceptions which may rather be explained as reciprocal altruism or as simple reciprocity (cf Bekoff and Wells 1982).

Alloparental care, commonly termed "helping" in the literature, can be defined as any rearing assistance of group members other than the parents that increases the survival of the offspring (cf Wilson 1975). Alloparental care is not necessarily restricted to female individuals. Guarding of young appears to be the most widespread manifestation of helping behaviour. Other forms of alloparental care include providing food, transport of young and assistance in territorial defense.

Emlen (1978 ex Von Schantz 1981) listed different potential benefits of group membership for breeders and non-breeders.

For breeders:

- (I) The non-breeders may help the breeders in care and rearing of their current offspring.
- (II) The non-breeders could function as an insurance back-up, increasing the probability that the offspring will survive if one of the breeders dies.
- (III) The experience gained by the non-breeders in rearing young could improve their ability to become successful breeders in the future. On the assumption that the non-breeders are close relatives to the breeders, their future success could increase the inclusive fitness of the original breeders.
- (IV) Competition for space and food between adjacent groups may favour a large group size.

For non-breeders:

- (I) Gained experience in caring for young.
- (II) Increased inclusive fitness by rearing relatives.
- (III) Access to the resources and security of the group which increases the chance of surviving to the age and status necessary for becoming a breeder.

In order to understand helping, these benefits and the costs that may accrue to breeders and to helpers as a result of the retention of the latter in the group must be carefully considered (Emlen 1982b). A non-breeder has two opposing options, the relative costs and benefits of which should determine which one to take:

- (I) dispersing and attempting to breed independently or
- (II) postponing departure and remaining as non-breeder in the group.

In the latter case alloparental care is often provided for increased inclusive fitness.

Whether it is advantageous for the non-breeder to leave the group depends on the cost (risk) of dispersal itself, and the likelihood of successful reproduction in such an event. This again depends upon the probability of obtaining a mate and on successful territorial establishment (cf Emlen 1982a). For the breeders the retention of non-breeders is however only of advantage if the costs of intragroup competition is not disproportionately severe. For mammals cooperative familial social organizations are thus predicted and found to occur under conditions of reduced intragroup and increased intergroup competition (see Von Schantz 1981, Bekoff and Wells 1982, Emlen 1982a and b).

4.1.5 Dispersal

Dispersal is usually defined in relation to an individual prior to first mating and as the movement away from its natal site and out of the home range of its parents to another site where it breeds or attempts to do

so. For an adult individual the term refers to movements away from its own (or group) home range to another area (Bekoff 1977).

Which individuals disperse and when may depend on a variety of factors such as sex, age, season, opportunities for colonization, density, physiological state, social environment and community composition (Lidicker and Stenseth 1985). It is usually assumed that dispersal allows each individual to maximize its own chances of reproduction (cf Bekoff 1977). Dispersal patterns are thus expected to be determined by factors which influence the gain in reproductive fitness to the dispersing individual. The ultimate costs and benefits of dispersal appear to vary primarily with food resources and population density (Packard 1980), with the direction of dispersal being from areas of high population densities or low food availability to those with lower densities or higher levels of food availability.

Dispersal is interlinked with all the sociological features introduced in this section. The group structure at any given moment is largely influenced by dispersal patterns. The dispersal pressures which operate are largely shaped by the sociospatial organization and the mating system of the species.

4.2 Methods

Data on social organization have come mainly from the general research programme rather than from planned studies of specific topics. These general data collection programmes have been described in detail in section 1.3. Relevant subsections are indicated below.

- (a) The data on group size and composition was forthcoming from
 - (i) the capture programmes, mainly on Goudveld State Forest, but also on Diepwalle, during 1981-1985 (1.3.1) and
 - (ii) whole-group culling in the Southern and Eastern Cape (1.3.2).

- (b) The bulk of the data on sociospatial organization resulted from radio-tracking on Goudveld State Forest (1.3.3) and the capture programme (1.3.1). Supplementary information on group integrity and agonistic behaviour, as related to sociospatial organization, was derived from introduction experiments in the study enclosure (1.3.4 and 5.2).
- (c) The study of the breeding system was based on information from three sources:
- (i) From the capture and culling programmes information on group composition and stability became available (1.3.1; 1.3.2).
 - (ii) Complementary information was derived from observations in the enclosure (1.3.4) especially during the study of rearing behaviour (5.3).
 - (iii) A specific radio tracking programme was initiated to monitor early post-parturient parental movement and paternal care. For this purpose the bushpig pair CT4(M)/CT3(F) was captured on Goudveld and temporarily kept in enclosure B. On 24.10.1986 the sow CT3 was inspected for pregnancy and colostrum was found in the mammae. On the same day both CT3 and CT4 were radio-collared. After an adjustment period of 6 days they were released into their territory on 30.10.1986. Results are reported in section 4.3.3.2.
- (d) Limited information on alloparental care became available as by-products of studies on rearing behaviour in the enclosure (5.3).
- (e) Most information regarding dispersal, albeit circumstantial, became available during the capture/recapture programme on Goudveld State Forest (1.3.1). Some related information was also derived from the culling and radio tracking programmes (1.3.2 and 1.3.3), as well as from observations in the study enclosure (1.3.4).

4.3 Results

4.3.1 Sociality

4.3.1.1 Group Size

The average size of bushpig groups for all study areas was 2,45 (Table 4/3).

| TABLE 4/3: GROUP SIZE FREQUENCY DISTRIBUTION | | | | |
|--|-----------------------------|-----------------------------|----------------------------|------------------|
| GROUP SIZE | SOUTHERN CAPE (CAPTURE) (a) | SOUTHERN CAPE (CULLING) (b) | EASTERN CAPE (CULLING) (c) | POOLED (a,b & c) |
| 1 | 23 | 17 | 11 | 51 |
| 2 | 18 | 16 | 10 | 44 |
| 3 | 11 | 5 | 9 | 25 |
| 4 | 7 | 4 | 9 | 20 |
| 5 | 2 | 1 | 3 | 6 |
| 6 | | 2 | 1 | 3 |
| 7 | 1 | | 1 | 2 |
| 8 | | | | |
| 9 | | | 1 | 1 |
| 10 | 1 | | | 1 |
| \bar{X} | 2,33 | 2,16 | 2,96 | 2,45 |
| n | 63 | 45 | 45 | 153 |
| s | 1,6164 | 1,3307 | 1,7832 | |

From the culling data a significant difference in group size is evident between the Southern and Eastern Cape. Solitary individuals and pairs were comparatively more common in the Southern Cape, whereas family groups predominated in the Eastern Cape ($G = 6,766$; $df = 1$, $P < 0,01$).

4.3.1.2 Group structure

The composition of 110 social units could be determined with reasonable certainty from the capture and culling programmes in both regions (Table 4/4).

| TABLE 4/4: GROUP COMPOSITION: SOUTHERN AND EASTERN CAPE | | | | | | |
|---|-------------|---------------------------|-----|------|----------------------|------|
| SOCIAL UNIT | COMPOSITION | SOCIAL UNITS | | | INDIVIDUALS INVOLVED | |
| | | Frequency | | % | Frequency | % |
| Solitary | M | 32 | 51 | 46,4 | 51 | 21,5 |
| | F | 19 | | | | |
| Pairs | MF | 20 | 22 | 20,0 | 44 | 18,6 |
| | MM | 1 | | | | |
| | FF | 1 | | | | |
| Family Groups | MFJ | 13 | 22 | 20,0 | 101 | 42,6 |
| | MFY | 3 | | | | |
| | MFJY | 3 | | | | |
| | MMFJ | 2 | | | | |
| | MMFY | 1 | | | | |
| Single-sex Adult/non-Adult Associations | MJ | 2 | 10 | 9,1 | 29 | 12,2 |
| | MY | 3 | | | | |
| | FJ | 1 | | | | |
| | FY | 2 | | | | |
| | MMJ | 1 | | | | |
| | MJY | 1 | | | | |
| Sibling groups | MMF | 2 | 5 | 4,5 | 12 | 5,1 |
| | MM | 1 | | | | |
| | MF | 1 | | | | |
| | FF | 1 | | | | |
| | | | 110 | 100 | 237 | 100 |
| M: Male (2y+) | | J: Juvenile ($\leq 1y$) | | | | |
| F: Female (2y+) | | Y: Yearling (1-2y) | | | | |

Solitary animals constituted 46% of all observed groups, whereas heterosexual associations of mature individuals (2 years and older) comprised 38% of all groupings (sibling groups excluded). Twenty-nine percent of social units involved mature/immature associations.

The family group (two parents and offspring), comprising 42,6% of the observed individuals, was the central and characteristic social unit. Heterosexual pairs, single parent/young groups and sibling groups were related to or derived from family groups. Mature multi-female/male(s) or multifemale/offspring associations were entirely absent and only 2 groupings out of 110 involved two mature females in the same social unit. One of these was a sibling unit and the other probably mother and daughter. This suggests a high level of intolerance between mature females. The association of boars with immature animals was as prevalent as that of sows, indicating a prolonged association of the male with the mother/offspring unit during the rearing phase and beyond. A boar, most probably the father, was in attendance in all 8 groupings with pre-weaning juveniles. The prolonged association of the boar with the sow during rearing of the young and the exclusively single-female family units provided convincing evidence that monogamy was the mating system of the bushpig populations studied.

It is noteworthy that the attachment between boar and juveniles or yearlings extended beyond the loss of the mother sow (for whatever reason) from the group. Seven such cases are recorded in Table 4/4 as opposed to only 3 sow/offspring units.

In 5 of the observed social units two adult males were present. In 4 cases they were associated with immature animals and in 3 cases with adult female presence (Table 4/4). Intragroup intolerance between adult males appears to be lower than that between adult females (4.3.3.1).

4.3.1.3 Group composition dynamics

Seasonal group changes are essentially a reflection of reproductive seasonality (10.3.5). Of the 20 heterosexual pairs, 12 were recorded during the months May to August, thus coinciding with the mating season ($\chi^2 = 6,39$; $P < 0,05$). Family groups with juveniles were most commonly recorded for the six months from October.

The capture programme allowed the monitoring of some pair bond sequences.

- (a) Adult boar CC3 was monitored for a period of nearly three years during which period pair bonds with 4 mature sows were established:

CC3 (ad M) + CC2 (adF) 7.8.1981
+ CU5 (YF) 22.2.1982
+ CL2 (sadF) 8.9.1982 - 1.9.1983
+ offspring CC5 + CC6
+ CW5 (adF) 6.9.1983 - 4.9.1984
+ offspring CI2, 4, 6+8
+ CT2 (adF) 5.1984

Boar CC3 remained in the same range over the recording period until his death or emigration in mid 1984. The succession of his mates was determined by the incidence of female territorial aggression, leading to displacement or death of the resident female.

- (b) A pair bond may be maintained over successive breeding seasons if no mortalities or changes in social status occur. Adult boar CH1 maintained an association with sow CZ1 from mid 1982 to mid 1985, producing 2 litters during this period. The pair bond was terminated with the death of CH1 due to prolonged starvation.

- (c) Pair bonds are often of a transient nature only.

CE1 (sadF) + CE2 (adM) 8.5.1981
CE1 (adF) + CM1 (adM) 31.8.1982

Sow CE1 died at the age of 4,7 years. The associations were only of short duration, CE1 being solitary for the intervening periods. No offspring were produced, probably due to failure to establish a territory and poor physical condition.

Adult boar CE6 and sow CE3 (ad) moved about on their own, but met at infrequent occasions (as indicated by capture events and radio

tracking). Both were relative newcomers to the area and may have been involved in a drawn-out pair bonding process.

There is some evidence indicating an increased occurrence of group fission under conditions of food stress. During the rearing of the first litter by the CH1(M)/CZ1(F) pair, both parents maintained reasonable condition and stayed together. After weaning of the litter in the subsequent year, boar CH1 moved about on its own. Both parents then were in poor physical condition. They still occupied the same range, but the degree of contact could not be ascertained. A similar segregation was observed for the CR1(M)/CL2(F) pair after weaning of CC5/CC6. Sow CL2 was in an extremely poor condition and died as a result a few months later. The segregation of sow CW5 from her family group, which included boar CC3 and two generations of young, may similarly have been triggered by poor post-lactational condition and the avoidance of intragroup feeding competition.

Family groups were essentially closed to attachment by foreign animals. No instances of any attachment to family groups was ever recorded in spite of over 4 years of monitoring. Group composition records, in general, support this finding. Introduction experiments in the study enclosure all failed, except for a case where six week old juveniles (TD6+7) were accepted. An introduced yearling boar TC2 was chased and harassed by the sow TD3 for many weeks before he was tolerated. Group integrity appears to pivot around the spatial intolerance of the alpha female. The dominant female appears to be intolerant to individuals of both sexes, with the exception of juveniles and potential male mates, i.e. males of relatively high social status (5.2). Although it is not impossible for yearling males to gain access to family groups, the available data indicates that this access is much easier to units formed by males only, with or without immature individuals, irrespective of sex. In respect of the former situation, the yearling boar CC6 was accepted by the CC4(M)/CC9(F) pair when 14 months old. The yearling sow CU5 joined up with the CC3/CR1 boar alliance. In both cases the biological parents of the yearlings were no longer alive at the time of the attachments.

Alliances between mature males or between males and sibling groups are possible, but are often only transient. Such transient associations were recorded for example, between boars CC3 and CR1, and CU4 with CU8. On 5.11.1981 adult boar CS1 was caught together with the sibling group CD1(F)/CD3(M) and on 9.11.1981 the same boar was associated with CP2 (ad M)/CP1 (juv.F).

Group composition data from the culling and capture programmes show that parent offspring groupings generally do not last beyond the second mating season experienced by the latter, then about 14-20 months old.

4.3.2 Sociospatial organization

4.3.2.1 Chronology of spacing patterns

(a) Analysis of spatial relationships: the approach

In this section animal locations from captures or radio tracking (4.2) were analysed to demonstrate the use of space by individual bushpigs. Depending on the amount and type of positional data available, one of three methods was used to describe sociospatial behaviour; least convex polygon range delineation, harmonic mean home range approximations and spot indications of presence (Figures 4/2 - 4/9).

(I) Least polygon range delineation

This approach provided an indication of maximum revealed range (6.1). It requires a minimum number of animal locations, but independence of data points is not required. It is suited for animals for which relatively many locations were available (16 - 244), mainly through movement tracking with half-hourly fixes. It was the preferred approach in cases where the "boundary problem" associated with the harmonic mean home range estimation method (6.1) made it difficult to delimit range boundaries precisely. The method was used to delineate the ranges of ten bushpigs.

(II) Harmonic mean home range approximations

The harmonic mean home range estimation procedure (Dixon and Chapman 1980) was applied in 12 cases for each of which between 5 to 14 locations were available. Home range estimates according to this approach are less dependent on large samples of animal locations (cf Anderson 1982). The 99% contours were taken to indicate range boundaries. The contour percentage selected may have resulted in overestimates, but this is not considered a problem where the main purpose is to test for range overlap. The reverse would more likely have resulted in erroneous conclusions. Independence of successive animal locations is required for this approach (6.2.1.1). It was achieved by eliminating all locations taken at intervals shorter than 6 hours. Since capture localities were used predominantly, it was seldom necessary to eliminate data points. In cases where disjunct home range centres were produced by the harmonic mean home range computations, these were linked by tangents enclosing the area between the centres, because the inspection of movement patterns indicated frequent movement between centres. Also, the lack of capture events between centres was found to be merely the result of poor capture locality coverage. Harmonic mean range boundaries are indicated with broken lines in Figures 4/2 - 4/9, whereas those determined with the minimum convex polygon method are shown as unbroken lines.

(III) Spot indications of presence

When the number of available fixes was low, i.e. between 1 and 5 animal locations, no attempt was made to provide two-dimensional indications of presence. The actual locations are shown in the relevant figures. The presence of 22 different bushpig individuals was determined in this manner. It is believed that the low number of capture points for these animals was mostly the result of transitory presence or limited ranges. This interpretation is favoured because of the relatively high density of capture corrals (one for every accessible 25 ha, amounting to over 12 capture corrals within the average bushpig home range) and the absence of any evidence of trap shyness.





Sampling intensity of animal locations was variable over time and in order to achieve adequate sampling, all available locations had to be used for range determination of most animals. As a result ranges were often delineated without being able to indicate spatiotemporal avoidance between animals or even range shifts for nomadic individuals. Such cases are however, pointed out in the explanatory text for each figure.

(b) Dynamics in spatial relations: Goudveld 1980-1985

Figure 4/2: Spatial relations of bushpig males at end of 1981

- (I) CP2(M)/CS1(M)/CD3(M)/CN1(M): occurred in overlapping ranges and transient group associations.
- (II) East of I: social unit CR1(M) with CT1(F).
- (III) Area surrounding (b): former territory of social unit TD5(M) + TD4(F) with offspring CD1-3 and TD6/7. Were translocated to study enclosure on 1.1.1981 (except yearlings CD1-3).
- (IV) Social unit CC3(M) with CC2(F)/CC1(Y = yearling). Apparent overlap with range CU1(M) is an artefact of analysis; CC3(M) occupied the overlapping area only after the death of CU1(M).
- (V) East of IV: social unit CU1(M) with CU6(F)/CU5(Y). To the south-east: CG13(M).
- (VI) North of V: social unit CL5(M) with CL1(F)/3Y.
- (VII) Overlap between social unit CH1(M)/2Y and CE2(M) is a presentation artefact. The range boundaries of CH1(M) were determined from all positions available, but he did not actually occupy the western portion overlapping the range of CE2 until after the disappearance of the latter (after 7/1981).
- (VIII) To north of VII: social unit CG1(M) with CK2(F)/J and CII(M). Range only partially overlapping capture locality grid.



| | |
|---|------------------------------------|
|  | State land boundary indication |
|  | River gorges (see Plate 4) |
|  | Least polygon range delineations |
|  | Harmonic mean range approximations |
| a, b, c, ... | Spot indications of presence |
| 1cm : 1km | See text for further explanations |

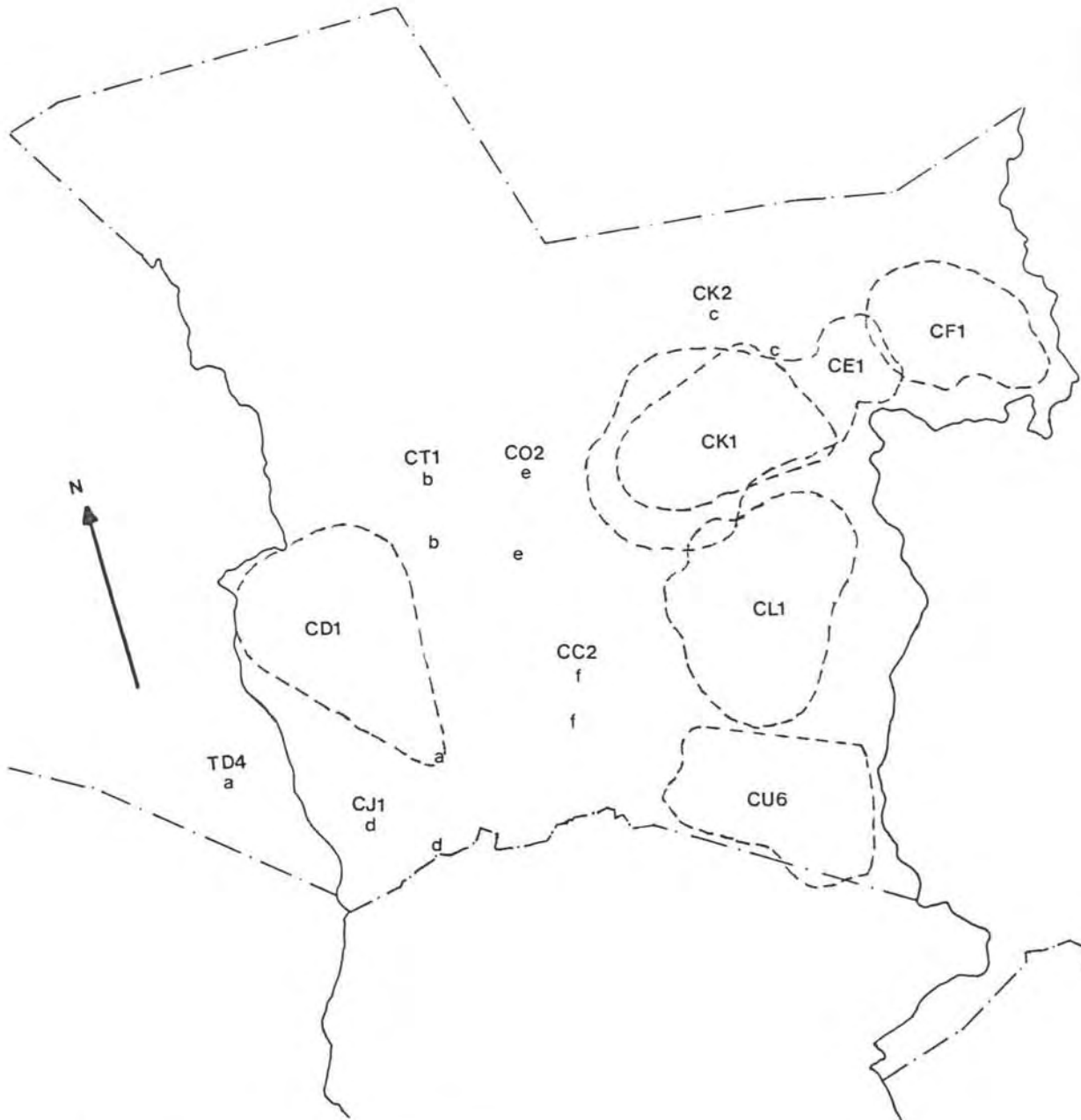
(IX) Paired males CC3, CL5 and CU1 basically without territorial overlap; in contrast with temporarily associating unpaired males CS1, CP2 and CD3.

Figure 4/3: Spatial relations of bushpig females at end of 1981

- (I) The ranges/positions of paired females are indicated as follows: TD4(a), CT1(b), CU6, CL1, CK2(c), CC2(f), with males TD5, CR1, CU1, CL5, CG1 and CC3 respectively. Subadult females: CD1, CF1; adult, unpaired females: CJ1(d), CD2(e), CK1, CE1.
- (II) Female CO2 died from interfemale fighting (locality e).
- (III) CK1(F) was not recorded after 26.7.1981 and CE1(F) was only recorded in the indicated range of CK1(F) from 23.8.1981 onwards. Female CE1 shifted westwards into vacated CK1 territory.
- (IV) No female range overlap is indicated, irrespective of social class (paired adults, unpaired adults, subadults).

Figure 4/4: Spatial relations of bushpig males at end of 1983

- (I) Social unit CP2(M) with CD1(F). Sibling brother CD3(M) of CD1(F) still in range, but CN1(M) and CS1(M) not recorded any longer. Male CY2 appeared to the north (a).
- (II) CR1(M) had left his former range (Fig. 4/2), presumably after the disappearance of his pair mate CT1(F), and associated with CC3(M). The CR1(M)/CC3(M) group was first captured on 8.3.1982. Transient association of CR1(M) with lactating CL2(F)/2J after CC3(M) had left the CL2(F)/2J unit. CC3(M) was later associated with CW5(F) and presumably left CL2(F) in favour of the former, who extended her range into that of CL2 (Fig. 4/5).
- (III) Social unit CV1(M) with CV5(F)/J. The overlap with the ranges of CR1(M) and CC3(M) is taken as an harmonic mean home range delineation artefact. Male CJ2(b) appeared to the west of the range of CC3(M).






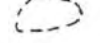
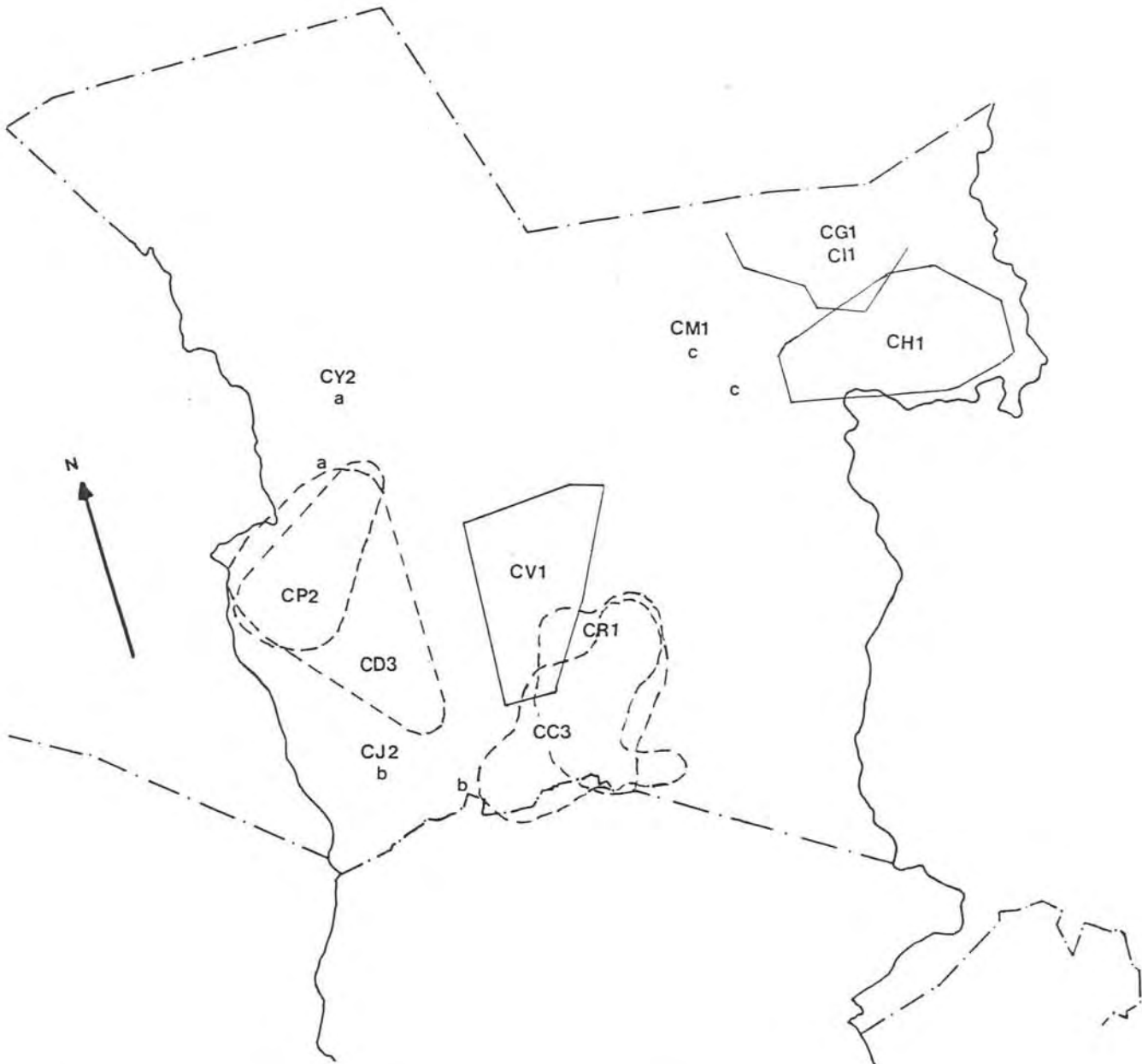
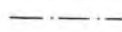



| | |
|---|------------------------------------|
|  | State land boundary indication |
|  | River gorges (see Plate 4) |
|  | Least polygon range delineations |
|  | Harmonic mean range approximations |
| a, b, c, ... | Spot indications of presence |
| 1cm : 1km | See text for further explanations |

FIG. 4/4

SPATIAL RELATIONS OF MALES AT END OF 1983



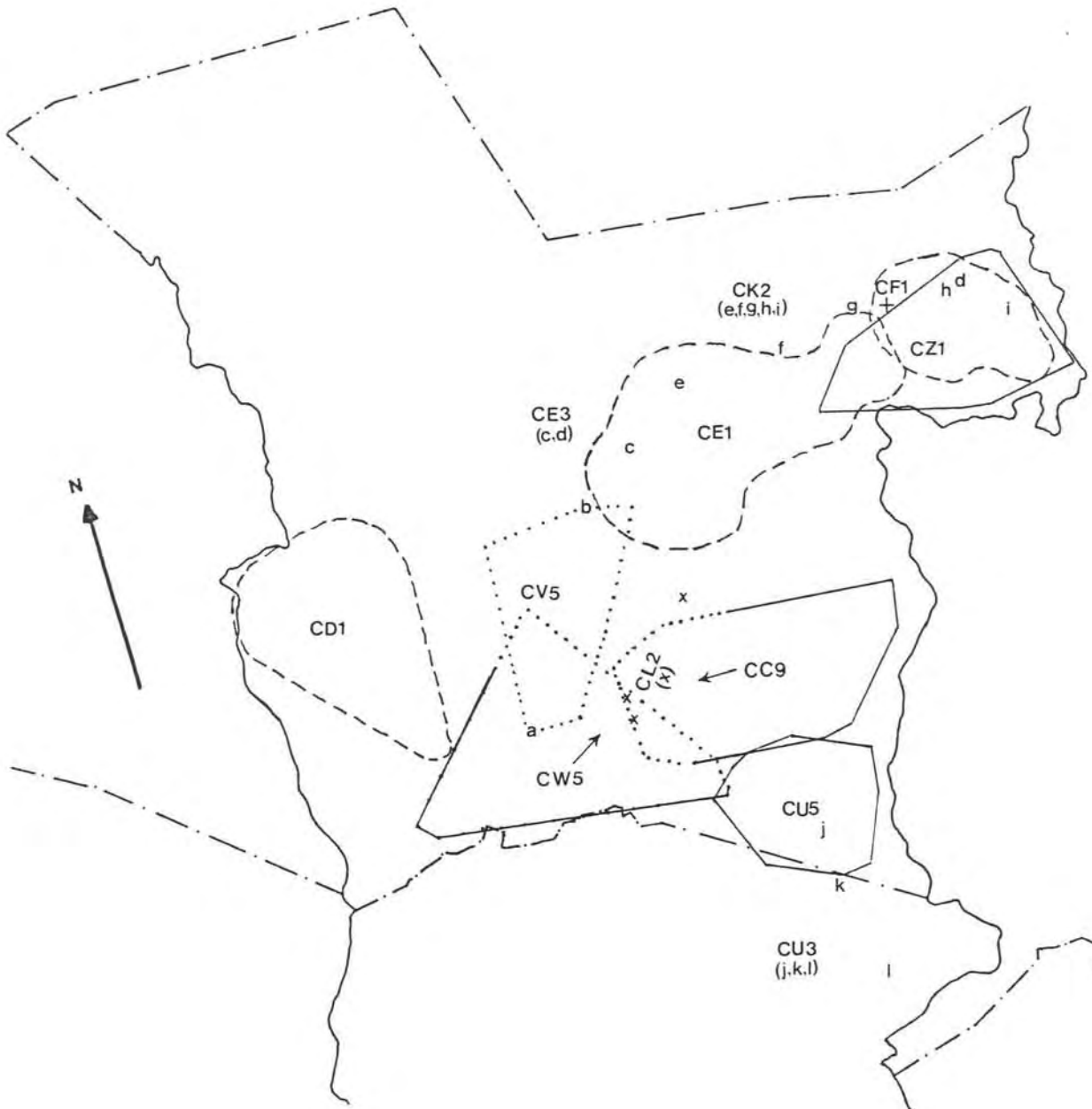
| | |
|---|------------------------------------|
|  | State land boundary indication |
|  | River gorges (see Plate 4) |
|  | Least polygon range delineations |
|  | Harmonic mean range approximations |
| a, b, c, ... | Spot indications of presence |
| 1cm : 1km | See text for further explanations |

- (IV) CH1(M), now paired up with CZ1(F), extended his range westwards into the former CE2(M) range. CE2(M) had disappeared. Range neighbourhood to males CG1/CI1 unchanged.

Figure 4/5: Spatial relations of bushpig females at end of 1983

- (I) CV5(F) was only recorded at localities a and b. A dot delineation of the range of CV1(M) with whom CV5(F) was associated serves to indicate the presumed range of the latter. Dot delineations also indicate the future ranges of CW5(F), later paired with CC3(M), and CC9(F), then paired with CC4(M). Arrows indicate ongoing range expansions of CW5(F) from the southwest and CC9(F) from the east, respectively.
- (II) CL2(F) was presumably displaced from her natal range, that of CL1(F)/CL5(M), by the westward extension of the older CC9(F) into the range of male CC3. Breeding with CC3 resulted in the birth of 2 juveniles during November 1982. CL2(F) was then only 2,1 years old. Boar CC3 left CL2(F)/2J during January 1983, presumably in favour of CW5(F) who was encroaching on the range of CL2(F). A transient association with CR1(M), a former associate of CC3(M), was recorded during February/March 1983. CL2(F) was seemingly restricted in her movements, being squeezed in between the ranges of females CV5, CW5 and CC9. She was in a very poor physical condition and died of exposure on 24.9.1983.
- (III) Towards the end of 1983, five unpaired, non-breeding females were recorded in the study area: CD1, CU5, CE1, CE3 and CF1. CE1(F) and CE3(F) exhibited "nomad" characteristics: far-ranging, but settling nowhere for any length of time (nomad CE3 captured at c and d only). CE1(F) shifted residence within the indicated range, but excluding the "overlap" zone with CZ1(F). During an extended period corresponding with the time when CE3(F) was captured at locality d, CZ1(F) did not occupy the northern portion of her indicated range.
- (IV) CK2(F) with CG1(M)/CI1(M) ranged north/northwest of CZ1(F), as during previous periods (Fig. 4/3). CZ1(F) only occupied the north-eastern portion of her indicated range during 1985.

FIG.4/5 SPATIAL RELATIONS OF FEMALES AT END OF 1983



| | |
|--|--|
| State land boundary indication River gorges (see Plate 4) | |
| | Least polygon range delineations Harmonic mean range approximations |
| a, b, c, ... | Spot indications of presence |
| 1cm : 1km | See text for further explanations |

(V) CF1(F) was a daughter of CH1(M) with which the territory holding CZ1(F) was paired. A seemingly substantial range overlap between CZ1(F) and CF1(F) is indicated. However, the ranges indicated for both animals span all available localities and thus mask any spatiotemporal avoidance between the two females. During 1983 CF1(F) frequented the northern portion of her range, when CZ1(F) was not recorded there during that time.

Nevertheless, the presumed spatial tension was resolved on 18.10.1983 through the death of CF1(F), due to interfemale fighting. CF1(F) was then 3,8 years old. Death resulted from sepsis of wounds presumably sustained when fighting either CZ1(F) or CK2(F).

(VI) After the death of its parents, CU1(M) and CU6(F), yearling CU5(F) was temporally associated with boars CC3 and CR1 to the north-west of the indicated range (1982). During 1983 CW5(F) and CC9(F) established their territories as indicated by dot delineation, whereupon CU5(F) became established in its indicated range.

(VII) CU3(F) in group association with CU8(M)/CU2(Y), had her range south of Goudveld as derived from a single radio tracking position (b) and the range of her paired boar CU8 (Fig. 4/5). The capture locality grid only covered the area north of her actual range, leading to an "excursion" capture at locality 1. Female CU3 died from capture myopathy in an attempt to translocate her to study enclosure B (13.2.1984).

CU3(F) was only captured inside the range of CU5(F) on two occasions, suggesting that these intruding visits were infrequent (capture at locality 1 on 28.5.1983 and 15.1.1984). During periods corresponding with these dates, CU5(F) resided in the northern portions of her range.

Figure 4/6: Spatial relations of bushpig females during February 1984

(I) Sow CV5 had disappeared and CL2(F) had died of starvation (refer to preceding Fig. 4/5). The ranges of CC9(F) and CW5(F) stabilized in their final form.

(II) CW5(F) and CC9(F) were paired with CC3(M) and CC4(M) respectively. CU5(F) was single. Range overlap among the 3 bushpig females is evidently minimal as is shown even more clearly by the distribution of the animal locations than the straight line least convex polygon range boundaries.

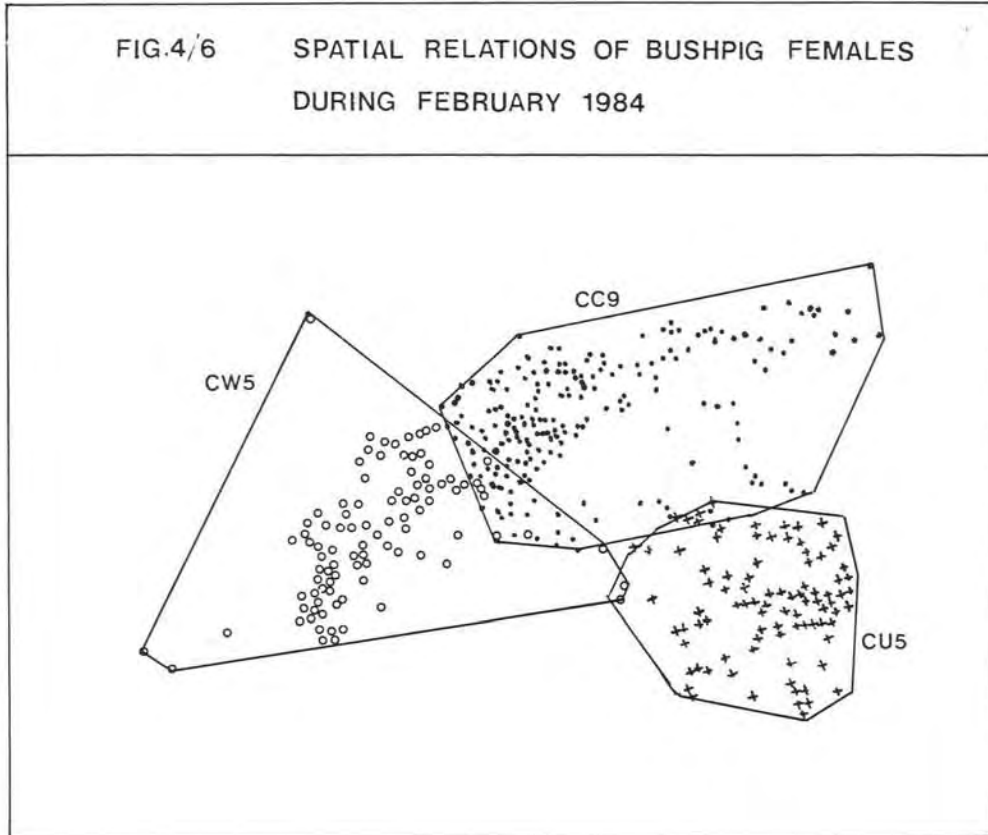
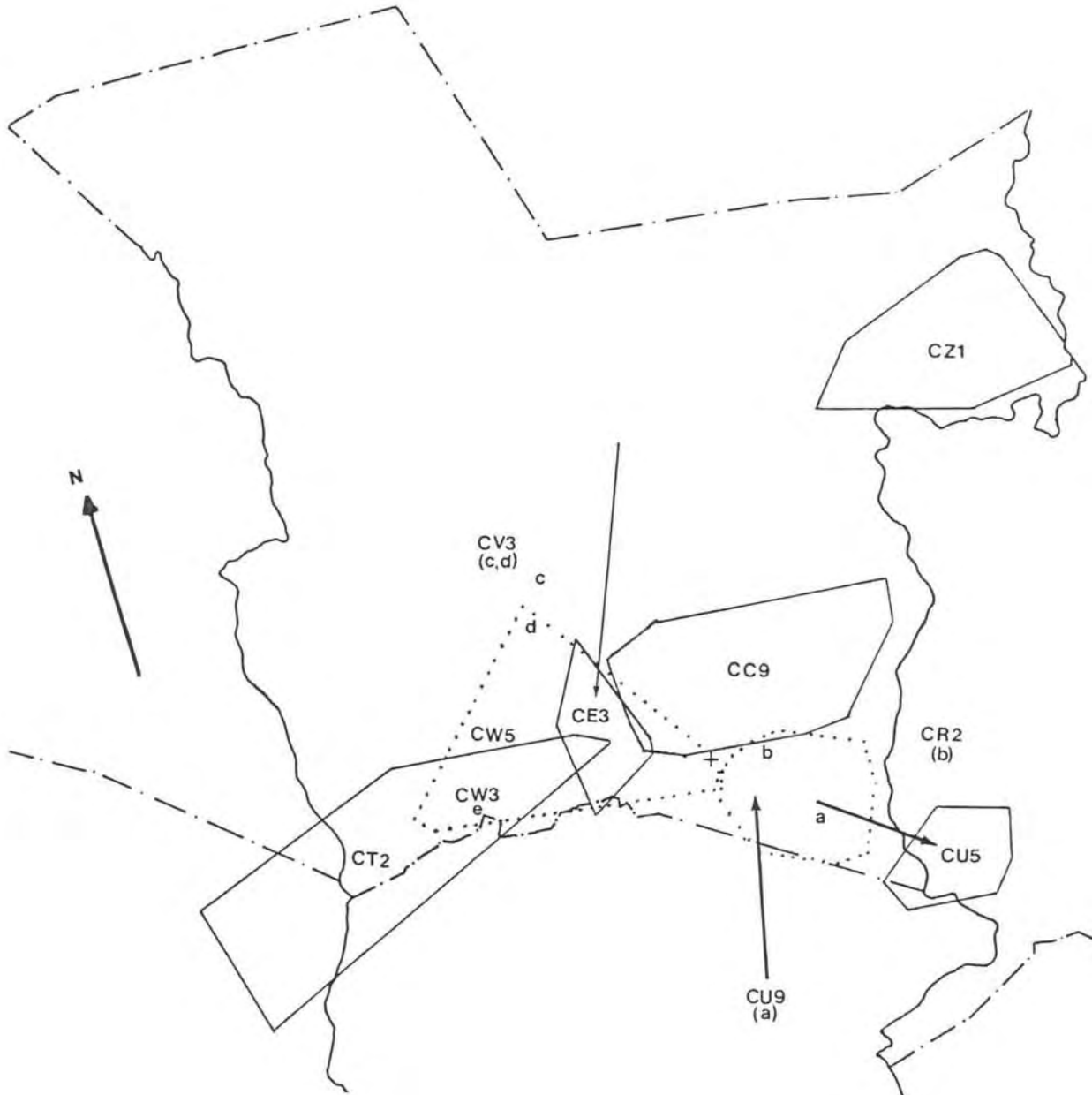






Figure 4/7: Spatial relations of bushpig females at end of 1984

(I) CW5(F) succumbed to fighting wound sepsis around 20.5.1984 (death locality marked +). At the same time CU5(F) was apparently evicted from her home range towards the south-west, across the Knysna river to Gouna. Tracking revealed that CU5(F) maintained the limited range, surrounded by other bushpigs. Tracking furthermore revealed that, although temporally associating with CU8(M), female CU5 remained within her new range and did not follow CU8(M) when the latter moved beyond her range boundaries.

FIG.4/7

SPATIAL RELATIONS OF FEMALES AT END OF 1984



| | |
|---|------------------------------------|
|  | State land boundary indication |
|  | River gorges (see Plate 4) |
|  | Least polygon range delineations |
|  | Harmonic mean range approximations |
| a, b, c, ... | Spot indications of presence |
| 1cm : 1 km | See text for further explanations |

A foreign female (designated "CU9") with a yearling was captured at locality "a" during May 1984, but escaped. The succession of events now could have been as follows: Removal of CU3(F) led to a range expansion of CU9(F) into the former territory of CU3(F) and intrusions beyond (see arrow). This led to clashes with CW5(F) and CU5(F). The unpaired, relatively young CU5(3,5 years) was permanently displaced and escalated fighting ensued with the paired CW5(F), subsequently leading to the latter's death.

- (II) The transient presence of female CR2 (2,3 years) south of the range of CC9(F), was recorded on 28.3.1984(b).
- (III) Nomadic CE3(F) moved southwards into the area formerly occupied by CW5(F). The first record of CE3(F) in her new range was on 25.7.1984.
- (IV) The range of CT2(F), established from all available locations, seemingly overlapped with the ranges of CE3(F) and CW3(F). However, a chronological analysis clarifies the situation.

CT2(F) was recorded within the indicated range of CE3(F) on 10.5. and 28.5.1984, but was never thereafter caught as far east when CE3(F) had established herself (7/1984).

CW3(F), who ranged in the southern parts of her mother's (CW5) former range, was pushed westwards by CE3(F) during the establishment of the latter's indicated range. Thus, during the period 7/1984 to 12/1984 CW3, paired up with an unknown male, presumably ranged west of the range of CE3(F) up to about the indicated capture locality "e". During this period, which was ended when CW3(F) died (immobilization casualty), CT2(F) was not caught at locality "e", presumably having retreated westward. CT2(F), now paired up with CT8(M), reappeared in the parts surrounding locality "e" from 1/1985 onwards, but mainly occupying the area to the west thereof, as determined from radio tracking locations. She was caught and shot on private land on 23.7.1985.

- (V) At this stage capture activities were only carried out on a limited scale. Due to easy logistics a capture corral was in continuous operation at locality "e" after the actual capture

programme had been terminated. On 2.8.1985, CI2(F) was caught at locality "e". She was a daughter of CW5(F) and reaching sexual maturity (1,8 years).

On 24.9.1985 CT3(F), paired up with CT4(M), while in the progress of expanding into the vacated CT2(F) territory, clashed with CI2(F). The latter sustained severe wounds from which she presumably died.

Figure 4/8: Spatial relations of bushpig males in the southern boundary zone at the end of 1984

- (I) Sibling brothers CW1(M) and CW2(M) had segregated, but still mainly frequented the former parental range. No overlap with the range of CU8(M).
- (II) At point "a" CU8(M) was caught with a foreign male CU4, which was interpreted as a transient consortship. This CU8(M)/CU4(M) grouping was only caught once on 2.3.1984.
- (III) CU8(M) associated with CU5(F) when in her range (around "b": Fig. 4/8).

Figure 4/9: Spatial relations of bushpig males in the southern boundary zone at the end of 1985

- (I) CW1(M) and CW2(M) were not in the southern boundary zone any more. Three immigrants were recorded in the area: CT4(M), CE6(M) and CT7(M).
- (II) In the western portion some range overlap of CE6(M) and CT4(M), as with CI4, was indicated. Some range overlap was also evident between CE6(M) and CC6(M) and with CT7(M) in the eastern portion of the range of CE6(M).
- (III) CE6(M) periodically associated with CE3(F) while in the latter's range (indicated with dotted line). In that portion no overlap with other males was recorded.

FIG.4/8

SPATIAL RELATIONS OF MALES
 IN SOUTHERN BOUNDARY ZONE OF GOUDVELD
 AT THE END OF 1984







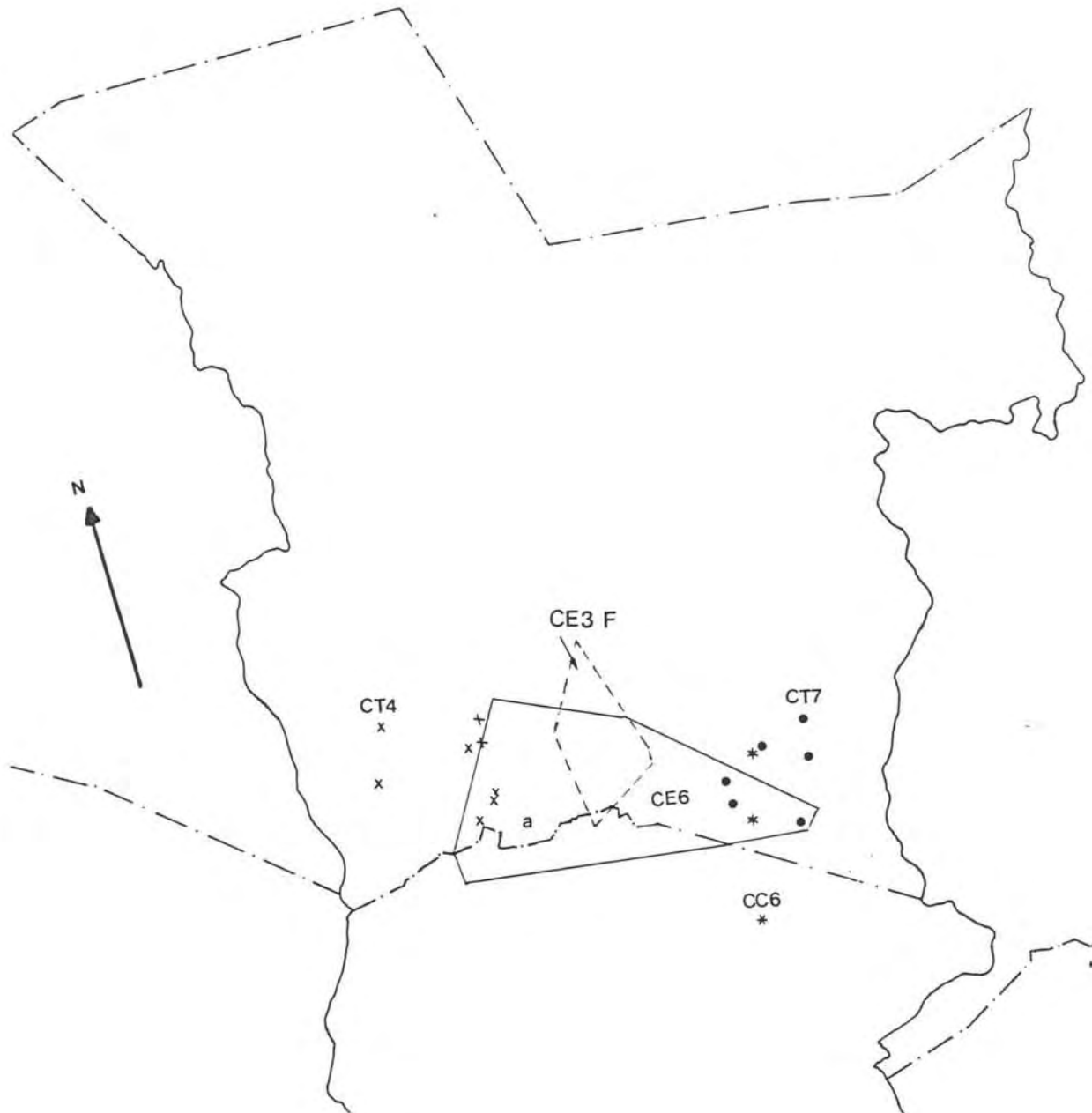




| | |
|--|------------------------------------|
|  State land boundary indication | |
|  River gorges (see Plate 4) | |
|  | Least polygon range delineations |
|  | Harmonic mean range approximations |
| a, b, c, ... | Spot indications of presence |
| 1cm : 1km | See text for further explanations |

FIG.4/9 SPATIAL RELATIONS OF MALES
 IN SOUTHERN BOUNDARY ZONE OF GOUDVELD
 AT THE END OF 1985



| | |
|---|------------------------------------|
|  | State land boundary indication |
|  | River gorges (see Plate 4) |
|  | Least polygon range delineations |
|  | Harmonic mean range approximations |
| a, b, c, ... | Spot indications of presence |
| 1cm : 1 km | See text for further explanations |

(c) Characterization of spatial patterns

In summarizing the spatial patterns presented in the previous subsection, a number of characteristic features emerge:

- (I) There is no overlap between the ranges of subadult or adult female bushpigs, paired or unpaired. Spatiotemporal avoidance is evident between residents and nomadic females. The latter tend to concentrate in range interstices and their presence in occupied ranges is exceptional and of short duration.
- (II) There is no significant range overlap between paired bushpig females and foreign subadult or even adult males. Subadult offspring are sometimes partially tolerated on the parental range.
- (III) No range overlap was recorded between continuously paired bushpig males and other foreign adult males. In cases where the male/female association was only intermittent, either because animals were in the initial stages of pair formation or due to small female ranges, male ranges may overlap those of other adult males when outside of the relevant female's range.
- (IV) Unpaired transiently associating males occur in mutually overlapping ranges.

4.3.2.2 Evidence for territoriality

(a) Spatial exclusivity

In the previous section it was demonstrated that spatial exclusivity is a prominent feature of the ranging relations between bushpig individuals. Furthermore it is evident that the female plays a central role in maintaining spatial exclusivity, while the role of the male is less clear. The territorial female appears to be intolerant not only towards other adult females, but also towards foreign subadult and subdominant males. From this and the year-round maintenance of spatial exclusivity, it is concluded that resource-based territoriality is involved, as opposed to the typical bovid male mating territoriality.

(b) Sociospatial classes

In terms of sociospatial relations bushpig societies are characterized by four classes (as derived from 4.3.2.1):

- (I) mated, territorial pairs; with or without associated progeny;
- (II) solitary individuals, usually adults, occupying home ranges which are non-exclusive in the case of males
- (III) dispersing individuals of either sex, sometimes still in sibling groups;
- (IV) nomadic adults, notably females, which may be viewed as being involved in extended dispersal.

Thus, some solitary bushpig show home range behaviour (females CK1 and CU5), while others are nomadic after dispersal (females CE1 and CE3). Nomadic individuals frequently change their living area and may cover large distances in relatively short periods. This behaviour may be viewed as either the consequence of continual aggression from territorial animals or the monitoring of new areas in search of vacant territories, or both.

It appears that offspring, even without noticeable family bonds, may preferentially use their parents' territory for an extended period (4.3.5). This is presumably only possible as long as parents can differentiate their offspring from intruders and tolerate them.

(c) Territorial maintenance

The comparatively large territories of bushpigs can presumably only be maintained through a combination of severe aggression towards intruders, regular presence in less intensely used portions of the territory (patrolling) and indications of occupation in the owner's absence (marking).

Fatal aggressive encounters among females in the field were documented in the previous section, relating to females C02, CF1, CW5 and CI2 (recorded over a period of six years, involving a population of 25 adult

females). Corresponding patterns of aggression of the dominant female towards introduced females were observed in the study enclosure. Female aggression was also directed towards foreign subadult and subdominant males (5.2.2.3). Bushpig marking behaviour is fully dealt with in section 5.1.2.1.

The usual pattern is for a bushpig to move about its territory in an irregular way, traversing most of it within a relatively short period, in a matter of a week (6.3). Regular presence is thereby maintained in most parts. Whenever territory owners do concentrate in particular portions of their territories for lengthy periods, territory-spanning patrolling bouts became discernable.

From July to December 1984 the territorial female CC9 predominantly occupied the western portion of her territory (Fig. 4/6 and 4/7). During 24-hour movement tracking CC9(F) would suddenly take off and visit the eastern boundary portions of her territory. Four such patrolling bouts were monitored. Back and forth movement lasted on average 9 hours at an average rate of movement of 470 m/h. These patrolling bouts were furthermore characterized by being routed along slippaths for long stretches, with regular ground scratch marking on the slippaths. From these features it is concluded that these movements bouts were unlikely to be associated predominantly with foraging. It is suggested that their function is primarily related to territorial patrolling.

The position of CC9(F) was monitored on altogether 28 days, during which four visits occurred to the eastern territorial outliers. If representative, this suggests a patrolling bout per week, on average. These findings link up with the data presented in section 4.3.5, which suggest that extended absence from any particular portion of the territory may lead to rapid encroachment, depending on the circumstances of neighbours and intrusion pressure.

4.3.3 Breeding systems

The breeding system is here considered to consist of two interdependent subsystems: the mating sub-system (4.3.3.1) and the rearing sub-system (4.3.3.2).

4.3.3.1 The mating subsystem

Monogamy is, *inter alia*, recognized in the field by one or more of the following features (cf Kleiman 1977):

- Close continual proximity of the members of an adult heterosexual pair, both during and outside periods of reproduction.
- An absence of adult, unrelated conspecifics from the pair's territory.
- Breeding by only one adult pair in a family group.

Data in respect of these sociological features, as presented below, strongly indicate monogamy to be the mating system in the bushpig populations studied.

- (I) Heterosexual associations of mature individuals with or without offspring, form the dominant group types (Table 4/4). Extended male presence (bonds) with females or female/offspring units follows from this data. Of the 15 social units with juveniles, 8 were with suckling juveniles. Males were present in all of them. Of the 32 adult/offspring associations (juveniles or yearlings or both), males were present in 29 (Table 4/4).
- (II) During the entire study only a single case of a group containing more than one adult female (3 years or older) was recorded. This interfemale intolerance is furthermore reflected in the high incidence of escalating fights between females, leading to severe wounding and often death (5.2.2.3). High intensity fighting between female bushpigs is also informally reported by naturalists (numerous personal communications). Similar interactions are not reported for females of other suid species.

(III) Spatial intolerance and exclusivity, particularly relating to females, is fully documented in section 4.3.2.

(IV) In no case was more than one breeding female encountered in a social unit (4.3.1.2). Also, the deferment of breeding by subdominant (daughter) sows was established (4.3.4, 10.3.1.2). This means that as long as daughter sows are still members of the parental group, they do not breed. However, as a rule they leave the group on reaching sexual maturity as yearlings.

In addition to the evidence presented here, monogamy is generally associated with male parental care. Evidence for substantial paternal rearing investment is documented in the section below.

4.3.3.2 The rearing subsystem

Rearing subsystems are characterized by the durations of the male/female and female/young bonds (Crook, Ellis and Goss-Custard 1976). For the bushpig rearing strategy "f" applies (Table 4/1): the male assists in the rearing and the young often remain with the pair-bonded parents long past weaning, dependence usually decreasing slowly with age until after birth of subsequent offspring (4.3.5.).

The close proximity to and concern for the young by the boar became evident from a) group structure patterns, b) behavioural observations in the enclosure and c) field observations aided by radio tracking.

(a) Group structure

In the preceding section it was indicated that all recorded maternal/young units were accompanied by a boar during the suckling phase (4.3.3.1). Thereafter the male/offspring associations predominate (Table 4/4), probably due to female segregation in certain cases and closer male/offspring bonding. Sow CW5 segregated from the male CC3/offspring association after weaning. After the death of sow CL1, the yearling offspring remained attached to the boar (CL5). The general pattern emerging is that bonds between boar and offspring after weaning

are more stable than those with the sow. Such bonds normally last through the yearling phase.

(b) Behavioural observations in the enclosure

- (I) Numerous observations in the study enclosure involved the juveniles staying with the boar while the sow was feeding, patrolling the enclosure fence or, on two occasions, building nests for protection against inclement weather.
- (II) Whenever the neonates or juveniles showed discomfort or discontent vocally, it was the boar who showed signs of concern by immediately joining up with the young or emitting warning grunts. Similar reactions were provoked from the boar by juvenile distress squeal playbacks, while the sow showed no response.
- (III) During sessions of observation on maternal behaviour (5.3.2.3), the boar frequently circled the sow and juveniles while they were bedded down. The same was observed in the field during the night of 10.11.1986 for the boar CT4 associated with sow CT3 and 3 neonates (see c below).
- (IV) With repeated routine capturing of the bushpigs in the capture corral within the enclosure, they showed less and less signs of distress or aggression on approach. However, whenever alpha boars were captured together with juveniles, they showed greatly increased aggression (threat charges and explosive growl-grunts).

On two occasions, when juveniles were handled and squealing inside the capture corral with the rest of the group outside, the whole group repeatedly approached the corral, milled around it and emitted alarm grunts. On both occasions the current alpha boars (TD5 and TD1) actually charged towards the enclosure while threatening with aggressive growl-grunting.

(c) Field observations aided by radio tracking

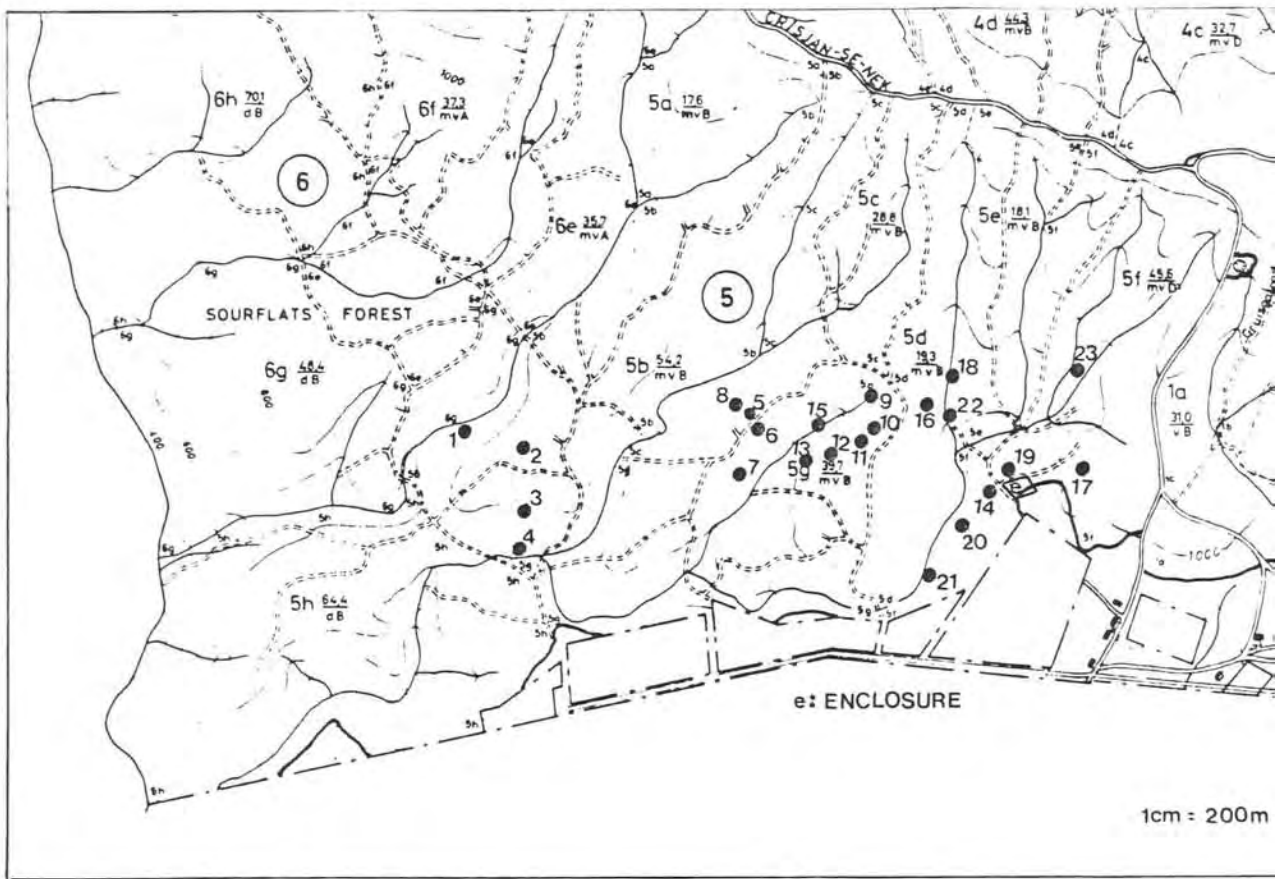
Boar CT4 with sow CT3, both fitted with radio-collars, were released into their territory on 30.10.1986 (4.2). The transmitter of the boar failed soon after and was also thrown off. A signal from the sow was last received on 3.12.1986. She was probably shot and the transmitter destroyed. During the period of about one month while the transmitter was operative, positions were determined as shown in Figure 4/10.

The sow CT3 gave birth to 3 young on 4.11.1986. During the succeeding month parental ranging was clearly restricted by limited juvenile mobility. The mean daily positional shift determined from position fixes on succeeding days during this period was 186 m ($n = 13$). The equivalent distance obtained for 6 non-lactating sows was 867 m, nearly 5 times as far ($n = 44$; $P < 0,001$).

Three phases of ranging behaviour could be distinguished:

- (I) The sow remained at the locality of birth for the first 3 days.
- (II) Some movement of the family, i.e. including the juveniles, over a few hundred meters, leading to daily shifts of the order of magnitude indicated above, took place during the first three weeks. Activities involving the juveniles took place mainly during day time (e.g. no movement from 18h00-01h00 on 10/11.1986). In addition, the sow undertook feeding excursions on her own while the boar remained with the young. During such excursions she visited the enclosure every evening on her own from 13.11.1986 onwards.
- (III) In order to facilitate observations a feeding spot was established at the enclosure on 16.11.1986. Only from the 22.11.1986 onwards did the boar and juveniles accompany the sow on her visits to the feeding spot. However the boar and the juveniles did not come up to the feeding spot until darkness. They remained in the vicinity while the sow was already feeding.

FIG.4/10 MOVEMENT PATTERN OF LACTATING SOW CT3



| DATE | POSITION | TIME | REMARKS |
|----------|----------|---|--|
| 30.10.86 | e | 10.00 ⁰⁰ | Released from enclosure (CT3+4) |
| 1.11.86 | 1 | 10.00 ⁰⁰ | |
| 2.11.86 | 2 | 15.00 ⁰⁰ | |
| 3.11.86 | 3 | 11.00 ⁰⁰ | |
| 4.11.86 | 4 | 15.00 ⁰⁰ | Birth locality |
| 5.11.86 | 4 | 15.00 ⁰⁰ | |
| 6.11.86 | 4 | 16.00 ⁰⁰ | |
| 10.11.86 | 5 | 15.00 ⁰⁰ | |
| 10.11.86 | 6 | 18.00 ⁰⁰ to 01.00 ⁰⁰ | Resting |
| 11.11.86 | 7 | 14.00 ⁰⁰ | |
| 12.11.86 | 8 | 18.30 ⁰⁰ | |
| 13.11.86 | 9 | 8.00 ⁰⁰ | |
| 13.11.86 | 10 | 18.00 ⁰⁰ | |
| 14.11.86 | 11 | 18.00 ⁰⁰ | |
| 14.11.86 | 19 | 19.00 ⁰⁰ | CT3(F) alone at enclosure |
| 15.11.86 | 12 | 9.00 ⁰⁰ | |
| 15.11.86 | 13 | 17.00 ⁰⁰ | |
| 16.11.86 | 14 | 9.00 ⁰⁰ | Captured previous night, CT3(F) alone, released 9.00 ⁰⁰ |
| 16.11.86 | 15 | 17.00 ⁰⁰ | |
| 19.11.86 | 14 | 19.00 ⁰⁰ | CT3(F) alone at enclosure |
| 20.11.86 | 16 | 17.00 ⁰⁰ | |
| 21.11.86 | 17 | 18.00 ⁰⁰ | |
| 22.11.86 | 18 | 10.00 ⁰⁰ | Visual contact |
| 22.11.86 | 19 | 18.00 ⁰⁰ | CT3(F) at feeding spot next to enclosure; CT4(M)/3J nearby |
| 23.11.86 | 19 | 17.00 ⁰⁰ | CT3(F) alone at feeding spot |
| 24.11.86 | 20 | 11.00 ⁰⁰ | |
| 24.11.86 | 19 | 17.00 ⁰⁰ | CT3(F) alone at feeding spot |
| 25.11.86 | 21 | 11.00 ⁰⁰ | |
| 25.11.86 | 19 | 17.00 ⁰⁰ | CT3(F) alone at feeding spot |
| 26.11.86 | 19 | 17.00 ⁰⁰ | CT3(F) at feeding spot, CT4(M)+3J in vicinity |
| 27.11.86 | 19 | 18.00 ⁰⁰ | As on 26.11.86 |
| 28.11.86 | 22 | 10.00 ⁰⁰ | |
| 29.11.86 | 21 | 16.00 ⁰⁰ | |
| 30.11.86 | 19 | 18.00 ⁰⁰ | CT3(F) at feeding spot, CT4(M)+3J in vicinity |
| 1.12.86 | 19 | 18.00 ⁰⁰ | As on 30.11.86 |
| 3.12.86 | 23 | 10.00 ⁰⁰ | |

In conclusion it is here suggested from the available evidence that the boar/juvenile association functions to enhance offspring survivorship and in sharing the energetic burden of rearing with the female. The breeding system of the bushpig is thus characterized by exclusive breeding of the alpha pair and substantial involvement in male parental care.

4.3.4 Alloparental care

Some evidence concerning the phenomenon of alloparental care by yearling daughter sows became available from maternal behaviour studies in the enclosure (5.3.2.3). Two opportunities for studying this phenomenon arose:

- (I) During December 1981/January 1982, when the maternal behaviour of sow TD3 with neonates TD8 and TD9 was monitored. TD2 was the associated yearling daughter sow (20 months) and
- (II) during October 1985, when the maternal behaviour of sow TD2 with neonates TD16 and TD17 was observed. TD12 was the associated yearling sow (22 months).

Alloparental care behaviour was observed in case I, but not case II.

(a) Alloparental care encountered (Case I)

Daughter sow TD2 showed definite alloparental care behaviour as manifested by tending of neonates, general close association and protective concern. Tending consisted of a type of grooming involving nosing or licking of or nibbling at the neonates while they were suckling from TD3, as well as on other occasions. This grooming is particularly noteworthy since it was otherwise hardly ever observed among bushpigs. The association with the TD3/neonate unit was pronounced, unlike her brother TD1. Protective behaviour was shown by consistently placing herself between the TD3/neonate unit and any approaching human observer. The protective behaviour exceeded that of the mother sow herself by far. On one occasion TD2 even staged a mock charge when an observer approached the young too closely.

(b) Alloparental care absent (Case II)

No alloparental care was observed in the case of the daughter sow TD12 during the rearing of TD16 and TD17 by sow TD2. Daughter sow TD12 broke out of the enclosure, presumably under agonistic pressure from TD2 on 26.11.1985.

The results are suggestive of a behavioural dichotomy for yearling daughter sows: staying with the maternal group in a non-reproductive state and providing alloparental care or dispersal in an attempt to become reproductive. The underlying hormone profiles of the daughter sows under the alternate options are of interest (Table 4/5).

| | DATE | AGE (month) | PROGESTERONE nMOL/l | ESTRADIOL (E ₂) pMOL/l |
|---------|------------|----------------|------------------------|---------------------------------------|
| a) TD2 | 24.09.1981 | 17 | <1 | n.a. |
| | 19.04.1982 | 23½ | <1 | n.a. |
| b) TD12 | 18.07.1985 | 19½ | 1,6 | 267 |
| | 6.10.1985 | 22 | 47,8 | 105 |
| | 19.11.1985 | 23 | <1 | <100 |
| | 28.11.1985 | 24 | 6,7 | <100 |

The hormone levels for TD12 indicate ovulation, unlike those for TD2.

4.3.5 Dispersal

Dispersal was not studied specifically, but some information became available and is presented in this section.

4.3.5.1 Dynamics of family group break-up

As revealed by group structure data, disassociation of offspring from the parental group usually takes place at the age of between 1,5 and 2,0 years. It is normally associated with the second mating season

experienced by the offspring. Animals below the age of 1,5 years without the company of at least one adult are very unusual and presumably the result of adult mortality or disruption of territorial tenancy. Orphaned yearlings apparently have a strong tendency to attach themselves to foreign adults (4.3.1.3). In the intensive study area, boar/yearling groups were a definite feature (4.3.1.2) resulting either from adult female mortality or segregation (see "c" below: sow CW5 segregated from boar CC3 with juvenile and yearling offspring). Parent/young or sibling group associations extending beyond 2,5 years were exceptional. Sibling groups were of a transient nature only.

From the few better documented recapture chronologies, four cases are reconstructed below. Sex, male (M) or female (F) and age, in years, are indicated in parenthesis.

(a) CF1(F)

- 11.7.1981 CF1(F1,5) with CH1(ad M) and sibling CF2(M)
- 1.82-6.82 CZ1(adF) established territory with CH1(adM); CF1(F) presumably nomadic.
- 28.9.1983 CF1(F3,7): in poor condition and with recent fighting scars.
- 28.10.1983 CF1(F3,8): mortally wounded through interfemale fighting in border zone area of the adjoining territories of adult females CZ1 and CK2.

(b) Siblings CD1(F); CD2(M) and CD3(M)

- CD2(M): died at age \pm 1 year
- 16.7.1982 CD1(F2,6) with CD3(M2,6): oldest captured sibling association.
- 26.5.1983 CD3(M3,5): solitary.
- 15.6.1983 CD1(F3,6) + CP2 (adM).

(c) Siblings CW1(M); CW2(M); CW3(F) and CW4(F)

- 8.1.1984 CW1-4(1,4) caught with parents CC3(adM) and CW5(adF) and juveniles CI2, 4, 6, 8 (CW4: immobilization casualty).
- 8.2.1984 CW1-3(1,5) + CC3(adM) + juveniles. CW5(adF) had segregated from the boar/offspring unit, as shown by tracking of the former and recaptures of the latter.
- 10.5.1984* CW1(M1,7): solitary.
- 20.5.1984 CW5(adF): death through interfemale fighting.
- 6.1984 CC3(adM): disappeared; probably shot.
- 13.7.1984* CW2(M1,9): solitary.
- 24.10.1984* CW3(F2,2): with unidentified adult male; gestating soon after.

(d) Sibling CI2(F); CI4(M); CI6(?) and CI8(F)

- CI6(?) disappeared at age 4-5 months.
- 10.4.1985 CI2(F) + CI4(M) + CI8(F): sibling group still intact; age 1,5 years.
- 4-9.1985 CI2(F) split from siblings.
- 24.9.1985 CI2(F2,0): mortally wounded by female CT3.
- 2.10.1985 CI4(M2,0) + CI8(F2,0).

These examples show that the young may remain with the parental group up to the onset of the third mating season, at an age of approximately 2,5 years. This is probably only possible because of deferred reproduction and as a result of helping. Usually groups break up earlier and the young of both sexes then disperse, spending varying periods in "floating".

* All three siblings were caught in different parts of the former parental territory.

4.3.5.2 Turnover in spatial occupancy

Changes in territorial ownership are indicated at 4 different localities (a-d: Fig. 4/11) where there was sufficient recapture data to make reliable reconstructions possible (refer also to 4.3.2.1 for territory delineations). Reconstructions of ownership are centred around the territorial females:

- (a) CZ1(F) + CH1(M) + various offspring: 12.10.1982 - 30.7.1985.
- (b) CC9(F) + CC4(M) + offspring: 6.1.1984-10.12.1985.
- (c) CB2(F) + CA1(M) + CB1(M) + 2 yearlings: 30.5.1980 - 9.7.1980.
CC2(F) + CC3(M) + yearling: 10.3.1981 - 10.8.1981.
CL2(F) + CC3(M) + 2 juveniles: 6.1982 - 24.9.1983.
CW5(F) + CC3(M) + offspring: 2.2.1984 - 20.5.1984.
CE3(F) + CE6(M): 25.7.1984 - 21.10.1985.
- (d) CW5(F) + CC3(M) + offspring: 2.2.1984 - 20.5.1984.
CW3(F) + unidentified M: 24.10.1984 - 7.12.1984.
CT2(F) + CT8(M): 17.1.1985 - 23.7.1985.
CI2(F): 28.3.1985 - 24.9.1985.*
CT3(F) + CT4(M) + 3 juveniles: 24.9.1985 - 3.12.1986.

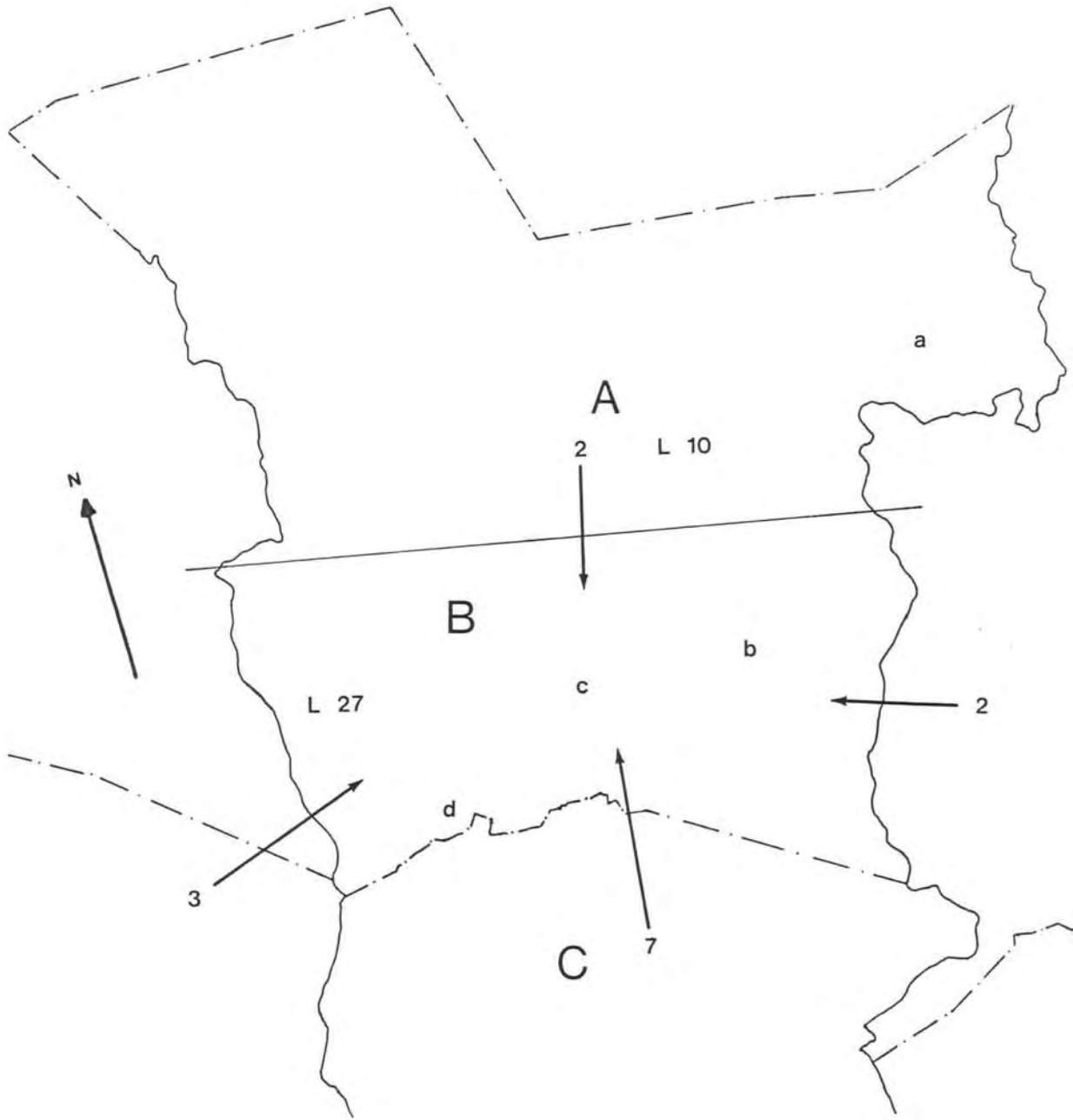
Territorial occupancy varied between relatively stable situations (a, b) and those with frequent succession of owners (c,d). The average time spans of territorial occupation per sow were 34, 24, 13 and 7 months for locations a to d respectively (territorial occupancy continued beyond the date of last capture indicated). The rate of turnover in territorial occupancy was directly related to the incidence of mortality in territorial sows. At locality c one sow died of starvation, one as a result of interfemale fighting and three were presumably shot while transgressing onto private land. For locality d two sows died from interfemale fighting, one due to immobilization effects and two were shot by adjacent private land owners.

Recapture data from the intensive study area (Goudveld) was analyzed in order to determine directional patterns in dispersal. The data were

* (CI2 was only 2 years old at the end of this period and thus sexually mature only for approximately the last 2-3 months of the period indicated).

FIG.4/11

BUSHPIG DISPERSAL TRENDS
 GOUDVELD 1980-1985



| | | | |
|-----------|---------------------|-------------------|--|
| A | Montane Zone | L | Losses/zone |
| B | Lower Foothill Zone | ↗ n | Number of recorded immigrants to zone indicated by arrow point |
| C | Upper Plateau Zone | | |
| 1cm : 1km | | a,b,c,d: see text | |

grouped in relation to three zones: A - the montane zone with fynbos and plantations as the predominating vegetation, B - the lower foothill zone, primarily under indigenous forest and C - the upper plateau, subject to agriculture and private ownership (Fig. 4/11). Towards the end of 1982 a complete capture record for the Goudveld bushpig population had been established (11.2.1). Any disappearances thereafter were taken as losses to the populations of the respective zones. It was generally not possible to distinguish between mortality and emigration. Additions to the populations were either by birth or immigration (Table 4/6).

| TABLE 4/6 FREQUENCIES OF BUSHPIG LOSSES AND ADDITIONS OVER TWO ZONES IN THE GOUDVELD CAPTURE AREA (1980 - 1985) | | | | |
|---|-------------------------------|-------|--------|----|
| | | | ZONES* | |
| | | | A | B |
| | Mortality or Emigration | M | 4 | 12 |
| | | F | 6 | 15 |
| | | TOTAL | 10 | 27 |
| | Natality | M | 2 | 8 |
| | | F | 4 | 5 |
| | Immigration | M | 0 | 8 |
| F | | 0 | 7 | |
| | | TOTAL | 6 | 28 |
| * see FIGURE 4/11 | | | | |

Two animals from zone A emigrated to zone B and of the remaining 8 animals lost, four were verified as mortalities. Eight of the lost individuals from zone B were verified as mortalities, while one was forced out to the neighbouring State forest Gouna (sow CU5).

The picture which emerged was one of greater stability of territorial ownership and zero immigration for zone A, and relatively high losses from and immigration into zone B. Immigrants to zone B originated from the surrounding areas as follows: 2 from zone A, 5 from zone B continuation areas outside the capture area and 7 from zone C. The immigrants showed no preponderance of any particular age class in either sex. Comparing population density indices of zones A and B revealed no signifi-

cant differences. Comparable population density indices were determined by expressing the sum of the periods of stay of individual animals within each zone, per unit area. Any animal only caught once was arbitrarily assigned a period of presence in the area of one month. The resultant indices reflected average relative density over the main capture period (1981-1984) between zones A and B. No data on population density were available for zone C, but according to subjective judgement no drastic differences to zone A or B were indicated.

4.4 Discussion

4.4.1 Sociality

4.4.1.1 Group size and composition

Bushpig group sizes determined in this study ($\bar{x} = 2,4$; largest: 10) were similar to those reported in the literature: Jobaert (1958): 2-12; Skinner, Breytenbach and Maberly (1976): usually 4-6, largest: 12, Breytenbach (1977): 2,6, largest: 6; Smithers (1983): 2-11; Ghiglieri *et al.* (1982): 3,2, largest: 11. Jobaert (1958) observed family groups as the typical social unit. He noted that solitary bushpigs were rare and observed no multifamily aggregations. There appears to be general agreement that the basic social unit is the family group, although larger group sizes suggesting aggregations have been reported. In respect of a group of 15 animals including 2 sows with litters, Breytenbach (1977) suggested that two sounders might have been involved. Large aggregations numbering up to 40 animals, such as reported by Dorst and Dandelot (1970) and Kingdon (1979) might also be attributed to observations of temporary aggregations of more than one sounder (cf Attwell and Bearder 1976). Multifamily aggregations were never observed in the course of this study and do not accord with the pattern of social organization found for the study populations (4.3.1; 4.3.2; 4.3.3). The aggregations reported elsewhere are thought to be associated with predictable and clumped food concentrations.

4.4.1.2 Group size determinants

Wittenberger (1980) suggested that, in mammals at least, sociality is largely a function of the reproductive or survival benefits that accrue to females in different sized groups. The social dispersion is accordingly considered to be determined by the adaptive mating system. Thus, although the basic group size is considered to be socially mediated, it will be argued in section 4.4.3 that the type of mating system is ultimately related to the nature of food resource dispersion. However, given any particular degree of social dispersion or gregariousness, group size frequencies exhibit changes and interpopulation differences. These will be discussed in this section.

For a given species, average group size may be a composite reflection of the

- (I) incidence of solitary individuals,
- (II) reproductive success and
- (III) stage of dispersal.

The higher average group size determined for the Eastern Cape is correlated with a lower incidence of solitary individuals (24 vs 37% of the social units were solitary individuals for the Eastern and Southern Cape respectively). The ratio of juveniles and yearlings to mature animals was significantly higher in the Eastern Cape (0,93 vs 0,40; $\chi^2 = 6,41$, $P < 0,05$), indicating a higher reproductive success or survival, or both. No reliable comparable data in respect of stage of dispersal for the two regions became available. Group size frequency data however revealed a significantly higher incidence of groups with 3 or more individuals relative to solitary and pair groups in the Eastern Cape compared to the Southern Cape ($\chi^2 = 6,315$; $df = 1$, $P < 0,05$). It is postulated that these regional differences related to average group size are linked to the availability of food resources.

Substantial evidence has accumulated that food dispersion underlies group size as indicated by the incidence of solitary individuals versus groups. According to Clutton-Brock and Harvey (1978), in some monogamous primate species the male and female spend most of their time apart.

This seems to apply either in species where feeding interference is intense because of the nature of the food resources or where species rely on crypsis to avoid predators. The most likely explanation for the association between food source size and group size is that group splitting occurs where food is widely distributed in small clumps, resulting in high costs of feeding competition (Clutton-Brock and Harvey 1977 and 1978). A low prey base increased solitary living among wolves (*Canis lupus*) and Messier (1985a) proposed that group living largely depends on the dispersion and abundance of food resources for carnivores generally. When food was scarce and dispersed, resident mated pairs and solitary individuals predominated in coyotes (Bekoff and Wells 1982). A similar interaction was found for the golden jackal, *Canis aureus*, by Macdonald (1979). Ghiglieri *et al.* (1982) suggested that bushpig group size may fluctuate according to food distribution and patch size, as in other fusion-fission societies. This study has shown that solitary living is similarly more pronounced in the Southern Cape, the region where food availability and concentration is considered lower (8.2.4). Some evidence was presented that the splitting of groups may be the result of food shortage (4.3.1.3).

As was pointed out earlier, family group size is determined by reproductive success and stage of dispersal and the corresponding changes codetermine average group size in the population. Among the semi-social canids, whose social organization is essentially identical with that of the bushpig (4.4; 4.5), groups larger than a single breeding pair appear to consist primarily of yearling offspring that have remained with their parents and may be related to conditions of clumped food supplies (Packard 1980). Wolf pack size is primarily determined by the rate of dispersal out of the pack (Page and Peterson (1985). Von Schantz (1983) found for red foxes (*Vulpes vulpes*) in Sweden that non-breeding group members mainly occurred during years of high food abundance. When food is in short supply, dispersal is usually more pronounced (Bekoff, Daniels and Gittleman 1984). It is postulated that the regional differences in bushpig group size frequencies found in this study may be similarly explained.

A comparison of data on ranging, activity budgets and frequency of social behaviour gathered over a range of group sizes for an omnivorous,

forest-living monkey, the long-tailed macaque (*Macaca fascicularis*), showed that the length of the day journey, the time spent travelling and searching for dispersed food items, as well as social tension, showed a monotonic increase with group size (Van Schaik *et al.* 1983). The authors also found that individual long-tailed macaques spent more time on vigil when they were alone. They concluded that predation pressure also seemed to influence the behaviour of forest primates and that predation risk may be lowered in larger groups. These results are in accordance with the postulates of Alexander (1974), namely that feeding efficiency will decrease with group size due to competition among group members and that predation selects for larger group sizes, thereby opposing the group splitting tendencies resulting from intragroup competition. From subjective observations it appears that solitary bushpig are more vigilant (e.g. they approach food sources more hesitantly; are more alert). In contrast to adult bushpig, immature animals are subject to predation (11.2.3) and the adaptive significance of groups formed by extended parent-offspring bonds seems evident.

Comparisons between species suggest that the two main environmental influences on group size are food and predation (Altman 1974, Krebs and Davies 1981). In this context, Altman (1974) formulated two central principles:

- (I) Sparse and patchy, slowly renewing resources are most effectively exploited by small groups.
- (II) Predation selects for large groups and groups containing at least one adult male.

In conclusion it is postulated that the nature and frequency of group sizes found for bushpig in this study are explicable by these two influences as found for other species and discussed in this section. The dispersed nature of the food resources which is typical of bushpig habitat leads to the characteristic social organization of the species (4.4.3). Within this socioecological framework, a favourable resource base allows or facilitates group formation for reproduction and rearing. Predation pressures could operate in favouring the maintenance of the family groups beyond weaning of the young.

4.4.2 Sociospatial organization

4.4.2.1 Comparative sociospatial organization in the Suidae

All well-studied suid species have hitherto been found to be non-territorial. In particular, this applies to the European wild boar (Brandt 1974, Beuerle 1975, Cumming 1984), the warthog (Frädrich 1964 and 1974, Bradley 1968, Cumming 1975, Kingdon 1979, Mason 1982) and the giant forest hog (D'Huart 1978, Haltenorth and Diller 1980).

For the bushpig Marberly (1967) stated "a sounder ranges a definite territory, in which it is aggressively antagonistic to intruders of its own species". Somewhat later Breytenbach (1977) suspected the bushpig to be territorial. He found bushpigs to move in well-defined areas and only when a large or special food source became available did more than one sounder occur in the same area (Breytenbach 1979). Kingdon (1979) reported on bushpig sows which were seen to chase off strange sows and even challenge strange boars.

These earlier reports and suggestions on the sociospatial organization of the bushpig were corroborated by this study. A clear pattern of female resource territoriality was found for this species. The possible underlying reasons for the different sociospatial organization of bushpig in comparison with the other suid species is explored in the following sections.

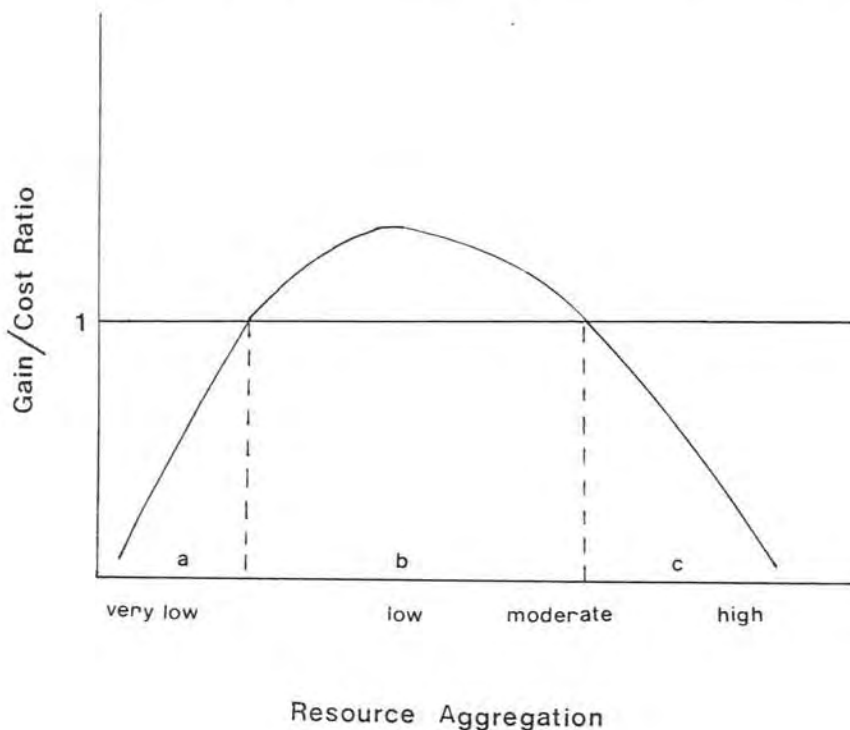
4.4.2.2 Socio-ecological basis of territoriality

Territoriality may be viewed as a social mechanism whereby individuals, through defence of space, ensure an adequate supply of resources for themselves and potential offspring (cf Bondrup-Nielsen *et al.* 1985). Whether a resource is subject to active or passive competition, in a territory or an undefined home range, is dependent on the defendability of the resource (Brown 1964). Both the possibility of resource defence and the need for it is of significance here. If the resource is defendable, active protection will ensue, provided the resource gain exceeds the cost of competition to the individual (Geist 1978a). Thus, territoriality can only evolve where a favourable cost/benefit ratio of

active competition can be achieved. This depends on the nature of resource aggregation and predictability (e.g. Clutton-Brock and Harvey 1977, 1978 and Geist 1978a).

Resource aggregation relates to the level of food abundance and its spatiotemporal concentration. According to the nature of food patch size, patch density and renewability food availability may be characterized along a continuum of low to high food resource aggregation. At the lower extreme food is scarce and scattered, while at the upper end of the continuum it is abundant and clumped. Under conditions of very low resource aggregation the costs of active defence per unit of resource would be relatively high due to the large area to be defended. Under conditions of high resource aggregation, defence costs would be high due to a high intruder pressure or defence benefits low due to a superabundance of the resource. At both extremes of resource aggregation a relatively low cost/benefit ratio would apply for active competition (Fig. 4/12).

FIG.4/12 GAIN/COST RATIO OF ACTIVE COMPETITION AS A FUNCTION OF RESOURCE AGGREGATION



At intermediate, i.e. low to moderate, levels of resource aggregation the intruder pressure is limited and defence costs thus relatively low. Defence gains may be relatively high due to the favourable effect on foraging efficiency achieved within an exclusive area. A favourable gain/cost ratio of active competition results and territoriality becomes adaptive (resource aggregation levels over range "b" (Fig. 4/12).

In addition to the actual level of resource aggregation, its predictability is of importance in this context. Any particular level of resource aggregation characteristic of a specific environment may be predictable or unpredictable. High intra-annual predictability means that resource levels fluctuate seasonally (temperate regions) or are relatively constant over the course of the year (aseasonal or weak seasonal pulses only). Low predictability usually refers to interannual fluctuations in levels of resource aggregation. Predictability may modify the implications of resource aggregation levels. Low to moderate levels of resource aggregation are thus considered to favour territoriality only when highly predictable (cf Wiens 1976). If they are not predictable, the situation resembles that for very low resource aggregation levels (Fig. 4/12 range "a").

In summary, passive means of competition are selected for whenever resources cannot be defended profitably such as when they are highly concentrated or widely dispersed (e.g. grassy plains or desert environments respectively for grazing herbivores). Year-round food resource territories are only found under relatively specific ecological circumstances, as in subtropical and tropical plant communities of moderate productivity (Geist 1978a).

The natural food resource base of bushpig in the Cape Province is characterized by small food patch size coupled with a low patch density. Pronounced seasonal pulses in food availability are not evident (8.1, 8.2.5). Food availability is thus characterized by low resource aggregation of high predictability. As a subordinate factor events of high resource aggregation with a low interannual predictability may also apply (e.g. synchronized fruiting, agricultural crops). In contrast the food availability for warthog (*Phacochoerus aethiopicus*) and the European wild boar (*Sus scrofa*) is typically subject to seasonal pulses

of superabundance. A situation of high resource aggregation with comparatively high predictability (being seasonal) prevails. In addition, a low interannual predictability caused by droughts or severe winters is superimposed on the basic seasonal pattern.

The dispersed nature of the bushpig food resource base is believed to have two significant implications:

(I) The search element is critical during foraging in view of small patch size and low patch density. Foraging efficiency would be critically affected through pre-emption by competing individuals. Territorial defense would accordingly be advantageous in terms of foraging efficiency (high gain).

(II) The low resource aggregation implies relatively low levels of intruder pressure (low defence cost). Bushpig population densities are generally substantially lower than those of warthog, European wild boar or giant forest hog (11.3.2).

The favourable cost/benefit relationship leads to territoriality as an adaptive competitive strategy for bushpig in contrast to the warthog and European wild boar. The giant forest hog as a bulk feeder on soft herbaceous material would correspondingly be predicted to be non-territorial (as also found by D'Huart 1978).

4.4.2.3 Maintenance of territorial integrity

Bushpig territoriality requires comparatively large areas to be defended effectively. The question of how territory holders achieve this naturally arises.

When food resource defence is not possible or beneficial, females tend to compete passively and lose or reduce their weapons, while males evolve strong defences, elaborate displays or low intensity interactions (Geist 1978a). Reduced canines in European wild boar females and protective dermal shields in males support this thesis.

In contrast "defence of resources needed for maintenance, reproduction (exclusive mates) and growth selects in both sexes for weapons maximiz-

ing surface damage" (Geist 1978a and b). Maximum negative conditioning to the locality of attack is achieved through the use of weapons that maximize surface damage and inflict pain well beyond the threshold of retaliation (Geist 1978a and b). Intrusion becomes a highly costly venture under these circumstances and area avoidance or immediate flight during encounters is adaptive for potential intruders in most cases. The data for bushpig fits this scenario. Sows have functional canines and play a central role in territorial defence. Non-ritualized, damaging fights invariably occur when a territory holding sow encounters a mature intruder of the same sex. Unfamiliar males of comparatively lower social status are also chased (5.2). Fighting among mature bushpig sows results in significant mortality (11.2.3). The chances of encounter and thus the risk to the intruder are increased by "patrolling" of the territory (4.3.2.2). Mobility about the range is considered essential for territorial maintenance (Eisenberg 1983, Mitani and Rodman 1979). Although bushpig territories are comparatively large, mobility is sufficiently high to allow the territory to be traversed within the time span of less than a day. Boundary visit intervals of between one and three weeks are indicated by limited data from this study. In comparison, Peters and Mech (1975) found that wolf packs travelled about their territories irregularly, but reached most parts at least every 3 weeks. Encounters with territory owners are not only costly to intruders because of their damaging nature, but the probability of such encounters is substantially increased by patrolling. The negative conditioning to an area is further reinforced through various intimidation behaviours such as group displays and charges observed during bushpig encounters (5.2). The advantage of group size for displacement between bushpig groups was implied by Attwell and Bearder (1976).

Gosling and Petrie (1981) suggest that there should be strong selective advantages for devices that assist in territorial defence at lower costs than those involved in direct interception of intruders. Demarcation of territorial occupancy by glandular secretions, urine and faeces may be such devices. The extensive olfactory marking observed in territorial species could be viewed as an olfactory intimidation mechanism still functioning in the absence of the owner (Geist 1966). In line with these authors it is here suggested that the frequency of boundary

patrols required for territorial maintenance is reduced through marking behaviour denoting the status of occupancy (5.1.3.1; 5.1.3.2). On two occasions the patrolling bouts of sow CC9 were actually followed with the aid of radio telemetry. A high rate of scratch marking was observed along the patrolling routes (5.1.2.1).

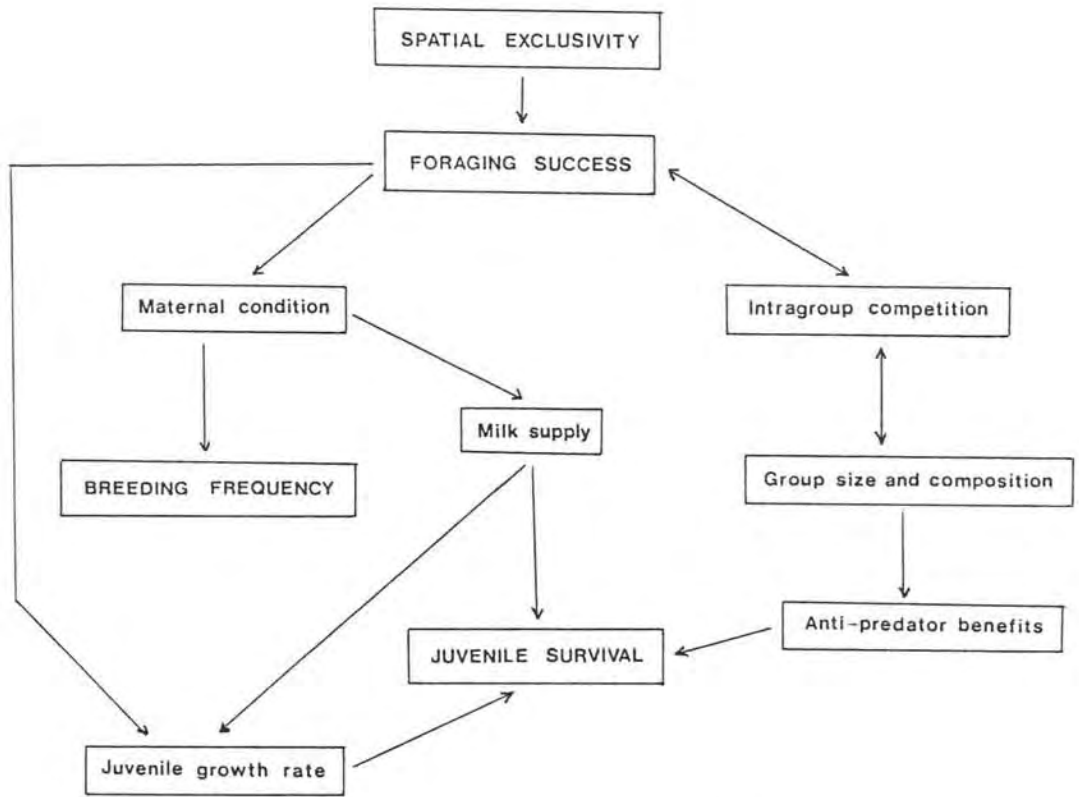
4.4.2.4 On the adaptive significance of territoriality

Given the diet of bushpigs and the patchy distribution of their food resources (8.1; 8.2), searching is an important element of foraging, as is the case for predators. It is suggested that foraging success is of critical importance for maintenance and reproduction. It is accordingly hypothesized that the adaptive advantage of territoriality relates primarily to the enhancement of foraging success for the territorial occupants. Protected foraging success is believed to have ultimate benefits in respect of reproductive and rearing success (Fig. 4/13).

Although considered of critical importance during the early post-parturient period, when movement is restricted by neonate mobility, it is suggested that exclusive access to the food resources contained in the territory is of significance for rearing well beyond weaning. Under conditions of lowered foraging success, a conflict may arise between subsequent breeding success of the parental female and juvenile survival or growth via intragroup competition for dispersed food items. The contention of Brown (1982) that the care of the young is more important than fecundity in group territorial species, is noteworthy.

Indirect evidence for the interrelationships illustrated in Fig. 4/13 will be dealt with in subsequent chapters. Conclusive proof would however require controlled observations and experimentation. The elements of adaptiveness of territoriality as suggested for bushpig may have wider applicability for group territorial species in general. As an example of a group territorial species, Messier and Barrette (1982) interpreted coyote territoriality as a form of year-round parental investment to ensure higher pup survival. They argued that pup survival

FIG.4/13 PLAUSIBLE BENEFITS OF TERRITORIALITY
FOR REPRODUCTIVE SUCCESS



primarily depended on the ability of the parents to obtain food readily from an initially restricted area and thus assumed exclusion of conspecific competitors from that area to be highly advantageous.

4.4.2.5 Territory "area maximization"

Bushpig territories are relatively large and it is difficult to conceive that such extensive areas are required or can be exhaustively utilized for foraging. In the Southern Cape resource levels are considered generally low, but fluctuating interannually with unpredictable periods of superabundance (8.2.5). The available data, albeit limited, suggest that substantial parts of a territory are not exhaustively foraged, although visited during patrolling bouts, and that territory sizes do not track resource availability levels.

"Area maximization" is commonly explained as prospective resource defence (Hixon 1980, Stamps and Tollestrup 1984). According to this

explanation, territory holding individuals may ignore short-term resource fluctuations because their territorial defence depends both on the present and expected future value of the resources in the territory. It is considered to apply to situations when resource fluctuations occur at shorter time spans than expected territory holding periods.

According to the rules of economic defendability many territorial species limit their territory size and therewith defence cost when the food supply increases beyond handling capacity (termed the "just-sufficient" strategy by Von Schantz 1981). In contrast, Verner (1977) suggested that an animal should defend a territory of a size larger than it needed. By defending a disproportionately large territory an individual would prevent others from obtaining a territory and breeding or would force them into suboptimal habitats with lowered breeding success ("super-territoriality"). According to this view super-territoriality acts as interference competition for the maximization of reproductive fitness by reducing the reproductive fitness of other individuals directly (cf Geist 1978a).

Following the model of Von Schantz (1981) a territorial and permanently resident animal in an interannually fluctuating environment should maintain a fixed territory size when food availability increases (the "obstinate" strategy). It then does not have to struggle for territorial enlargement later when food availability decreases. This model is supported by data for red foxes (*Vulpes vulpes*) in central Sweden (Von Schantz 1981). Individuals adopting the "obstinate" strategy would be more fit during the low years, since they maintain an optimal territory size more economically than the "just-sufficient" strategists. During years of high resource abundance "just-sufficient" strategists benefit most since they maintain an optimal resource gain/defence cost ratio, whereas obstinate and super territory strategists have territories that contain a resource surplus. However, it was demonstrated that, unless some benefit was derived from the resource surplus, such strategies cannot become evolutionary stable in the population (*op. cit.* Von Schantz 1981). Von Schantz (1981) however proposed that such a benefit might be derived through kin selection, which was defined by Maynard Smith (1964) as "the evolution of characteristics which favour the survival of close relatives of the affected individuals". Such behaviour

is selected for because the inclusive fitness of the particular individual involved is increased. Accordingly, an individual allowing its close relatives to exploit a resource surplus, should be selected for. The obstinate strategists would therefore gain by allowing some of its offspring to remain in the territory during years of high resource abundance, resulting in higher offspring survival (Von Schantz 1981).

Territories of the sizes containing more resources than needed for the breeding pair and their current offspring are a prerequisite for multi-generation group living as found *i.a.* in the bushpig. For territory holders in bushpig populations it is basically a matter of allowing yearlings (1-2 year olds) to remain in the territory; be it in the parental group or separately (4.3.2). Possibly associated kin selective advantages of such behaviour could be higher probabilities of yearling survival to dispersal, of territory inheritance by genetically related individuals and of adoption of current offspring in the event of death of the territory holders.

Where fecundity is of overriding importance as opposed to kin selected parental investment the "just-sufficient" strategy is assumed to be most appropriate. Dispersal of offspring then takes place after weaning and offspring generation overlap within the same social unit is uncommon. As discussed, the "obstinate" strategy is linked with an interannually fluctuating environment. Where full reproductive success leads to offspring generation overlap due to the inclusive fitness derived from extended parental care, the "territory size maximization" strategy is postulated to apply. This strategy may be seen as a form of prospective resource defence, not in anticipation of resource lows, but of increased needs for successive second generations of offspring to be accommodated in the territory until they disperse.

It is postulated here that bushpig territorial behaviour conforms to the "territory size maximization" hypothesis. According to this hypothesis, territorial pairs would strive for the maximum defendable area. This maximum defendable area would presumably be lower under conditions of territorial saturation. The available sociospatial data on bushpig (4.3.2.1) suggests that territorial animals regularly probe neighbourhood occupancy and making use of possible opportunities for

expanding into vacant neighbouring terrain. An instability of territory boundaries can thus be expected in the absence of territorial saturation, as found for the study area in the Southern Cape.

It is the bushpig female which occupies the more prominent role in spatial intolerance. Although this study has produced no direct evidence, the possibility that female territorial aggression has implications in terms of female sexual selection, should not be disregarded. Intrasexual female competition through territory size maximization could operate through the limitation of competing breeders and possibly also the protection of maximum male rearing investment (4.4.3.4). If applicable, interference competition of the kind indicated should however not be considered the initiating factor in the evolution of territoriality, but a resultant adaptive function thereof (cf Verner 1977).

4.4.3 Breeding system

4.4.3.1 Suid breeding systems

The rearing unit in the European wild boar (*Sus scrofa*) is the matriarchal sounder consisting of one or more females with young. Males are normally segregated (Frädrich 1967, Gundlach 1968, Eisenberg and Lockhart 1972, Stubbe and Stubbe 1977, Santiapillai and Chambers 1980). Cross maternal suckling was reported by Stubbe and Stubbe 1977, but contradicted by Hennig (1981). A similar social structure has been reported for the warthog, *Phacochoerus aethiopicus* (Bradley 1968, Cumming 1975, Frädrich 1974, Kingdom 1979, Mason 1982). Both species thus have a typically polygamous mating system.

The breeding system of the giant forest hog (*Hylochoerus meinertzhageni*) is not as clearly determinable from the literature. The basic social unit appears to be the family group, with one or more females and with extended male presence (Dönhoff 1942, Frädrich 1967, D'Huart 1978, Kingdom 1979). The defence of piglets is suggested by Kingdom (1979). The preponderance of females in the population (sex ratio oscillating around 1 male to 2 females; D'Huart 1978) and the multifemale groups suggest polygamy. However, only one female is reported to breed during any particular season (D'Huart 1978) and Martys (1985) consider the

giant forest hog to be monogamous. On the basis of the available information the breeding system may be termed "serial harem polygamy". Any further investigation of the giant forest hog breeding system should take cognizance of its possible common ancestry with *Potamochoerus*, its evolution as a grazer and its secondary adoption of forest habitats (cf Thenius 1981).

In this study monogamy was found to be the breeding system of bushpig (4.3.3). Observations suggestive of monogamy, such as restriction of breeding to the dominant female, extended male presence with suckling females and paternal care behaviour, have been recorded by a number of authors (Maberly 1967, Attwell and Bearder 1976, Skinner, Breytenbach and Maberly 1976, Kingdon 1979). Possible reasons for differences between suid species in their breeding systems are discussed below.

4.4.3.2 Environmental correlates of monogamy

Monogamy is usually associated with a carrying capacity within the home range of a group which allows only one female at a time to rear a litter (Eltringham 1979, Eisenberg 1983). This is normally the case where food is energetically costly to collect (Bekoff, Daniels and Gittleman 1984) because it is spatiotemporally dispersed. Stable habitats of relatively uniform, but moderate productivity tend to select for monogamy (Geist 1974).

The nature of the food resource commonly associated with monogamy largely resembles that indicated for the bushpig (8.2.5). Bushpig food resources tend to be scattered in space and time and foraging is thus energetically costly. This probably results in significant inter- and intragroup competition. Under such conditions it then becomes adaptive for breeders to safeguard foraging success by spatial defence (territoriality) and by reducing intragroup competition to unimaternal social groupings (monogamy). In contrast, both the European wild boar, a temperate zone inhabitant and the warthog, a savanna grazer, inhabit environments with seasonal pulses of superabundance. In both species the phase of critical nutrient requirements during lactation falls within the period of predictable superabundance (flush of new growth in spring). Multimaternal groupings are then probably advantageous in

terms of predator evasion and intragroup competition is negligible. Territoriality, as a food resource defence strategy, and monogamy may thus both be adaptations which minimise the cost of searching for high quality dispersed food items (as opposed to scramble feeding on clumped, low quality food resources).

4.4.3.3 Sociobiological correlates of monogamy

In contrast to species with a polygynous mating system, the females of monogamous mammals appear to exhibit high levels of intrasexual aggression (Kleiman 1977). Coupled with this female aggressiveness is the retention of functional, damaging weapons similar to those of the male. Unlike the situation in the bushpig where the female has fully functional canines (4.4.2.3), the canines are reduced in female wild boar compared to the male. This not only refers to size, but also to function. Female canines terminate their growth whereas those of the male grow continuously, thereby compensating for wear (Landolt 1968). We thus have the sociobiological dichotomy of aggressive females with fully developed weapons and monogamy - represented by the bushpig - and females showing reduced aggression and bearing reduced weapons associated with a polygamous mating system represented by the European wild boar and the warthog.

Suid males of the polygamous species are not only better armed than females, but also larger bodied (Jarman 1983). Some male to female mass ratios from the literature are 1,54 (Sludskii 1956); 1,46 (Briedermann 1970); 1,50 (De Vos and Sassani 1977) and 1,21 (Hennig 1981) for European wild boar and 1,40 (Mason 1982) and 1,62 (Rodgers 1984) for the warthog. In diverse mammalian groups monogamous species are less sexually dimorphic in size. Clutton-Brock and Harvey 1977, Kleiman 1977, Ralls 1977, Jarman 1983). This trend is once more reflected in the bushpig, which has an adult male/female mass ratio of only 1,06 (9.3.1).

The breeding system must be expected to affect the degree of intrasexual competition for mating access. In strongly polygynous species intermale competition should be intense, while in monogamous species it should be reduced. Consequently, traits affecting competitive ability, such as

body size, should be better developed in males of species which usually breed polygynously than those that breed monogamously (Clutton-Brock and Harvey 1978). However, if increased size confers only a slight advantage in terms of fitness during agonistic encounters for access to females, it would also be selected for among monogamously breeding males. However there may be opposing selective pressures such as reduced survival of larger-bodied individuals due to energetic constraints. Thus, as Ralls (1976 and 1977) correctly indicates, sexual selection is but one of the selective pressures affecting size. Other pressures and those affecting female size (e.g. neonate or litter size) all contribute to the final degree of sexual dimorphism in size.

Sexual selection favouring large body size may be counterbalanced by ecological factors (including *i.a.* energetic constraints) which presumably limit body size increases (cf Clutton-Brock and Harvey 1977). It is accordingly suggested that sexual dimorphism depends on a sex differential balance between sexual and ecological selection and not on the intensity of intermale competition *per se*. The sexual dimorphism often encountered in polygynous species is thus explained by sexual selection operating in a way where larger size confers a competitive advantage, operating on males only, and relaxed ecological selection. The latter entails environmental conditions allowing growth to and maintenance of larger body size. This generally applies to environments with seasonal variation in resource availability (Boyce 1978, Geist 1978a). Environments with seasonal pulses of increased resource availability both favour large body sizes and the incidence of polygamy (4.1.3). Ralls (1977) identified two trends - a greater frequency of polygyny in larger mammals and the larger the mammal, the greater the degree of size dimorphism. Both trends can be explained on the reasoning presented above.

The monomorphic body size in bushpig may be explained by sexual selection involving physical agonistic encounters in both sexes. Such equalized selection pressures are theoretically expected for monogamous mammals (cf Trivers 1972) and the observed pattern of aggression in bushpig of both sexes is in accordance with this expectation. Tighter ecological counterselection against body size increases which diverge from the energetic optimum are similarly to be expected under conditions

of continuous K-selection in stable habitats with a relative resource scarcity (Geist 1978a). Low food availability produces selection for small individuals with lower nutritional demands. Body size monomorphism in bushpig may thus be related to equalized sexual selection or tight ecological counter-selection, or both.

4.4.3.4 Paternal rearing investment

There is a close association between monogamy and paternal care among mammals (e.g. Clutton-Brock and Harvey 1977 and 1978, Kleiman 1977, Ralls 1977). Kleiman (1977) discussed evidence suggesting that Type II monogamy is favoured whenever the carrying capacity of the habitat is not great enough to permit another female simultaneously to raise a litter in the same home range and associated with circumstances where rearing of the young by more than a single individual is adaptive. Crook et al (1976) argue that the male will only stay with the female/young unit through gestation and rearing if his presence enhances parental fitness, i.e. reproductive output. Male presence may enhance parental reproductive output in two ways: by increasing survival of offspring and by sharing the energetic burden of rearing with the female, thereby allowing the latter to maintain a higher breeding frequency.

The evidence for substantial male rearing investment in the bushpig (4.3.3.2) fits the theoretical expectations from its monogamous mating system and is in agreement with previous reports regarding the close association between boars and juveniles (Attwell and Bearder 1976, Skinner *et al.* 1976, Kingdon 1979).

In most monogamous species, males help in territorial defense, thereby defending food reserves used by their mates and offspring (Kleiman 1977, Clutton-Brock and Harvey 1978). Particularly for group territorial species, aiding the female in defence of the territory is suggested to be a significant part of male parental investment (Kleiman 1977, Brown 1982). To what degree and in which ways male bushpigs assist in territorial defence is not clear. No direct evidence became available, but it is conceivable that such assistance does take place through, for example, double scent marking (5.1.2.1) and group displays and attacks against foreign groups. However, the evidence for paternal rearing

investment in bushpig which did become available, is interpreted to operate by improving offspring survival and female energetics.

Bushpig juveniles are vulnerable to predation (11.2.3) and a guarding function of the male bushpig can clearly be derived from the evidence in section 4.3.3.2, involving close proximity and responsiveness to the young. Directly defensive behaviour was also recorded. This guarding association may last into the yearling stage. The relatively high incidence of boar/yearling associations is noteworthy (4.3.1.2). Protection of juveniles against heat loss through huddling is another conceivable survival enhancing function of the boar, particularly during periods of temporary absence of the sow.

Bushpigs normally forage over larger areas than is possible during the first one to two months post-partum, when the neonates have limited mobility. This limitation, together with the demands of lactation and subsequent post-weaning intragroup feeding competition, may conceivably subject the sow to energetic deficits (9.3.2). By sharing rearing duties, the boar could indirectly enhance the survival and growth of his offspring through improved lactational output and defence of food resources by the sow. Both are partially dependent on her physical condition. From the available evidence it is suggested that the boar performs this function (4.3.3.2). By guarding the young he allows the female to roam more widely on her own to feed and patrol the territory than would otherwise be possible without detriment to survival of the offspring. A similar function has been reported for the males of monogamous bat-eared fox (*Otocyon megalotis*) pairs (Malcolm 1986).

Depletion of the female's energy reserves during rearing has implications for the frequency with which she rebreeds (10.4.1.4). The longer the period of mate fidelity, the greater the importance of its partner's future physical condition (cf Emlen and Oring 1977). It thus becomes adaptive for the boar to equalize the energetic burden of reproduction by sharing in parental care, as outlined. There appears to be a tendency towards post-weaning segregation of the female if the yearling generation is also part of the family group (4.3.3.2). This is presumably restricted to conditions when food resources are scarce and is explained as an attempt by the sow to avoid intragroup feeding

competition in order to gain sufficient condition for rebreeding. The post-weaning juveniles or yearlings or both remain attached to the boar, presumably benefitting from his defensive capabilities. Such behaviour could explain the incidence of some of the boar/offspring groups and constitute another form of male investment in parental care.

4.4.3.5 Male-male associations

Unlike adult bushpig females, which are totally intolerant towards each other, male consortships or alpha/beta-relationships do occur. Five social units involving two adult males are recorded in Table 4/4 (4.3.1.2). In addition, male TD1 in the study enclosure occupied the beta position to male TD5 until his takeover of the alpha position from the latter (5.2.2.4).

Of interest is the following sequence recorded during the capture programme:

8.3.1982 CC3(M) + CRI(M)
21.3.1982 CC3(M) + CRI(M) + Y
16.1.1983 CC3(M) + CL2(F) + J (suckling)
16.2.1983 CRI(M) + CL2(F) + J (suckling)
8.1.1984 CC3(M) + CW5(F) + J + Y

It is suggested that territorial encroachment by female CW5 into the territory of female CL2 (4.3.2.1) led to the desertion of male CC3 and bonding with CW5(F), leaving only male CRI with the CL2(F) + J unit. Both members of the alpha-beta male association appear to be subject to some form of bonding to the maternal/young grouping. Observations in the study enclosure indicate that both show concern for juveniles perceived to be in danger.

Male-male associations are not uncommon among mammals (e.g. cheetah, *Acinonyx jubatus*, Caro 1985; wolves, *Canis lupus*, Zimen 1982) and the question as to the costs and benefits for participants naturally arises. A plausible benefit which the beta male may derive from consortship with the alpha male is free access to the group territory, since he is accepted by the alpha female. Some evidence suggests that foreign low-

ranking males are otherwise chased off (4.3.2.2). The beta male is also the probable successor of the alpha male. Where there is a male-biased adult sex ratio, beta male status may be the strategy with higher fitness prospects than searching for an unmated female and establishing a territory. Male consortships are however unlikely to occur unless the alpha male (or alpha female) also derives some benefit therefrom. Increased "resource holding potential" against intruding contestants may be such a benefit (cf Frame *et al.* 1979). For example, the beta male may function to increase the intimidatory content of group displays and charges. Assistance with paternal care, particularly defence of young against predators, may constitute another benefit to the alpha male.

Future studies should determine whether female promiscuity is associated with multimale groups. A polyandrous element would then be introduced, as found, for example, in wolves (Zimen 1982). Within persistent multimale social groups, females may increase their reproductive success by mating with several males if they can thereby induce those males to provide care for their young (Stacey 1982). The model developed by Stacey (1982) suggests that when promiscuity is advantageous to the female, a male should not interfere with copulations by other males. Male-male cooperation is assumed to be important to the survival of the young and subordinate males are likely to leave the group if prevented from breeding. The model indicates that when males provide some form of parental care, female promiscuity and its tolerance by males, can actually increase male reproductive success under certain conditions, rather than decrease it. Functional monogamy and complete promiscuity (where all mature males copulate equally with the female during her reproductive period) could then accordingly be viewed as opposite extremes of a continuum of degrees of access to females, rather than fundamentally different types of mating systems.

4.4.3.6 Sexual competition strategies

In this section an hypothesis is proposed to explain the strategies of sexual selection manifested by the bushpig's breeding system.

As suggested in section 4.4.2.2, food resource territoriality is considered to be related to the dispersion of food resources. A

consequence of anti-herbivore defence mechanisms of plants is that high quality food items for herbivores are generally dispersed in space or time. In the case of the omnivorous bushpig suitable food items tend to occur in small patches which are widely distributed, dispersed both in space and over time. Omnivorous foraging thus involves a considerable "search" element, unlike bulk feeders such as grazers, and thus resembles predatory foraging. Bushpig foraging accordingly involves time and mobility, and the rate of resource depletion and renewability become critical factors affecting foraging success. Since reproductive success of the female bushpig is dependent on sufficient access to food resources, particularly during lactation, it is postulated that female sexual competition pivots around the defence of this access through spatial intolerance, i.e. territoriality. Female territorial defence concerned with access to environmental resources is suggested for diverse mammalian species, i.a. for lesser bushbabies (*Galago senegalensis*) by Bearder and Martin (1980) and bears (*Ursus* spp.) by Bunnell and Tait (1981).

Neonates, especially when altricial, require protection against predators and inclement weather and have limited ranging capabilities. The requirements of offspring survival during the early post-parturient period are thus in conflict with far-ranging parental foraging. Restricted foraging is considered particularly important for the lactating sow, since her energy balance has consequences for both lactational output and the probability of rebreeding. Male parental care in the form of guarding the young while the female is foraging would thus substantially increase her access to dispersed food items. It is therefore postulated that the bushpig female competes for male parental and alloparental care through maximal extension of her territory ("super-territoriality" *vide* 4.4.2.5). This interpretation is supported by the intensity of intrasexual female aggression found in bushpig (4.3.2; 4.3.3). The reproductive success of a female would be reduced if by tolerating breeding of her mate with another female, she risked losing paternal care critical to the survival of her offspring. Since male parental care represents a resource for a reproductive female (cf Trivers 1972), the degree of interfemale sexual rivalry should be related to the importance of this resource (Burley 1977). This correlation between intense female intrasexual intolerance and extensive

paternal care is a well-documented phenomenon (e.g. Van Schaik and Van Hooff 1983).

The mating strategy of the male is adapted to the dispersion, grouping and predictability of occurrence of females (Jarman 1974). If females are spatially dispersed and the distribution of receptive females synchronized in time, the potential for maximizing the number of inseminations is low (Emlen and Oring 1977). The opportunity to mate with more than one female is accordingly low for the male bushpig. As a result of this and the opportunity for increased fitness through paternal care, the best mating strategy for the male is to enter into a prolonged pair bond with the female. If two parents can raise twice as many offspring, or if the chance that a deserting parent will remate is small, then monogamy with both parents caring for the young is the likely evolutionary stable strategy (Maynard Smith 1977). In the context of intrasexual competition, males prevent access of other males to their pair-bonded female through direct defence using a previously established individual reference for dominance. The previously established dominance rank is presumably communicated with the aid of tusk gland scent marking and facial display features (5.1.2.1; 5.1.2.3; 5.2.3).

In summary thus, the emerging scenario of bushpig sexual competition is one of female-dominated intergroup spacing and adjustment of the male mating strategy to female dispersion and opportunities for male parental care. The resultant monogamy is considered to be ultimately linked to food dispersion and proximally to female spacing and intrasexual male aggression (see Mitani 1984 for a comparable situation in monogamous gibbons, *Hylobates muelleri*).

Populations living in seasonal environments are subjected to periodic food shortages (Boyce 1978), but also to seasonal superabundance. Such populations usually experience higher mortality during a period of famine. This will lower the average population size and consequently competition is lower during the growing season. This would be expected to apply for the warthog as a savanna grazer and Jezierski and Myrcha (1975) also suggest lack of food competition between breeding European wild boar sows. Since competition is not an important factor, multi-maternal groups are possible during the period of lactation. The sows

can take turns in guarding and do not need to move for feeding and as a consequence be absent from their young for lengthy periods. The bushpig sow and monogamous mammals in general, are confronted with a totally different set of circumstances: low density food supplies (cf Clutton-Brock and Harvey 1977) requiring extended foraging; intense feeding competition (cf Van Schaik and Van Hooff 1983) precluding multi-maternal groups and altricial young (cf Zveloff and Boyce 1980) with reduced initial ranging capabilities and vulnerability to predation.

Under the given set of circumstances it is obvious that the sow would not be able to perform both guarding and suckling functions without seriously impairing her lifetime reproductive success. With a low potential for access to multiple mates due to female dispersion, taking over the guarding function logically presents itself for the male. Territorial patrolling and supplementary feeding for maximum lactational output are both optimally performed together during foraging. The male contributes to offspring survival both directly and indirectly and has the added advantage that accrues from energetic maintenance and subsequent reproductive success of the female to which he is pair-bonded.

4.4.4 Alloparental care

"Helping" has been reported in an increasing number of mammals (and birds). It is a phenomenon in which older, potentially reproductive offspring ("auxiliaries") assist in the rearing of their younger siblings in various ways. A number of possible advantages of such behaviour may be postulated for both auxiliaries and parents (4.1.4) and its evolution may involve a complex interaction of individual and kin selection (Emlen 1978, cf Harrington, Mech and Fritts 1983).

The presence of auxiliaries and implied helping behaviour is usually associated with monogamy (Eltringham 1979, Bekoff, *et al.* 1984) and has been documented for most monogamous territorial carnivore species. It is generally associated with increased food abundance (e.g. Macdonald 1979, 1980 and Von Schantz 1981) or increased habitat saturation (Von Schantz 1981, Emlen 1982b and Lott 1984), or both. The retention of sexually mature offspring within the parental group (philopatry) thus

appears to depend on sufficiency of resources and reduced likelihood of successful breeding after dispersal (Emlen 1982a). From studies on the red fox (*Vulpes vulpes*) in Sweden, Von Schantz (1981) suggested helping to be a consequence of group living rather than a cause of it and group living to be a consequence of a resource surplus. In addition, habitat saturation was considered a fundamental prerequisite for group living. Harrington, Mech and Fritts (1983) believe that auxiliaries remain with the parental group for reasons that need not be associated with helping. By remaining with the parental group, for whatever reasons, opportunities for helping arise. Helping may thus simply be an epiphenomenon of nondispersal and postponed breeding.

For the bushpig, Maberly (1967) reported behaviour patterns of a daughter sow reminiscent of alloparental care similar to those observed in this study. For the bushpig female philopatry seems to be restricted up to and including the yearling subadult transition phase, i.e. potentially including only the first breeding season. The opportunity for increased fitness through helping behaviour similarly appears to be restricted in comparison to, for example, the canids where food provisioning may be involved. In line with the authors cited above it is here postulated that helping behaviour is not the significant phenomenon in the evolution of philopatry, but rather that philopatry should be seen as a form of extended parental care. Helping would merely follow as adaptive behaviour as a consequence of philopatry.

The postulated extended parental care could take on various forms: by allowing the yearling daughter sows to remain in the family group; to remain attached to the alpha boar, with the alpha sow segregated, or to remain on the parental territory, but alone or in sibling groups. All three forms have been encountered and are presumably related to resource availability and habitat saturation. The likely advantages for the parents would be increased survival of their yearling offspring. Not only is dispersal and territorial establishment particularly risky for subadult sows, but the probability of successful breeding is also comparatively low (10.3.6). First litters often succumb and the energetics of combined body growth and lactation are probably unfavourable (9.4.4).

When remaining in the parental group or territory, yearling/subadult sows do not breed. From the limited available evidence it appears that a yearling daughter sow either remains within the parental sphere of influence as non-breeder, with alloparental care involvement when the opportunity arises, or disperses in an attempt to breed. The factors underlying these options and their respective hormonal correlates remain as yet unverified for the bushpig.

4.4.5 Dispersal

The term dispersal is here used to include all spatial shifts by non-reproductive but sexually mature individuals of both sexes which thereby at least potentially improve their chances of successful reproduction. These spatial shifts may either follow the disassociation from the parental group or may take place at any other stage in the animals life. The "floating" phase may span variable periods until spatial attachments are established again.

Dispersal in mammals is commonly associated with the attainment of sexual maturity, but is not confined to this stage (Caughley 1977). Subadult and adult dispersal both feature prominently in the bushpig. Whereas the incidence of adult dispersal varies with territorial stability and availability of food resources, subadult dispersal is an obligatory event. It occurs either at the onset of sexual maturation or may be delayed over an additional mating season. Attwell and Bearder (1976) reported of both bushpig parents becoming increasingly intolerant of the young beyond six months of age. According to the results of this study, young do not disperse at such an early age.

Delayed dispersal until after the first potential breeding season is interpreted as the outcome of extended parental care (cf Bekoff 1977, Brown 1978, Emlen 1978 and Packard 1980). It may be argued that delayed dispersing individuals have an advantage in that they will be older and more experienced and have a higher survivorship (Bekoff 1977). If age or experience were an important determinant of competitive ability then parents that allowed their offspring to remain on the natal territory for an extended period would tend to produce more competitive young (Brown 1978, Emlen 1978). Dispersal increases the likelihood of encoun-

tering foreign counterparts and escalating agonistic incidents and does appear to involve considerable risk for dispersing bushpig, particularly for females (5.2.2.3). Competitive ability, as determined by age or experience does appear to be important for reproductive success. This is shown by increased reproductive success with increasing age of bushpig females (10.3.6).

Functional explanations for dispersal normally invoke competition for mates or resources and inbreeding avoidance (Stacey 1982, Dobson and Jones 1985). The "competition for mates" hypothesis successfully predicted that young males were the predominant dispersers in many polygynous mammals and that both sexes disperse in most monogamous mammals (Dobson 1982). In bushpig the maturing individuals of both sexes disperse which is according to expectation for a monogamous mammal. However, according to Dobson (1982), inbreeding avoidance and competition for mates may often be synergistic influences on dispersal in mammals. Males do not appear to be more philopatric in bushpig than females, presumably because the territorial sow is intolerant of both maturing and foreign males (4.3.2.2). Also, male consortships have never been observed to involve father and son.

No differences in population density or food availability could be established between zones A and B with certainty (4.3.5.2). Both factors presumably fluctuated substantially in zone C, depending on the level of population control exerted and the spatiotemporal availability of agricultural crops. Both were presumably higher than for zone B during some periods and lower during others. Many immigrants from zone C were in better condition than zone B residents (9.3.3.1). No immigration into zone A was observed, in strong contrast with zone B (Table 4/6; Fig. 4/11). No clear trends in dispersal relating to zone B and population densities or food availability of adjacent zones were evident. The relatively high rate of immigration into zone B was however, correlated with a high rate of disappearances and turnover in territorial occupation. The high rate of losses in zone B is largely attributed to artificial mortality through the killing of bushpig on privately owned land in zone C.

Theoretically, immigration into an area is expected to be proportional to its food availability and inversely to its population density, compared to adjacent areas. This appears to be borne out by data for the European wild boar. It was found that emigration is high with high and immigration high with low resident population densities (Kozlo 1970, Andrzejewski and Jezierski 1978). Immigration was also particularly induced by conditions of excess food availability. For a territorial animal, food resource availability would be expected to be of less direct importance. Immigration would require territorial vacancies or unoccupied spaces. From the data presented for the bushpig, it is suggested that the rate and direction of dispersal is primarily governed by the availability of spatial vacancies.

4.5 Synopsis

The social organization of the bushpig may be characterized by the following features:

- (I) Bushpig sociality is centred around the family group, usually consisting of a boar and a sow with one or two generations of offspring. There is typically only one adult sow per family group.
- (II) The average group size for the study populations was 2,4 individuals, ranging between 1 and 10.
- (III) Resource group territoriality is maintained by spatially-related high levels of aggression, notably between females, patrolling and marking behaviour.
- (IV) Populations may be subdivided into four sociospatial classes: territorial male/female pairs with or without progeny; solitary individuals occupying non-exclusive home ranges in the case of males, dispersing individuals which are mainly yearlings or subadults and nomadic adults.
- (V) The mating subsystem: extended male/female pair bonds lasting beyond mating and rearing periods; breeding by the alpha female only in each territorial group; breeding deferment of sexually

mature, pre-dispersal daughter sows and alloparental care involvement.

- (VI) The rearing subsystem is characterized by substantial male parental care, the young remaining with the parents long past weaning. Dispersal usually proceeds when the offspring are between 1,5 and 2,0 years old.

The specific sociobiological syndrome of resource territoriality and monogamy, with its associated features such as interfemale intolerance, body size monomorphism and male parental care, as found to characterize bushpig social organization, is interpreted as a set of adaptations to the nature of food resource dispersion typically encountered by the species. The spatiotemporally dispersed nature of food resources is considered to result in the search being important during foraging. It leads to relatively low population densities and conditions where inter- and intragroup competition is critical. Safeguarding foraging success through spatial defence (territoriality) and reduction of intragroup competition to unimaternal social groupings (monogamy) is accordingly considered adaptive.

Some caution is appropriate in extrapolating the social organization established for the bushpig study populations to the species over all parts of its range. Populations elsewhere may differ, particularly where food resources are more concentrated than in the study area. For example, in more productive habitats female black bear (*Ursus americanus*) territoriality is replaced by an increasing degree of home range overlap (Powell 1985). Instances of intraspecific variation in social systems suggest that in some species selection has produced a social predisposition that can result in more than one social system, depending on individual history and current circumstances (Lott 1984).

5. ELEMENTS OF SOCIAL BEHAVIOUR

5.1 Communication

5.1.1 Introduction and methods

Communication can be defined as a process adaptive to the genome of the sender of signals. Accordingly, signs and signals are adaptations by which the sender sends messages that act as stimuli on the receiver (Geist 1978a). According to another view, true communication is only established if it is also advantageous for the receiver to change its behaviour upon receipt of the signal (cf Alcock 1979).

One or more of olfactory, auditory or visual signals may be involved in communication within a specific functional context. Bronson (1983) emphasized the functional role of chemical cues in support of mammalian breeding activity through (I) ensuring an appropriate dispersion of social units, (II) by playing a role in acute, short-range identifications that precede sexual or aggressive interactions and (III) by evoking stereotyped endocrine responses, thereby scheduling related physiological events. Chemical communication appears to be particularly important in nocturnal situations of densely vegetated habitats and with widely scattered individuals or social groups (Bronson 1983). Vocalizations may be particularly important in spacing, recognition and antipredator behaviour, whereas visual communication predominantly involves close range social signals, often within the functional context of agonistic behaviour (display). Signals of all three avenues of communication may modulate physiology and behaviour and ultimately regulate spacing between social units, thereby contributing in adjusting populations to their resources and general environment (Müller-Schwarze 1983).

Information regarding bushpig communication became available through opportunistic observations in the field (*i.a. vide* the capture programme 1.3.1), during formal enclosure studies (1.3.4, 5.3.1.2) and from scent marking reaction experiments.

5.1.2 Results

5.1.2.1 Olfactory communication

(a) Sources of odorous substances (Review and results)

Apart from urine and faeces, a number of glands are involved in the production of odorous substances in the bushpig.

Tusk gland (Plate 7c)

The large buccal pouch in the male bushpig was described by Marlow (1956) and the fact that the pouch is lined with sebaceous follicles was brought to light by Jones (1978). Externally the pouch appears as a large swelling on the cheek, extending from the edge of the upper lip behind the canine. The pouch opens around the base of the upper canine (Jones 1978). Fragments of bark and wood abraded off in the process of applying the gland to a tree accumulate in the pouch (Jones 1978). During tusk gland marking the tusks tend to score the tree, leaving scratch marks, together with traces of pouch debris. Microbial activity may be suspected where sebaceous glands occur in cavities and pouches (Albone *et al.* 1977) and Estes *et al.* (1982) deemed it likely that bacterial decay plays an important role in modifying and enhancing tusk gland odour.

The males of both warthog and the domestic pig have glands equivalent to the tusk gland of the bushpig (Estes *et al.* 1982)

Glands in the orbital region

Kingdon (1979) refers to secretions "dribbling from the forward corner of the eye" in bushpig. Milky exudates in the forward corner of the eyes were observed in both sexes on a few occasions during this study. Dark stains sometimes observed running down from the eyes were presumably associated with such exudates. Similar orbital secretions were noted for the giant forest hog (Dönhoff 1942) and the warthog, in the latter case taken as originating from Harderian glands. On inspection, large Harderian glands (with a wet mass of ca 40 g each)

were found behind the eyes in the bushpig. The species lacks preorbital glands, which are present in the giant forest hog (Ewer 1970, Beuerle 1975) and the warthog (Estes *et al.* 1982).

Glands along the nape

According to Ewer (1970) and Kingdon (1979) sebaceous secretions originate from a glandular area running down the midline of the neck in bushpigs. This could not be verified. Enlarged sebaceous glands on the back and sides of male domestic pigs produce a characteristic odour (Gosling 1985).

During rolling behaviour observed in the bushpig, the nape made prominent contact with the ground surface. Tusk gland marking was frequently followed by vigorous neck-rubbing against the trees, particularly with the area immediately behind the ears. The same marking behaviour was observed in the tame bushpig of Cumming (1975). Relatively unspecialized glands of the body surface may provide a source of signal odour (Gosling 1985) and vigorous body rubbing may be a means of depositing scent.

Digital glands (Plate 7a + b)

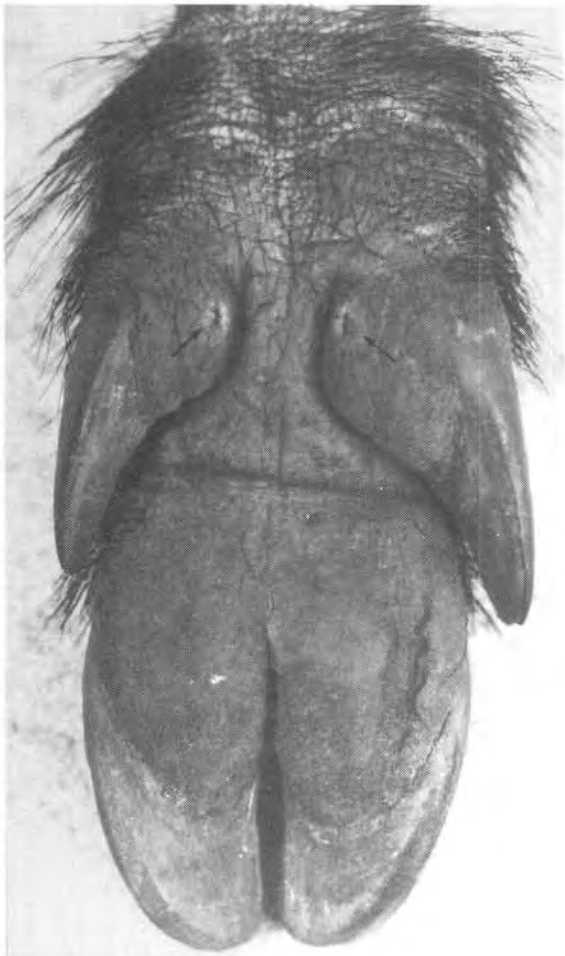
Digital glands in the bushpig were first recorded by Pocock (1916). A pair of these glands occurs on the forefoot, one of them opening upon the skin of the lower side of the second digit and the other in a corresponding position of the fifth digit. Each is visible externally as a small pore with a thickened circular rim. The sac of the gland, about 4 mm in diameter is filled with a white waxy secretion. By pressure the secretion may be squeezed from the orifice of the gland. The hind foot has two similar glands in corresponding positions and in addition, a third unpaired gland nearly resembling these, but opening in the centre of the sole of the foot (Plate 7b).

PLATE 7

- a. Front hoof: digital glands marked with arrows.
- b. Rear hoof: visible digital glands marked with arrows.
- c. Inner surface of tusk gland pouch, showing numerous individual glands.

PLATE 7

a



b



c

Digital glands occur in both males and females. They are not recorded for any of the other suid species, but may be functionally analogous to the carpal glands of the European wild boar.

Preputial glands

As with the other suid species, the male bushpig has a preputial gland which lies above the distal end of the penis. The median aperture opens in the dorsal wall of the prepuce.

(b) Scent marking

Marking in bushpigs primarily involves tusk gland marking by the male and ground scratch marking by both sexes. Tusk gland marking is performed by wiping the opening of the pouch gland on objects, usually up and down stems of smaller sized trees (Plate 8a). Ground scratch marking entails forcefully scratching the ground surface with the front feet, leaving clearly visible slashes on the ground (Plate 8b). Urination onto the marks occurs occasionally. In states of particular excitement, rolling in scratch marks occurs. It appears that during such rolling the nape and shoulder region form the central point of ground contact. Whether this is related to the assumed glandular area on the nape and dorsal crest line is unknown. The various components of scent marking are often performed in combination. They are intensive and more frequent in reaction to encounters with foreign individuals or scents. It is noteworthy that ground scratch marking outside the study enclosures only occurred when these were occupied. An agonistic context is inferred. For example, on 2/2/1986 a bushpig pair just outside enclosure B was observed performing the full complement of marking behaviours with an aggressively excited male TD7, jaw clamping and erectile dorsal crest, just inside the enclosure.

Tusk gland marking

Sus and *Potamochoerus* mark in much the same way (Beuerle 1975, Cumming 1975). The boars run the side of the mouth down a tree trunk, repeating the wiping movement with both sides of the muzzle on opposite sides of

PLATE 8

- a. Tusk gland marking on yellowwood tree.

- b. Bushpig scratch markings on forest floor.

- c. Alpha boar TD5 sniffing tree prior to tusk gland marking
(Enclosure A, Goudveld)

PLATE 8

a



b



c

the tree. During this process tusk marks are also inadvertently left on the trunk. Brushing up and down the tree sometimes also involves the orbital region of the forehead. It could not be verified whether the deposition of orbital gland secretions is involved, as surmised for European wild boar by Beuerle (1975). Ground scratch marking often occurs in a behavioural sequence with tusk gland marking.

Tusk gland marking was only observed on tree trunks. Trees selected for marking were associated with paths in most instances (as also found by Skinner *et al.* 1976). Not all trees along paths were marked, the ones selected tending to be conspicuous, jutting into the paths and of a convenient diameter. The minimum diameters appeared to be governed by the ability of the trunks to withstand the horizontal pressure applied during marking. Trees with diameters lower than 20 cm appear to be preferred for ease of marking on two sides during up and down brushing and possibly also because they have smoother bark types.

From observations in the study enclosure it is concluded that tusk gland marking is done largely, if not exclusively, by the dominant boar in the group (Plate 8c). Signs of marking normally reached up to about 85 - 95 cm above ground level. The contention that bushpig boars mark as high as possible in order to advertise size-related dominance status (Estes *et al.* 1982) was not verified. Cheating by marking whilst standing up on the hind legs would be conceivable if height of tusk gland marks was of importance.

Ground scratch marking

Both sexes perform ground scratch marking. It takes place mainly in perceived contact zones (intrusion zones). Radio tracked female CC9 ground scratch marked on all her patrolling bouts into the south-eastern corner of her territory. Males often ground scratch mark in association with tusk gland marking. It is incited in both sexes through contact with foreign individuals or scents (enclosure observations). For example, 49 ground scratch marks were counted along 140 metres of enclosure fence (17.5.1985). While patrolling along Slangpad slippath, female CC9 ground scratch marked 18 times over 750 meter, i.e. on average once every 42 meters.

Ground scratch marking leaves visually conspicuous scratches on the substrate. It is not clear whether the main purpose is to deposit digital gland secretions or to leave a visual signal. Whereas digital glands occur on both back and front feet, only ground scratch marking with the front feet was observed. Ground scratch marking may thus involve both olfactory and visual signals.

Reactions to foreign scent

In order to gain more insight into the functions of scent marking, reactions to introduced foreign scent material were observed in the study enclosure. Scent material from captured or culled animals was applied to tree trunks or to the ground at the feeding site and reactions were observed when the study animals came to feed. To facilitate observation, feeding took place after dark when the animals were more at ease. Artificial light did not seem to disturb them.

Results are presented in Table 5/1. From the limited number of observations only a few tentative conclusions are indicated:

- (I) Only males react to the tusk gland scent from foreign males. An overmarking reaction is largely confined to the alpha boar. Countermarking invariably occurred, except in the case of SH42 (9,1 years old), who may have been regarded as of superior dominance(?) Vigorous ground scratch marking and rolling was however incited.
- (II) The alpha female reacted to female digital gland material and "body odour" from the donor by ground scratch marking and searching for the intruder.

Digital gland material only elicited reaction when presented with the feet from which the digital gland sacs had been removed. Intruder search behaviour consisted of restlessly moving about the vicinity of the feeding place, in clear contrast to the normal behaviour in the absence of foreign scent.

- (III) Male marking behaviour was also observed in reaction to foreign female digital gland and body odours. Whether this was in direct

| TABLE 5/1: OBSERVATIONS ON REACTIONS TO FOREIGN SCENT MATERIAL (GOUDVELD STUDY ENCLOSURE) | |
|--|--|
| OBSERVATIONS | SOURCE AND TYPE OF SCENT MATERIAL: |
| 1. <u>26/3/1985</u> Prompt countermarking by alpha boar TD5 | CT4 (M:2,4) Tusk gland |
| 2. <u>10/4/1985</u> Overmarked by TD5(M); alpha TD2(F), TD1(M) and TD7(M) took no notice. | CI4 (M:1,5) Tusk gland |
| 3. <u>1/6/1985</u> All group members present. Sow and daughter sow smell digital gland material. After addition of feet from culled LK10: TD2(F): Vocal signals of disturbance; ground scratch marking and intruder search behaviour. TD5(M): Tusk gland and ground scratch marking. | LK10 (F:11,1) Digital gland |
| 4. <u>7/6/1985</u> TD5(M) Countermarked 4x TD1(M) Sniffing; imitation marking 2x TD2(F) Sniffing; slight orbital marking movements | CE6 (M:3,3) Tusk gland |
| 5. <u>9/6/1985</u> TD2(F) Disturbed; aggressive grunting; sniffing and intruder search behaviour (only feeding intermittently) TD5(M) Tusk gland marking (3x) and ground scratch marking alongside trees. Marking behaviour repeated at enclosure fence. | K15 (F:4,0) Digital gland |
| 6. <u>4/10/1985</u> The CI4 material elicits sniffing only, in contrast to the CC6-material: a) Repeated overmarking by TD5 (M) : to a lesser extent also TD1(M) Tusk gland marking was also extended to other non-scented trees. b) The tusk marking behaviour also involved eye sweeps and neck rubbing. c) Both TD5(M) and TD1(M) moved about; ground scratch marked and engaged in rolling. d) No marking reactions by TD2(F); yearling males and TD7(M): only sniffing. | CC6 (M:3,0) CI4 (M:2,0) Tusk gland |
| 7. <u>7/10/1985</u> a) Male yearlings, alpha TD2(F) and beta TD12(F): no reaction. b) Males TD5 and TD1 arrived late and reluctant. Acutely disturbed. No overmarking, but tree biting by both. c) Vigorous ground scratch marking and rolling by both. | SH42 (M:9,1) Tusk gland |
| 8. <u>8/10/1985</u> a) Digital gland material alone: no reaction. b) With feet added: some sniffing, no marking reaction. | SH42 (M:9,1) Digital gland |
| 9. <u>19/1/1986</u> a) Digital gland scent alone: only sniffing by TD2(F). b) After addition of feet: TD1(M) sniffed; TD2(F) concerned. Ground scratch marking (2x) by both. | EC22 (F:6,0) Digital gland |
| 10. <u>27/1/1986</u> a) Yearlings sniffing. b) TD1(M) elaborate sniffing; moves off. Then ground scratch marking and rolling in marks. | CC6 (M:30) Tusk gland |
| M: male; F: female; Figures in brackets: age in years | |

reaction to the foreign odours or aggressive excitement induced by female marking behaviour, is unclear.

- (IV) In general the presence of foreign individuals or odours resulted in excitement, which manifested itself in agonistic behaviour involving ground scratch marking and rolling as well as tusk gland marking by the dominant male.

(c) Deposition of faeces and urine

Urination did not show any clear patterns but seemed to occur more frequently at latrines, in wallows and occasionally also on ground scratch marks than elsewhere. The use of latrines by bushpigs has been reported by Breytenbach (1979), Kingdon (1979), Breytenbach and Skinner (1982) and Jones (1984). The role of faeces in communication remains unclear, but definite defecation patterns were also noted in this study. Not only did defecations tend to be concentrated in latrines, but these were sited according to specific patterns.

Latrines consist of scattered accumulations of faeces which appear to be used intermittently over long periods of time. Whether describable as a latrine or not, faeces accumulations are sited predominantly where the ground surface is clear of vegetation. Openings in the tree canopy also appear to influence site selection. Faeces accumulations are mainly found on bare stretches of paths and roads, as well as in canopy openings. They tend to be visually conspicuous, indicating a possible role in communication.

5.1.2.2 Auditory communication

Sounds made by the bushpig (Table 5/2) resemble the grunts, squeals, snarls and snorts recorded for other Suidae (Frädrieh 1974). The vocal repertoire presented in Table 5/2 is not considered complete. For one, no opportunity arose to record mating/courting calls, well-known in the European wild boar (Klingholz *et al.* 1979, Briedermann 1986).

| TABLE 5/2: TENTATIVE VOCAL REPERTOIRE FOR BUSHPIGS | | |
|--|--|---|
| FUNCTIONAL CALL TYPE | DESCRIPTION | CONTEXT |
| CONTACT | <ol style="list-style-type: none"> 1. Irregularly repeated soft, short contented-sounding grunts, with interspersed occasional "squeak" sounds. 2. Rhythmic, low-pitched, more accentuated, short grunts. 3. Single to few, common short grunts. | <p>Group contact</p> <p>Mother-young contact</p> <p>Recognition, "greeting"</p> |
| WARNING | <ol style="list-style-type: none"> 1. Suppressed, drawn-out, soft "oomph" ("Blasen"). 2. Deep, throaty, low-pitched "oomph" ("Blasen"). 3. Deep, low-pitched snarl-grunt. 4. Hoarse, throat-snort. | <p>Suspicion</p> <p>Warning</p> <p>Acute warning</p> |
| ALARM | <ol style="list-style-type: none"> 1. Short, intense snort. 2. Abrupt grunt-snort. 3. Grunt-bark. | <p>Alarm</p> <p>Alarm</p> <p>Startled</p> |
| AGGRESSION and THREAT | <ol style="list-style-type: none"> 1. Abrupt sneeze-grunt. 2. Hoarse, explosive bark-grunt. 3. Drawn-out growl-grunt. 4. Sharp, coarse, loud growl-grunt. | <p>Anger or impatience</p> <p>Calling juveniles to order</p> <p>Acute aggression: e.g. charging</p> |
| DISTRESS | <ol style="list-style-type: none"> 1. Repeated, drawn-out squeal-growls. 2. Short, high-pitched squeal. 3. Drawn-out, repetitive whining squeal. 4. Discontented, grumbling (squabbling) squeal-grunt. 5. Drawn-out complaining squeal. | <p>Cornered</p> <p>Fear/pain</p> <p>Heat stress</p> <p>When displaced at feeding site</p> |
| GROUP CONCERN | Concerted, repetitive intense-excited contact grunting | Group reaction to juveniles squealing in distress |

The calls listed tended to form a continuum, none being specific to one situation, although some were more characteristic of particular situations (cf Wood-Gush 1983). Transient forms of the vocalizations may occur according to varying motivational states of the animals. This is in agreement with Klingholz and Meynhardt (1979), who found that the calls of pigs in general are not discrete signals, but rather form a continuum with components which may have highly specific structural and functional properties.

The most common vocalization by bushpigs is undoubtedly contact grunting. The call is a relatively soft, monosyllabic grunt ("Presslaut"); these are occasionally interspersed with more penetrating squeaks which are presumably nothing else but high-pitched contact grunts. Contact grunting is typical when the group forages along in extended, loose formation. It is made by all members and presumably functions to inform one another of position in order to maintain contact. Group contact is easily lost since members may be spread out over 100 m² or more and move at varying rates, depending on individual food search success. Grunting frequency increases with rate of movement and ceases when the group is stationary while feeding. When foraging at normal rates, a contact grunt may be emitted every 5 - 10 seconds (cf Breytenbach 1977). Relatively little contact grunting occurs before the onset of darkness.

European wild boar similarly emit contact grunts, repeated at intervals modified by the rate of movement (Klingholz *et al.* 1979, Briedermann 1986). They are also particularly prevalent during the hours of darkness as well as in dense cover (Hennig 1981, cf Wood-Gush 1983, Briedermann 1986). The noises associated with foraging, like chewing and breaking, are presumably also involved in the maintenance of group cohesion (Briedermann 1986). Whether contact grunts function in individual recognition, as in the case of the European wild boar (Klingholz *et al.* 1979), could not be determined for the bushpig.

5.1.2.3 Visual communication

Evidence for a visual element in communication was found in scent marking and male dominance displays. The deposition of ground scratch marks and faeces in visually conspicuous places, usually with good

background colour contrast, strongly suggests a visual element in these behavioural patterns (5.1.2.1).

The bushpig is characterized by dorsal and facial coat colour patterns. The white forehead and cheek beard, and darker ears with tassels are conspicuous (Plate 2). The forehead in males is distinctly whiter than in females. Snout knobs, tusk gland pouches, gonial and malar protuberances are facial structures confined to the male. They may all add to the total effect during frontal or latero-frontal dominance displays.

In congruence with their display function, the snout knobs have a tendency to be allometric to body size (partial correlation: 0,629) and, more important, continue to grow with age (partial correlation: 0,582). This was determined by multiple regression analysis of 39 data sets involving a maxillary flange index (MFI) and the two variables mandibular length (ML) and age (A). The maxillary flange index acted as an index of snout knob dimensions and was determined by the sum of maxillary flange height and dorsal length (cf Seydack 1983). Mandibular length was taken as an index of skeletal size.

$$\text{MFI (cm)} = -114,09 + 1,677 \text{ A(yrs)} + 0,801 \text{ ML (mm)}$$

Both variables were statistically highly significant ($P < 0,001$).

5.1.3 Discussion

5.1.3.1 Patterns in olfactory communication

The widespread occurrence of scent glands in mammals and their significance in chemical communication have been highlighted in various review papers: Ralls (1971), Eisenberg and Kleiman (1972), Johnson (1973), Mykytowycz (1974), Brown (1979), Stoddart (1980), Gosling (1985) and MacDonald (1985). Most mammals apparently have a highly developed olfactory sense which they employ in social communication. Many use specialized motor patterns to deposit the chemical signals on objects or other animals of the same species. Such behaviour is referred to as scent marking or marking (Ralls 1971).

The deposition of odoriferous gland secretions, urine or faeces to form a scent mark, is a part of an animal's system of olfactory communication. It is distinct from the release of pheromones, i.e. the release of volatile scents directly from an animal. Both are part of the olfactory system of communication (Johnson 1973). Odours can be produced directly by glands or indirectly by urine constituents, dietary products or bacterial fermentation (Müller-Schwarze 1983). Often glandular secretions take on a characteristic odour only after being metabolized by bacteria that colonize the skin and glandular pouches (Albone *et al.* 1977). Thus, a distinctive odour may be caused by a combination of three factors: the internal metabolism and hormonal state, the chemistry of the scent gland and the action of external micro-organisms (Brown 1979).

The Suidae are endowed with a remarkable variety of scent glands (Mohr 1960, Schaffer 1940 ex Estes, Cumming and Hearn 1982). As exemplified by the European wild boar, olfaction is well developed in suids. This is advantageous in thick vegetation and during nocturnal activity (Briedermann 1986). Referring to *Tapirus*, Moehlman (1985) remarked that the accumulation of odour through urination, defecation and wallowing may be important for species typically inhabiting dense vegetation and which generally occur in low numbers.

During the rutting season, European wild boar males perform salivary marking through the application of salivary foam onto saplings, twigs or the apices of small trees (Beuerle 1975). Such salivary marking is often part of a behavioural sequence with spurt urination, ground pawing ("Stemmscharren") and "yawning". It is not known whether scent material from the carpal gland is deposited during ground pawing. Ground pawing is only recorded for male wild boar. It is performed in a stationary position, with the hind feet firmly pressed into the substrate. The front legs are shifted forward in small alternate steps, resulting in the front part of the body being lowered, with the dorsal crest line sloping downwards and the head lowered with the snout virtually touching the ground. In this position pressing movements are carried out with alternating feet (Beuerle 1975). Ground pawing in European wild boar typically occurs during marking at the feeding site, olfactory inspection of female spoor, prior to aggressive encounters and courting of

females (Beuerle 1975). Tusk gland marking in bushpig males may be considered equivalent to salivary marking in European wild boar, and ground scratch marking to ground pawing. However, the latter is also performed by bushpig females and male bushpig marking is apparently not as seasonally concentrated as in the European wild boar.

In canids, scent from interdigital glands may be deposited by ground scratch marking (Bekoff 1979). A visual component is also implicated: (I) visual scratches on the substrate may convey some message and (II) the act of ground scratching might serve as a visual display to other individuals, who see it performed. Thus, Bekoff (1979) concluded that ground scratching should be viewed as a composite signal, combining chemical and visual components. Radke and Niemitz (1989) presented a similar interpretation of scratch marking and ground pawing sequences in the warthog. It has also been suggested that secretion from the pedal glands in ungulates is transmitted to the substrate during pawing, that is drawing the forefeet backwards in contact with the ground. This interpretation is only possible for glands in the forefeet, since artiodactyls never paw with the hind feet, even though glands of hind feet are common (Gosling 1985). Also in the bushpig, digital glands are found on both front and hind feet, although ground scratch movements are only performed with the front feet. For the European wild boar, Briedermann (1986) suggested that carpal gland secretions result in an olfactory trail during movement. The same may be true of digital gland secretions in the bushpig. However, the continual release of digital gland material in order to create a "trail" is unlikely and difficult to reconcile with antipredator considerations. Rather it is conceivable and postulated here that digital gland scent material is expelled and thus deposited through the muscular tension arising from forefoot pawing. This requires a firm stance, so that and muscular tension is also applied to the hind feet, facilitating expulsion of digital gland material. Ground scratch marking in the bushpig is thus tentatively considered to involve the deposition of digital gland material and the creation of a visual mark. Whether the ground scratch mark constitutes a visual mark in its own right or merely serves to advertise digital gland material or urine deposition, remains to be determined. An additional possibility is that scratching up of earth may also attract

an animal's attention through the smell of fresh earth itself (cf Eisenberg and Kleiman 1972).

Faeces and urine are rarely used to mark objects in the artiodactyla, but faeces may be deposited conspicuously in dung piles, or merely faeces concentrations which have both visual and olfactory significance (Gosling 1985). Regularly used defecation sites have been reported for the giant forest hog (Kingdon 1979) and bushpig (Kingdon 1979, this study). Although Frädrieh (1965) and Cumming (1975) observed warthog using particular spots for defecation, Bradley (1968), Cumming (1975) and Mason (1982) found no clear evidence of warthog marking by means of faeces. Urine may also have some signal value, in addition to the specialized additions of preputial glands (Gosling 1985). From the results obtained in experiment by Meese *et al.* (1975) it became clear that domestic pigs can be taught to distinguish between the odours of urine from different animals, thereby providing evidence for the potential transmission of social information via odour (Meese *et al.* 1975).

Some artiodactyl species lie or roll in faeces and urine. The same effect, presumably self-marking (cf Gosling 1985) may be achieved through wallowing. Communal wallowing, as in pigs, might have group marking functions. Group scents could also be obtained by sequential object marking, by lying on a substrate impregnated with secretions, faeces or urine or simply by resting in body contact (Gosling 1985). Sebaceous glands on the general body surface presumably contribute to individual odour in pigs (cf Briedermann 1986). Bushpigs have not been observed to roll in faeces, but they urinate into wallows. Family group odour may be maintained by communal resting and wallowing, as also suggested for the European wild boar by Briedermann (1986). Neck rubbing in sequence with tusk gland marking and rolling in conjunction with ground scratch marking observed in male bushpigs may similarly play a role in odour exchange.

The association of high rates of marking with dominance is a widespread phenomenon in mammals (Ralls 1971, Drickamer *et al.* 1973, Wells and Bekoff 1981, Macdonald 1985). No such correlation was observed in the warthog, however (Radke and Niemitz 1989). In territorial species,

dominance implies territorial ownership and for many taxa also established pair bonding. For example, marking by solitary canids is rare or absent (Rothman and Mech 1979, Barrette and Messier 1980, Wells and Bekoff 1981, Macdonald 1985). Double-marking is common-place, generally involving the alpha male overmarking the urine of the alpha female (MacDonald 1985). In the bushpig marking is also performed mainly by dominant individuals (5.1.2.1). Dominance is associated with territorial ownership and established pair bond. Both pair members usually mark, thereby indicating their paired, territorial status to foreign intruders.

A widespread mammalian trend is that marking is more frequent during and after encounters with individuals with which they do not normally associate, i.e. in a context of intolerance (Ralls 1971, Stoddart 1980). This was likewise observed in the bushpig (5.1.2.1, Table 5/1). For the warthog, Cumming (1975) found that scent-marking was often associated with agonistic encounters and he noticed scent marking behaviour in tame individuals from the age of 6 - 7 months.

Marks and time available for marking are limited resources. Marking should therefore be done economically. This implies placing marks where the chance of intrusion or encounter is high and avoiding areas where these are unlikely. It further implies placing marks on conspicuous spots or advertising their presence (Gosling 1982). Mammalian scent marks are universally made as obvious as possible by being deposited high up on a structure (e.g. tree trunk), or by being placed close to an obvious landmark, or by being made to contrast startlingly with the environment (Stoddart 1980). Placing a scent mark as high as possible above the ground presumably enhances the "active space" of the point source of the scent (Wemmer *op cit.* Eisenberg and Kleiman 1972). This explanation for the tusk gland marks of bushpig being made as high as possible is favoured, rather than that size is advertised in this way, as suggested by Estes, Cumming and Hearn (1982).

Marks are thus placed in a way which increases the likelihood of attracting the attention of the desired recipient of the message. In closed habitats, intruders are more restricted to trails and marks occur at high densities along trails (Gosling 1982, 1985). In the bushpig,

this seems valid for tusk gland and ground scratch marks, as well as the deposition of faeces. Bushpig faeces are deposited at visually conspicuous sites or where they are otherwise likely to attract attention, e.g. on paths and bare ground in canopy gaps. On paths, faeces concentrations are predominantly on parts devoid of ground vegetation and where there is a clear colour contrast between the dark faeces and the substrate, e.g. lighter soil surface or light brown dry leaf litter. The siting of latrines is often on roads or in canopy gaps. This is similar to the pattern found in other animal species: civets (Von Saldern *et al.* 1987); European badgers (Kruuk 1978); and in many canid species (Macdonald 1985). Bushpigs studied in the St. Lucia lakes area (Zululand) used ecotonal areas as latrine sites (Breytenbach 1979, Breytenbach and Skinner 1982). Bushpig latrines in the Matopos (Zimbabwe) were associated with game paths (Jones 1984). The giant forest hog is also reported to prefer conspicuous defecation sites; e.g. in the bare earth of the hole caused by a treefall (Dönhoff 1942).

5.1.3.2 Functional interpretation of marking behaviour

Four main functional categories of chemical communication may be recognized: identification, breeding and rearing facilitation, antipredator behaviour and social status (after Eisenberg and Kleiman 1972, Mykityowycz 1977, Müller-Schwarze 1983, Macdonald 1985).

(a) Identification

Odours may signal presence and provide specific information on individual, species, racial and sexual identity. Individual recognition by odour has been demonstrated in virtually all species that have been investigated (Müller-Schwarze 1983). Chemical signals have the important characteristic of also functioning in the dark (Geist 1978a).

(b) Breeding and rearing facilitation

Odours commonly provide information on reproductive status, play a role in reproductive synchrony and promote mother-young cohesion (e.g. Müller-Schwarze 1983). In many mammals the urine odours of females in

oestrus act as attractants to males and advertise the state of oestrus (Stoddart 1980). Frädrich (1965) and Bradley (1968) have reported on mature male warthogs smelling the urine of mature females. Male warthogs were noted to urinate onto spots where females had urinated (Mason 1982). Lordosis in the female may be elicited by male pig saliva from the submandibular salivary gland. The lordosis response is also elicited by a mixture of boar urine and preputial gland fluid (Melrose *et al.* 1971 *ex* Gosling 1985) or by the preputial fluid alone (Signoret 1970 *ex* Gosling 1985), none of which contain the steroids found in the salivary glands. No information was obtained on the role of odours in bushpig reproduction during this study.

(c) Antipredator behaviour

Scent may function as an alarm signal by the transmission of volatile components, without scent marking *per se* being involved (Johnson 1973). There is an abundance of evidence implicating olfaction in the transmission of alarm within the vertebrates, but the involvement may only be secondary to an alarm posture, visual signal or cry (Stoddart 1980). When a male black-tailed deer (*Odocoileus hemionus columbianus*) is chased by a dog or a human, it releases an odour from the metatarsal gland on the outside of its hind leg (Müller-Schwarze 1971 *ex* Claus 1979). An alarm odour may possibly also function as a decoy for a predator (Müller-Schwarze 1983). According to various bushpig hunters, an alarm or fear scent is apparently emitted by bushpigs during close encounters with pursuing dogs. In association with the cryptic coloration and freezing posture of bushpig juveniles, such an "alarm" scent, emitted by adults, may function to confuse predators and lower the likelihood of them finding the juveniles.

(d) Social status

Priority access to resources is regulated via the social hierarchy. The dominance status within any particular social hierarchy may either be spatially related (territoriality) or based on absolute rank. Information exchange or territorial ownership or resource holding potential (RHP) among the individuals of a population is crucial to the functioning of a dominance hierarchy, i.e. the partitioning of resources with a

minimum of escalated aggression. Odour is generally considered to be one of the possible information vectors in this context (cf Mykytowicz 1977, Brown 1979, Jannett 1984, Gegory and Cameron 1989).

Many territorial mammals put much effort into marking their territories with odorous substances. An intruder entering the territory may thus quickly perceive that the area is already occupied. The intruding individual can identify the resident as such if the smell of the latter corresponds to that of the environment. Any dispute may then be settled based on an asymmetry between the two contestants in the gain to be expected from escalating the fight (Gorman 1984). For this mechanism to operate it is imperative that the intruder recognizes the territory holder as such. This demands that scent marks should be dispersed in the territory in such a way that an intruding individual will quickly encounter the marks and realize that the range is already occupied. It also demands that a scent mark should contain information on the individual identity of the animal leaving the mark (Gorman 1984). According to the "scent-matching" hypothesis formulated by Gosling (1982, 1985), the function of territory marking is to provide an olfactory association between the resident and the defended area which allows intruders to identify the resident when they meet and thus reduce the frequency of fighting.

Marks are accordingly considered to provide a way for an intruder to assess the quality of a potential competitor, the resident. An intruding individual is expected to withdraw in most cases, based on the contention that an animal that can defend an area long enough to mark it comprehensively is likely to win most encounters because of its physical quality. It will thus pay low status intruders to withdraw from encounters with an identified resident. Only a minority of high status intruders might chose to escalate an encounter with a resident in an attempt to displace it. Under the scent-matching hypothesis the following predictions may be formulated (Gosling 1985). They are in general agreement with observed mammalian scent marking behaviour.

- (I) The owner should mark the territory in a way that maximizes the chance that marks will be detected by an intruder.

- (II) The owner should mark itself with the substances used to mark the territory (e.g. urine or faeces), except when the odour is available to an intruder at its site of production (e.g. from scent glands).
- (III) The owner should make itself available for scent-matching by the intruder.
- (IV) The owner should remove or replace marks in the territory that do not match its own odour.

Bushpig marking behaviour, particularly that of the male, corresponds with these predictions.

Territoriality in ungulates functions as a system of male breeding competition (Leuthold 1977). Within this context two crucial components of the scent-matching hypothesis, namely identification of the resident and territory ownership as an indication of resource holding potential, makes good sense. However, it is argued here that the hypothesis is less appropriate for resource territoriality, where an indication of spatial occupancy is important as such and usually results in avoidance of the occupied area by non-residents. Marking then functions to facilitate the avoidance of occupied territory and thereby minimizes the chances for risky encounters. This is the sense in which scent-marking functions from the perspective of the bushpig female as the central figure in bushpig resource territoriality. Scent-marking in this form of territorial rivalry may be viewed as constituting an important signal in a game where an intruder has to consider the costs and benefits of trespassing (cf Dawkins and Krebs 1978). The response of an intruder to a scent mark then depends on the risk of injury if a direct encounter occurs. For animals ranging over large areas and living at relatively low densities, the frequency of encounters is probably quite low (cf Messier and Barrette 1982 in respect of wolves and coyotes). Territorial animals under these conditions must demonstrate a high degree of aggressiveness during encounters, thereby maintaining a high risk of injury for a trespasser and enforcing obedience to scent marks (e.g. many incidences of fatal encounters, particularly between bushpig females). Neighbouring residents presumably rarely meet and scent marking may communicate continued occupancy. Failure to replenish these

marks may prompt intrusions. There is evidence that territorial coyotes, foxes and tigers quickly respond to changes in the ranging behaviour of neighbours and expand into vacated areas (Gosling 1985). The same was observed in the case of bushpigs (4.3.2) and scent-marking may also function in confirming the status quo between neighbours.

As in the case of territoriality, dominant males should make their odour available for matching and this may explain the high frequency of marking during agonistic encounters (Gosling 1985). In the case of the European wild boar, Beuerle (1975) believes that the outcome of agonistic encounters is often determined through individual odour control of opponents. For bushpig males it is suggested that tusk gland marking conveys information on the social status of the donor. Whether the role of olfactory status advertisement is linked to the identification of the scent donor as the pair-bonded territory occupant or on advertisement of absolute status via an associated odour quality, cannot as yet be assessed. Rank indication based on the height of scent mark application above ground level, thereby presumably advertising size, as suggested by Estes *et al.* (1982) is however deemed unlikely (5.1.2.1b).

5.1.3.3 Auditory communication in suids

The vocal repertoire of European wild boar (cf Klingholz *et al.* 1979, Hennig 1981) and bushpig are very similar. Generally, mammals occupying habitats rich in cover and exhibiting nocturnal activity tend to have well-developed acoustic communication systems. This is exemplified by the domestic pig, corresponding to the forest habitat of the ancestral pig (Wood-Gush 1983), the European wild boar (Briedermann 1986) and the bushpig. The extensive vocal repertoire of the collared peccary *Dicotyles tajacu* also indicates that auditory communication is important and Bissonette (1976) suggests that the rich repertoire of sounds used by tayassuids probably evolved as the most appropriate method of communication in the densely vegetated habitats which they inhabit, or at least evolved in.

A range of vocalizations used by warthogs in the context of courtship, alarm, aggression and other contexts have been described by Cumming (1975). Mason (1982) found the most commonly heard vocalizations to be

alarm grunts, the rhythmic "chugging" grunting during courtship and squeaks and "chirring" of very young warthogs. Most of the vocalizations are similar to those of the other suids, with contact grunting notably absent or rare. Warthog are apparently seldom heard in the field (Cumming 1975) and were found to be generally less vocal than other suids (Frädrich 1965). This is presumably linked to the more open habitat this species occupies, where visual communication is of relatively greater importance.

The vocalizations of pigs have been well described by Grauvogel (1958) and Kiley (1972) while other authors have made detailed studies of those of piglets (*op. cit.* Walser 1986). Opinions appear to differ as to whether pigs convey specific messages to other individuals in specific situations (Grauvogel 1958) or whether their vocalizations indicate a change in general motivation (Kiley 1972). These two interpretations are not necessarily mutually exclusive, however. Acoustic signals in the European wild boar were used in combination with other channels of communication (sight, smell). This is in accordance with mammalian auditory communication system patterns in general. Most vocal signals operate in combination with other modalities or contextual cues and are graded in relation to motivational state (Gould 1983). This may explain the lack of prompt or consistent reaction to seemingly similar vocal signals which was observed in the bushpig at times.

5.1.3.4 Visual communication

Although olfactory and auditory communication are particularly well developed in suids, sight is not altogether unimportant. The visual apparatus of pigs is unspecialized (Briedermann 1986); excepting the warthog, with its special adaptations for vigilance in an open environment (3.3.1).

Display behaviour is reported for all the better studied suid species (cf Kingdon 1979, Briedermann 1986). According to Geist (1978a) displays may be defined as abstract signals recognizable by various criteria. These include apparent enlargement of the body or weapon size, orientation towards conspecifics, the use of attention-guiding organs and optical illusions and an indirect approach, probably designed

to generate arousal by robbing the opponent of predictability. Sensory stimulation is normally maximized during dominance displays by filling all channels of communication, i.e. visual, auditory, olfactory and even tactile (Geist 1978a).

The emphasis in the European wild boar is on broadside display where contour enlargement through pilo-erection of the dorsal mane and contour accentuation through darkened dorsal mane, ears and the upper forelegs are employed (Briedermann 1986). In accordance with the more latero-frontal display of bushpigs we find an increasing cephalization of display features in males. These include snout knobs, tusk gland pouches, gonial and malar protuberances, a strikingly white forehead, cheek beards and ear tassels. The latter two are also found in females. In addition, the dorsal mane and tail are likely to play a part in maximizing display effect. Colour contrast patterns are most developed in the western bushpig races (3.2.2). Frädrich (1968) has described their display postures. The back is arched in a way which enhances the visual effect of the white dorsal hairline, while at the same time, the head is turned towards the conspecific and the long pointed and tasseled ears are held horizontally in lateral extension.

Although the snout knobs in males may somehow be involved in fighting, they are believed to be primarily display organs. That they are not indispensable for fighting is shown by the fact that females, who lack them, seem to fight more frequently than males. The white forehead in males forms a striking contrast with the dark tusk gland pouches and the latero-frontal display posture seems to enhance the assessment of snout knob size by creating an appropriate silhouette (Plates 2 and 8c).

Snout knob dimensions scale to size and age (5.1.2.3) and may thus, just as horn size gradients (cf Geist 1966), function as rank indicators which parallel fighting potential. Male snout knobs are accordingly taken to function as indicators of dominance, i.e. their sizes convey information upon which strange conspecifics may base appropriate behavioural reactions. According to Geist (1966) rank indicators probably allow the existence of "open" societies where strange

conspecifics can integrate with a minimum of combat, damage and energy loss. Bushpig male-male associations (4.3.1; 4.4.3.5) may similarly be facilitated by the postulated rank indication system of male snout knobs.

5.2 Agonistic behaviour

5.2.1 Introduction and methods

Dominance may be characterized as an attribute that provides its holder with access to certain resources in precedence over other individuals, without actual contest. Dominance hierarchies thus generate predictability in competitive social interactions, allowing individuals to behave appropriately in terms of maximizing their reproductive fitness (Geist 1978a). To maximize its reproductive fitness an individual must obtain all the scarce resources essential for reproduction. Such resources of necessity being limiting resources, competition can be defined as a process in which an individual uses all means to his disposal to obtain more than an equal or proportional share of the relevant resources. Agonistic behaviour may now be defined as the behaviour associated with active competition, i.e. aggression in its widest sense, including combat, threat, dominance displays and the strategies of their application, as well as submission and appeasement behaviour (Geist 1978a).

In this section systematic, as well as casual, but mainly qualitative observations are presented and tentatively interpreted. The bulk of the information on agonistic behaviour resulted from formal observations in the study enclosure (5.3.1.2) and from experimental introductions of non-resident bushpigs into the enclosure.

5.2.2 Results

5.2.2.1 Dominance interactions

A variety of behaviour patterns were observed in the bushpig during threat and dispute, mainly at the feeding site in the study enclosure.

They closely resemble those reported for the European wild boar (Frädrieh 1965, Beuerle 1975).

- (a) Threat gestures. The slight, almost inconspicuous movement of the head by a dominant individual was often enough to keep others out of particular zones at the feeding site. A fully developed threat gesture, as observed only once with alpha boar TD5, consisted of the head held high, with the mouth partly open. Other, more determined expressions of threat include jaw champing, rushing forward and pawing the ground with the front feet.
- (b) Snout thrusting. The general method of suids to keep competitors away from food is the snout thrust, a vigorous upward swipe of the head in the direction of the antagonist. This entails a directional movement of the snout from below upwards, seldom making contact with the other animal. The intensity of this behaviour may be variable, from weak threat intention to contact, where the snout is pushed under the body of the antagonist with vigorous shovelling-like movements, pushing it away or even overthrowing it. Snout thrusting may also take the form of sideways snout butting. It is then more an aggressive form of making place, rather than a threat.
- (c) Pushing aside. Performed mainly by subdominants or younger individuals, also towards adults. It involves pushing or wedging in between others which are orientated in parallel. Sideways pressure is applied with the flanks and rear end of the body.
- (d) Squabbling. This behaviour, also termed mouth-mouth wrangling, may be described as mutual threatening during which two animals, their heads placed side by side, take inhibited bites at each others snouts. This is accompanied by pushing and wrestling with the snouts, with some suppressed vocalizations. Such squabbles arise suddenly and are of short duration. Squabbling in a similar fashion was also described for the collared peccary, *Dicotyles tajacu* (Schweinsburg and Sows 1972, Bissonette 1976).
- (e) Snap biting. Occasionally snap bite movements are directed at group members e.g. when two animals approached the same food item.

Snap biting is not directed at any specific part of the antagonists body and actual contact seldom occurs.

- (f) Chasing-off. Dominant animals were observed to chase off group members of lower rank subsequent to snout thrusts or by suddenly rushing towards them. Such chases were usually observed at feeding sites and took place over variable distances, but were mainly over short distances only (short run-up chases). In most cases the chased animal came back soon afterwards, without necessarily being immediately chased again.

In reaction to or in anticipation of threat, submissive or appeasement behaviour occurred. The typical submissive posture of artiodactyls is a lowered, outstretched head and neck (Ewer 1968). That of suids (Cumming 1975 for warthog, this study for the bushpig) is essentially similar and varies from a lowering of the head to the final submissive gesture of ducking and fleeing. Ducking or dodging is sometimes accompanied by a submissive squeal. The following submissive behaviour patterns were observed in the bushpig:

- (a) Nose down, head low, turned away. In this pattern, the nose and head are lowered while at the same time the nose is turned away from the aggressive animal. This was a common response in submissive encounters.
- (b) Back up. Submissive animals sometimes retreated from a threat by taking a few steps backwards, whilst staying orientated towards the dominant animal.
- (c) Sink back, crouching down. Here the submissive animal rocked back, while keeping all four feet firmly on the ground. With increasing submissiveness of the response, the sink back became a crouch. The animal crouched back and down until the belly touched the ground. The nose was lowered further and the head turned away. Lying down on the stomach with the nose stretched out and the chin placed on the ground was the culmination of the sequence in response to a very strong threat. Vocalizations sometimes occurred. Crouching down was usually alternated by dodging and fleeing when under acute threat, as on approach in the capture corral.

(d) Lying down. As an anticipatory appeasement posture, subadults were often found feeding at the feeding site in a lying down position. Lying down in submission has been found in collared peccary, warthogs and bushpigs (Martys 1985). Ewer (1968) considered evidence to support the view that appeasement postures in mammals are derived from intention lying down. Our observations, and those on warthog by Cumming (1975), support Ewer's (1968) view that submissive postures in the artiodactyls may be intention movements of lying down.

At feeding sites in the study enclosure all group members usually fed peacefully close together. On 14 occasions, snout butting and chase-offs, generally directed at subordinates, were observed (Table 5/3).

| TABLE 5/3: DOMINANCE INTERACTION AT FEEDING SITES (GOUDVELD STUDY ENCLOSURE) | | | | | | | |
|--|-----------|-----------|------------------------|-----|-----|-----|-------|
| FREQUENCIES OF UNIDIRECTIONAL INTERACTION EVENTS | | | | | | | |
| RECIPIENTS | AGE (yrs) | MASS (kg) | INITIATING INDIVIDUALS | | | | TOTAL |
| | | | TD5 | TD2 | TD1 | TD7 | |
| TD5 (M) | 12 | 70 | - | | | | 0 |
| TD2 (F) | 5 | 80 | 4 | - | 2 | 2 | 8 |
| TD1 (M) | 5 | 83 | 4 | 3 | - | | 7 |
| TD7 (M) | 4 | 73 | 3 | 14 | 5 | - | 22 |
| YEARLINGS | 1-2 | 30-60 | 4 | 24 | 3 | 3 | 34 |
| TOTAL | | | 15 | 41 | 10 | 5 | 71 |

- (I) The interactions recorded in Table 5/3 normally took the form of chasing the opponent away for a few paces and were initiated by butting, snout thrusts and sudden rushing towards the recipient of the aggression. In most cases the chased animal returned promptly and continued with feeding. However, sometimes certain subordinates did not return and waited at a distance. Juveniles were always tolerated, but had disputes among themselves.
- (II) Chases are interpreted as dominance status reinforcements and not as attempts to prevent subordinates from feeding. The rank relationship between the alpha female (TD2) and her brother, the beta male TD1, was not entirely clear. TD2(F) was clearly

dominant over the younger male TD7. The latter only drove off the former twice when it was returned to the enclosure after having been starved for some days.

- (III) In some species, dominance relationships tend to be unidirectional, i.e. the submissive animal does not retaliate or challenge the clearly dominant one. In other species, such as the domestic pig, the relationships are reported to be bidirectional, i.e. the relatively subordinate animal may retaliate (Beilharz and Cox 1967). Contrasting the incidences recorded in Table 5/3, cases of "challenging" the higher ranking or retaliation were only rarely observed (TD1 + TD2 versus TD5; TD7 versus TD1; yearling versus TD1). During most of such cases the higher ranking animal did not react to the "challenge", but sometimes vigorous counteraction followed (e.g. TD1 challenged TD5 at the feeding site with snout butting. TD5 retaliated and drove TD1 away).
- (IV) "Chain reactions" were observed twice; e.g. in reaction to being chased by TD5, TD2 chased TD7.
- (V) The limited evidence presented in Table 5/3 is suggestive of a system of age-graded intragroup dominance ranking, at least among males. Judging from the much higher incidence of aggression of the female TD2 towards subordinates and particularly yearlings, it is presumed that the female acts as the primary force in expelling subordinate members from the group.

Adult female bushpigs drove off or threatened human onlookers through mock charges, consisting of a short rush towards them (compare Cumming 1975 and Hennig 1981 for similar mock charges in warthog and European wild boar respectively). Male bushpigs did not undertake mock charges, but TD5 (M) once charged human observers from ca 20 metres away, with fully opened gape. The charge was carried through right into the enclosure fence, unlike the mock charges of females.

5.2.2.2 Display and fighting behaviour

Displays as distinct from threat postures (cf Walther 1958, 1974; Geist 1978a), occur comparatively rarely in suids (cf Martys 1985).

Opportunities to observe suid display behaviour therefore are inherently limited. Only very rudimentary and transient display behaviour was observed during this study, but the limited observations conform to descriptions of bushpig display behaviour in the literature (Attwell and Bearder 1976; Skinner, Breytenbach and Maberly 1976).

Skinner, Breytenbach and Maberly (1976) give an account of display contests between two bushpig boars:

"During the challenge they advance rather cautiously towards one another with white and black shoulder bristles raised high. This is accompanied by a series of little runs or quick steps, while lashing their tails from side to side and slashing their short formidable canines. In turn, they paw the ground savagely, sending clods of earth and fragments of grass flying in all directions. Finally they lie down roll over and over in the grass and dusty ground before leaping up once more to advance on one another again. Opponents always face one another. As one makes a little charge, the other retreats a pace or two and presently the situation is reversed, they sometimes circle one around and always at a trot. This manoeuvring may cover an expanse of ground while the contest continues. However, slowly one boar begins to lose confidence, his advances becoming more cautious and he retires more frequently. Concomitantly encouraged by this change, his rival increases the aggressive vigour of his attacks until his opponent turns and bolts with the dominant boar in hot pursuit."

Display contests are apparently confined to males and presumably function in the mutual evaluation of the opponent's resource holding potential. Actual fighting is accordingly rare in male bushpigs since one of the contestants tends to lose confidence during the ritualized display preceding potential clash situations (cf Kingdon 1979).

Characteristic of the display stance of male bushpig is the erected dorsal mane, the latero-frontal posture, i.e. the body is parallel to the opponent and the head directed towards him, and the ears held in sideways extension. These features of the display posture clearly facilitate the demonstration of body surface and the conspicuously marked head (cf Frädriich 1967). As in some other suid species, the

cephalization of display organs is marked in the bushpig. The head is clearly marked and set off against the body. Some subspecies have a black mask-like face contrasting with the bright red body and others have a white forehead contrasting with the darker body (5.1.2.3). The lack of display behaviour in the female bushpig corresponds to the absence of display structures and pronounced facial colour patternings.

Fighting was only observed between juveniles and between adult females. The juvenile play fighting between TE1 (M) and TE2 (M) was reminiscent of adult fighting as described (Frädrich 1965, Cumming 1975) and observed. The contestants faced each other, with crest hairs erect and snouts crossed. Following a sudden disengagement, they charged at each other, the point of contact being the region of the male protuberances. After moments of snout pushing, charging was repeated or alternatively butting bouts ensued during which the contestants tried to get in underneath with head thrusts to overthrow or slash the opponent.

The fighting between the two adult sows, TD3 versus TD4 in the study enclosure, consisted of rapid thrust and pushing movements with the snout, and side blows or slashes whenever the opportunity arose. Forehead contact formed a central part of the contest and the snouts were held in the form of crossed swords against each other. The contestants push-butted each other with vigorous forward movements of the head, continuously striving to regain close head contact. Fighting usually ends with a sudden turn-about of one contestant which is then pursued by the other. If the losing individual is too weak to flee rapidly, heavy gashes may be sustained from the rear.

Bushpig fighting described by Frädrich (1965) between females and males against females fully agrees with the observations made during this study. The fighting style has aptly been termed "nose fencing", compared to "tusk wrestling" in warthog and "snout ramming" in the giant forest hog (Kingdon 1979). All three fighting types conform to the frontal style in contrast to the other basic suid style, namely lateral fighting, described by Beuerle (1975) for the European wild boar.

No account of fighting between bushpig males is as yet available. Although presumably similar to the form described, the heavier snout and

the male snout protuberances, providing an additional anti-slip projection, may result in some differences.

5.2.2.3 Female aggression

Four cases of fatal female wounding were recorded for the free-ranging study population on Goudveld during 1981 - 1986. All 4 sows (COI: 11,1; CFI: 3,8; CW5: 5,0; CI2: 2,0 years of estimated ages) were severely wounded on shoulders, flanks and paunches and succumbed to wound sepsis (4.3.2). No similar cases in males are known for this population. Anecdotal reports by hunters and naturalists of bushpig fights also mainly involve encounters between females. An account of aggressive encounters in the study enclosure provide more insight into the nature of female aggressiveness in the bushpig.

- (I) Sow TD3 (11,5 y old), with her two yearlings TD1 (M) and TD2 (F), resided in the study enclosure when TD5 (adM); TD4 (F: 10,7 y) with juveniles TD6 and TD7 were introduced. Escalated fighting immediately ensued between the two adult sows, finally leading to the death of TD4 (F). The boar TD5 and juveniles TD 6 + 7 were accepted, or at least tolerated, within hours of introduction.
- (II) The 10 - 11 month old male TC2 was introduced into the enclosure. He was chased for prolonged periods and was only accepted after about 6 weeks. The threshold of aggression of sow TD 3 towards TC 2 remained low for many months.
- (III) Sow DG1 from Diepwalle was released into the study enclosure on 1.2.1982. The entire resident group approached the "intruder" and chased her around. Although all tried to follow closely during the initial stages of the chase, only the dominant resident sow inflicted wounds and persisted with the chase. Unlike TD4 of case I, sow DG1 (3,5 y) never fought back.
- (IV) On release of male DF1 (3,0 y) into the study enclosure (10.2.1983) the complete resident group approached and then chased him around. Failure to retreat fast enough, led to clashes and slashes being dealt out by both the dominant boar TD5 and sow TD2.

The boars soon lost interest in the chase, but again the sow TD3 persistently continued with the chasing.

- (V) Enclosure B was inhabited by the bushpig pair DJ1 (M: 4,5 y) and DI1 (F: 12,0 y; 80,5 kg). On 4.7 and 6.7.1983 the alpha sows of both enclosures, i.e. DI1 and TD2 (3,4 y), were observed to antagonistically move along the separating fence, both "jaw champing".

On 7.7.1983 DI1 (F) and DJ1 (M) broke into the enclosure of TD2 (F) and her group. Both TD2 and TD5 chased DI1 (F). The juveniles of TD2 followed along with the chase. Persistent chasing and occasional contact with the fleeing DI1 was conducted by the alpha sow TD2, while TD5 soon lost interest. The intruding boar DJ1 was not chased at that stage. However, he was chased the following day by TD2, after DI1 had been removed from the enclosure and the attention of TD2 thus freed to be redirected towards male DJ1.

Boar DJ1 was chased less intensely by sow TD2 than the intruding sow DI1. No slashes were inflicted on DJ1 and it appeared as if he was only chased away; in contrast DI1 was actually persistently attacked and wounded. Boar DJ1 was apparently accepted after about a week.

- (VI) During the residence of another bushpig pair TH1 (M) and TH2 (F) in the adjoining enclosure B, the two sows, namely TH2 and TD2, again attempted to fight each other through the separating fence. No aggression between the corresponding alpha males were observed.

- (VII) Daughter sow TD12 (3,0 y) to TD2 (F) broke out of the enclosure under agonistic pressure of the latter between 7 and 10.1.1986.

The evidence presented strongly indicates that the alpha female is the dominant aggressive force, particularly in relation to spatially related intolerance. Female spatially related aggression is also directed towards intruding males. These findings verify the observations made by Skinner *et al.* (1976) in this regard: "Although a boar will not usually chase off a strange sow, a sow of the dominant sounder will always do so and she will also attack an intruding boar of another sounder who will retreat without opposition".

5.2.2.4 Male aggression

Unlike female bushpigs, adult males may form male-male associations (4.3.1.2), presumably alpha-beta consortships (4.4.3.5), and males also have display structures and colour contrast patterns concentrated on the head (5.1.2.3) as well exhibiting display assessment behaviour (5.2.2.2). These sociobiological features suggest the existence of dominance status differentiation. In accordance with this, two cases are on record from the free-ranging study population where two adult males had been fighting, but subsequently stayed together. On 8.3.1982, male CC3 (8,5 y; 60 kg), with a deep cut on his right flank, was caught together with male CR1 (7,5 y; 69 kg). These two males remained together and were both later associated with female CL2 and her juveniles. On 8.3.1984 males CU8 (8,9 y; 65kg) and CU4 (5,9 y; 70 kg), both with fresh fighting wounds, were captured together. These records are interpreted as representing cases where two foreign males had met and in the process of consortship formation could not decide on relative status based on display assessment alone.

In the study enclosure two cases of intermale fighting were recorded, although not directly observed.

- (I) On 7.7.1983 male DJ1 (4,5 y; 66kg), together with DI 1 (F), from enclosure B had broken into the main study enclosure and was accepted within a few days, after some chasing by the resident female TD2. During the first few days of August 1983, i.e. about a month later, fighting with male TD5 (10,3 y; 71 kg) resulted in wound sepsis, from which DJ1 then died. He had sustained deep gashes on both sides, shoulder and flanks (Plate 9a).
- (II) Male TD5 had alpha status in the study enclosure from the time of his introduction on 1.1.1981 and TD1 occupied the beta position since he reached maturity. On 26.11.1985 it was discovered that TD5 (12,5 y; 74 kg) had forcefully broken out of the enclosure, while TD1 (5,8 y; 85 kg) remained together with the resident female. TD5 was recaptured on 8.12. 1985, showing fighting gashes on the shoulder. He was placed back into the enclosure and 3 days later was found dead with additional wounds. It then became clear that TD5 had broken out of the enclosure on 26.11.1985 subsequent

to escalated aggression, as a result of which TD1 had asserted the alpha position.

Both fighting events coincided with back-dated conception, i.e. oestrous periods of female TD2. It thus appeared that escalating dominance probing was triggered by situations of competition for mating access.

5.2.3 Discussion

According to the postulates of Geist (1977, 1978a), weapons that maximize surface damage to the body and therefore "pain" are associated with the defence of food resources. The factors in the adaptive syndrome are monogamy, prolonged pair formation, the use of damaging weapons and a relatively low level of display organs and display behaviour. This appears to be valid for both sexes in certain monogamous species occupying pair territories, like the Cephalophinae. There both sexes are bound into a system of relative, i.e. spatially related dominance. For the bushpig this appears to be valid only in the female. Social interaction in the bushpig female is characterized by spatial exclusivity and aggressivity and the absence of an intrasexual dominance hierarchy. Bushpig females avoid each other or immediately enter into escalated fighting. Aggression of the territorial female is also extended to strange intruding, relatively low-ranking males. Agonistic interaction among bushpig males is strikingly different. Assessment display behaviour, display organs and absolute dominance relationships are prevalent. An attempt is made below to interpret these differences according to evolutionary theory of animal contest.

For reasons of energy conservation and risk of injury it will usually pay individuals in competitive situations to avoid becoming involved in escalated fights (Barnard and Burk 1979). Parker (1974) and Maynard Smith and Parker (1976) stressed the significance of asymmetry in settling contests without escalating. Asymmetry denotes a bias towards one individual in the probability of winning an escalating fight. Asymmetries are used as assessment cues in predicting the outcome of an escalated fight and enable the likely loser to withdraw before escalation (Barnard and Brown 1982). Three categories of asymmetries are generally recognized (Parker 1974, Maynard Smith and Parker 1976):

PLATE 9

- a. Fighting wounds: male DJ1 (Enclosure B)
Death through wound sepsis.

- b. Resting hollow in enclosure A (Goudveld).

- c. Resting place below stinkwood stump (Goudveld State Forest).

a



b

c



resource holding potential (RHP), resource value or reward (V) and "uncorrelated" asymmetries (prior residence).

(a) Resource holding potential

RHP asymmetries are based on differences in individual fighting/competitive ability. Contests in which there is an RHP asymmetry may be settled on the basis of assessment cues like body size, size of weapons or display organs (horns) or display vigour, which are assumed to provide estimates of relative RHP (e.g. Clutton-Brock *et al.* 1979). Any cue correlated with RHP may be used for assessment and thus used to settle contests, resulting in stable dominance hierarchies (cf Barnard and Burk 1979).

(b) Resource value

The contested resource may be worth more in terms of fitness units, to one opponent than the other (Parker and Rubenstein 1981). This may arise, *i.a.* because one contestant has been deprived of the resource for longer or has better information about its availability. Defined alternatively, resource value V is the difference in fitness between obtaining the disputed resource, versus leaving to search for an alternative, usable resource (Parker and Rubenstein 1981). A general rule in this regard postulates: withdraw if in role B and persist if in role A; where A and B are defined by $V_a/K_a > V_b/K_b$ and V = resource value and K = rate of contest costs.

Parker and Rubenstein (1981) define a role as being set by the interaction between asymmetries in RHP and in V . Contests will be settled peacefully only if reliable estimates of RHP and V can be obtained quickly and cheaply (e.g. by a short assessment phase or display). Weak role asymmetry between opponents, undetectable by assessment, will lead to escalation, but they may use the contest itself to increase information. Assessment displays are accordingly seen primarily as adaptations to obtain information about an opponent.

(c) Residence advantage

Under certain conditions e.g. where resource availability is high, contestants may use an arbitrary cue such as priority of residence, which is unrelated to RHP or V asymmetries, to settle a contest (cf Maynard Smith 1974 ex Parker and Rubenstein 1981, Barnard and Brown 1982). The commonplace adoption of "owner wins" conventions is often taken as evidence that uncorrelated asymmetries exist in nature. However, as Parker and Rubenstein (1981) correctly note, it is not clear how such conventions can be maintained by selection in the face of RHP and V asymmetries.

There is much evidence that "owner wins" conventions do exist in nature, i.e. ownership is respected unless detectable RHP disparity is very large (Parker and Rubenstein 1981). It is suggested here that some correlation presumably always exists between ownership and RHP or V, resulting in "owner wins" conventions. Presumably more than one type of asymmetry influences the outcome of a contest. While the results of the experiment by Barnard and Brown (1982) show that the outcome of social interactions between captive common shrews (*Sorex araneus*) is influenced by prior residence, its effect was influenced by variation in food availability and differences in competitive ability between animals. The resident advantage was strongest when no food was available and weakest when a high density of food was available.

In connection with bushpig female territoriality it is theoretically plausible that ownership is respected, resulting in spatial avoidance, under the following conditions (cf Parker 1974, Parker and Rubenstein 1981):

- (I) unless detectable RHP or V disparities in favour of the attacker are very large,
- (II) whenever there is a positive correlation between ownership and V or RHP or both,
- (III) the owner is identifiable as such, and

(IV) within the zone where ownership is respected (relating to I), opponents lack information when it would pay to break the convention of "owner wins".

Thus, over a range where information about roles A and B is difficult to obtain (V_a/K_a close to V_b/K_b), an "owner wins" convention may be respected. Parker (1974) indicated that at least long-term tenure of territories would most likely be correlated with V. For example, in prolonged guarding of feeding territories, it seems likely that learning the characteristics of the resource will increase the rate of resource uptake. The remainder of the resource may thus be worth more to the holder than the attacker.

Ownership status thus functions as a correlated cue that is available to both opponents, whereas exact information on role asymmetries may not be readily available (Parker and Rubenstein 1981). This interpretation only requires that, within the range where prior residence is respected, ownership has an expectation of correlating positively with $V_a/K_a > V_b/K_b$. If asymmetries in pay-off between roles A and B are slight and costs of assessment are high, assessment may not evolve. If search costs are high, i.e. alternative territories not readily available, role asymmetries may diminish and result in attack rather than withdrawal (Parker 1974, Parker and Rubenstein 1981).

The features of agonistic behaviour outlined above are in line with corresponding observations regarding female bushpig behaviour (respecting of ownership status; mutual avoidance or obligatory high intensity aggression). If this interpretation is applicable, it logically follows that territory-holding females must ensure that their ownership status is known, or else they risk frequent conflict escalation. Also, any violation of the ownership convention should be reacted upon with immediate high intensity aggression. Marking, patrolling and the presence of a pair-bonded male, himself marking, presumably all contribute to convey information on territorial ownership status to potential contestants.

Males can secure a female directly by (I) defending a female against competitors at the time of mating or (II) through a previously established dominance; or indirectly by (III) defending some resource

(e.g. food supply, nest site, mating territory). There is evidence that the food access and the mating access rank orders are not the same in the European wild boar (Beuerle 1975). Age-graded rank appears to be prevalent in terms of access to food (Beuerle 1975, Hennig 1981), whereas directly size-related contest determines mating access during the relatively short mating season. For this species with its polygamous social organization, females are aggregated and may be monopolized by the strongest during multimale escalated contest (strategy I). The sociobiological context and features of bushpig males, notably with cephalized display organs for dominance assessment and pair-bonding to dispersed females, suggest that strategy II may apply.

The snout knobs in male bushpigs are interpreted as being central to the assessment of relative RHP during dominance displays. The white forehead presumably facilitates the assessment of snout knob dimensions by fixing the attention to and accentuating the snout knobs. The dorsal mane may guide vision to the forehead in latero-frontal display. In addition, male snout knobs may function in binding together the heads of opponents during pushing contests. Snout knob dimensions are correlated with both body size and age (5.1.2.3), and can therefore function as assessment cues of RHP. Among other possible features, size and experience are often involved in determining of RHP in animals (Parker 1974). Dominance hierarchies may accordingly be established and maintained without frequent resorting to overt aggression. Particularly in more gregarious species this may lead to substantial savings in energy (cf Geist 1966).

Dominance hierarchies enhance the predictability of social relationships and can exist in groups of individuals that differ little from each other. They then depend on the knowledge of each individual about the fighting ability of its companion (Geist 1966). There is however no such predictability of social relationships if a number of strange, similar individuals are united. Such predictability may however be preserved if some assessment system exists which parallels RHP and thus absolute dominance rank. Predictability is thus preserved even if strange individuals meet (Geist 1966). An equivalent function is suggested to operate among bushpig males. This pattern differs from that

applicable to bushpig females and also between males of certain monogamous and territorial species. The possible adaptive significance of the observed pattern remains to be clarified and is discussed further below.

It is selectively advantageous to an individual not to be involved in escalated contests with equal or superior opponents. Equal or superior opponents may be identified through territorial ownership (relative dominance) or signals of absolute dominance rank, like horn size gradients. Antler and horn size appear to be judged directly in many ungulate species and fights occur only between closely matched opponents. "Assessment" of RHP obviously only implies that the individual responds differentially to opponents on a basis of their RHP relative to their own and the "real assessment" of what the appropriate response is, is the unconscious one performed by selection (Parker 1974).

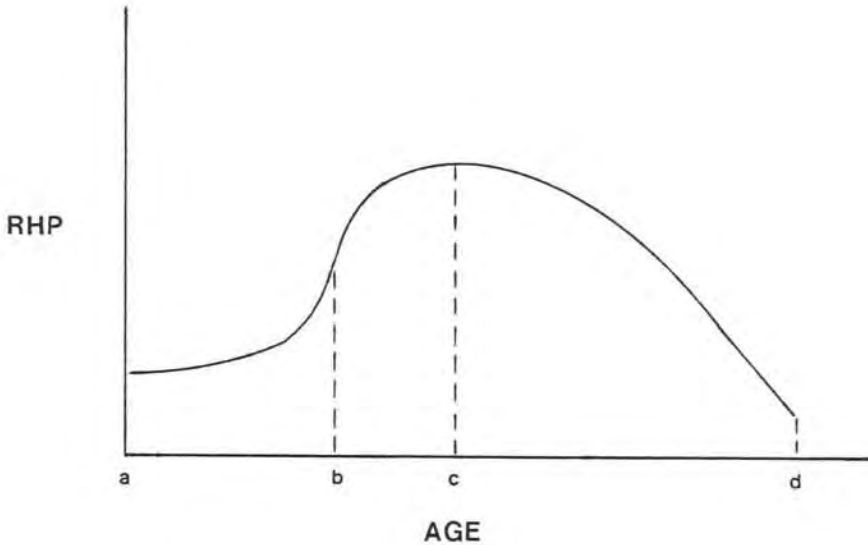
As suggested by Geist (1966), one of the main significances of absolute rank indicators is probably that they allow the existence of "open" societies, where strange conspecifics can integrate with a minimum of conflict. Bushpig alpha/beta male associations may be made possible thereby. The possible advantages of such associations were discussed in section 4.4.3.5.

The social organization, particularly dominance status and agonistic interactions, described for lesser bushbabies *Galago senegalensis* (Bearder and Doyle 1974, Bearder and Martin 1980) is closely reminiscent to that of the bushpig. Noteworthy here was that the social position in the male hierarchy of lesser bushbabies was found to be largely dependent on relative age. An age-graded hierarchy was similarly recorded for male dwarf mongooses (*Helogale parvula*) which also live in monogamous family groups (Rood 1980). In the bushpig, the size of male snout knobs, possible display organs, increases with age. The role of age as determinant of social rank and its relation to RHP is intriguing.

Monopolization of spatially aggregated females results in high intensity competition with success largely dependent on RHP; mainly related to body size. When females are dispersed, "monopolization over time" presumably may become the superior strategy (cf 4.4.3.6). Reproductive fitness variance i.e. the proportion of offspring produced relative to

competing individuals, is then more a function of effective reproductive life span, as opposed to the number of females inseminated per mating season. Age may then be of increased significance. A schematic and hypothetical relationship between RHP and age is presented in Figure 5.1.

FIG. 5/1: HYPOTHETICAL RELATIONSHIP OF RESOURCE HOLDING POTENTIAL (RHP) TO AGE



In "polygamous" situations the effective reproductively competitive life span of males is presumably depicted by interval b - c (Fig. 5/1); but may extend to ages beyond peak RHP in "monogamous" situations.

Age may be directly linked to RHP through the competitive advantage resulting from "experience". Emphasis is however here placed on the effect of age on V/K role asymmetries. For prolonged resource guarding situations (e.g. exceeding one mating season as with monogamous pair bonding) it seems likely that the average age of holders exceeds that of attackers (Parker 1974). In fighting with a reasonable chance of fatal outcomes, as in the bushpig, the overall risk in terms of fitness of the younger combatant will be higher than that of the older, since a larger proportion of its reproductive life span is at stake (relative high K).

Resource value (V) asymmetries occur where the disputed resource is worth more to one contestant (Barnard and Brown 1982). Resource value is expected to increase as RHP decreases, since an individual of declining RHP has a lower probability than one of high RHP of finding a resource occupied by an individual of lower RHP (Parker and Rubenstein 1981). The older contestant thus incurs a relatively greater loss in fitness through resource loss. It is hence postulated that size and age related male snout knobs serve as assessment cues for RHP (b - c of Fig. 5/1) and V/K role asymmetries (beyond c of Fig 5/1). Males would thus aim to extend resource tenureship beyond point c (Fig. 5/1). This would however represent a form of "bluff", which would eventually break down under probing (challenge) by an individual with higher RHP. The essential feature of a bluff is that it should increase apparent size or whatever feature being used as assessment cue, without altering RHP in an escalated contest. If bluff cannot be distinguished from actual RHP, then it will be established (Maynard Smith and Parker 1976). In other words, as long as the relationship between the assessment cue and RHP is no more than a statistical correlation, it is open to cheating/bluff (Barnard and Burk 1979). It is clear that selection will favour individuals capable of distinguishing bluff from actual RHP and this is likely to limit the extent to which bluff is employed in animal contests. It is however possible for extensive bluff to evolve as a stable strategy within a population even though the bluff could be detected. This is more likely in species in which serious injury is possible (Maynard Smith and Parker 1976), as in the bushpig.

5.3 Rearing Behaviour

5.3.1 Introduction and methods

5.3.1.1 Introduction

Mother-infant relationships of ungulates were reviewed by Lent (1974) and maternal behaviour in mammals generally *i.a.* by Walser (1977). Detailed accounts of rearing behaviour for free-ranging suids are available for the European wild boar (Gundlach 1968, Meynhardt 1978, Martys 1982, Briedermann 1986).

Pigs are the only true multiparous ungulates; having relatively small neonates and characteristically preparing farrowing nests (Frädriich 1974). Paternal care provides an additional component in bushpig rearing (4.3.3).

In contrast to the pattern found in other suids, rearing in the bushpig takes place in the context of a monogamous social setting (Chapter 4). This will be discussed in conjunction with reproduction (Chapter 10), population dynamics (Chapter 11) and when interpreting life history strategies in the bushpig (Chapter 12).

5.3.1.2 Methods

The systematic observation programme in the study enclosure involved altogether 41 x 24 hour, i.e. round-the-clock, observation sessions (Table 5/4).

| OBSERVATION PERIOD | 24-HOUR SESSIONS | SPECIAL STUDY FOCUS (REMARKS) |
|--------------------------|------------------|---|
| 01/02.06 - 05/06.06.1981 | 5 | Thermoregulation |
| 19/20.12 - 22/23.12.1981 | 4 | Rearing (TD3 + 2 juveniles) |
| 29/30.12.1981 | 1 | Rearing (TD3 + 2 juveniles) |
| 08/09.01 - 12/13.01.1982 | 5 | Thermoregulation Rearing (TD3 + 2 juveniles) |
| 11/12.07 - 15/16.07.1982 | 5 | Activity |
| 06/07.01 - 10/11.01.1983 | 5 | Activity |
| 11/12.01 - 15/16.01.1983 | 5 | Activity |
| 08/09.03 - 10/11.03.1983 | 3 | Rearing (TD2 + 1 juvenile) |
| 04/05.07 - 08/09.07.1983 | 5 | Activity |
| 10/11.12.1983 | 1 | Rearing (TD2 + 1 juveniles) |
| 24/25.10 - 25/26.10.1984 | 2 | Rearing (TD2 + 3 juveniles) |

The observations were carried out by single observers in shifts of between 4 and 8 hours, depending on schedule preference and number of observers available. During the observation period 8/9.1 - 12/13.1.1982, two observers worked simultaneously; one for unin-

errupted observations of rearing behaviour, while the other was primarily responsible for recording weather parameters and monitoring body core temperature.

Observers were able to observe from distances between 5 to 20 meters without unduly affecting the behaviour of the study animals, especially after about the initial 12 hours when the animals had become accustomed to the presence of the observers. At night the enclosure was illuminated (1.3.4). Comparison with pre-illumination pilot observations during moonlight or with the aid of torches or mere auditory contact indicated that activity or behavioural patterns were unaffected by dim artificial illumination. Individual recognition of most bushpig group members was possible due to size-, age- or sex-related differences.

All observations were recorded on standard observation forms (Fig. 5/2). The observation variables used are defined below.

(a) Weather description

The overall weather pattern was described for 3-hour periods in respect of cloud cover, wind-direction and speed and whether warm or cold. Ambient temperatures were measured hourly in the forest and the fynbos. Onset, termination and intensity of rain was also noted.

(b) Behavioural states and events

Behavioural states have appreciable durations and provided information on the percent of time spent in some activity; whereas events were instantaneous and provided information on frequency of behaviours (Altmann 1974).

FIG.5/2: OBSERVATION RECORDING FORM

(See text for abbreviations)

DATE: 9.3.1983

OBSERVER: A. SEYDAEK

WEATHER: clear, cool, SE breeze.

| | | | |
|-------------|---|--|-----------------------------------|
| 18.00-18.10 | BSP (For) R | $T_{IF} = 16,8^{\circ}C$ $T_{F_{in}} = 17,7^{\circ}C$ | |
| 18.10-18.20 | BSP (For) F _c | | |
| 18.20-18.30 | BP (For) L _a S (For) F _c | | |
| 18.30-18.40 | BSP (For) F _c | | |
| 18.40-18.50 | BSP (For) F _p G (For) F _p | P suckled from S in standing position while she was feeding. | |
| 18.50-19.00 | G + BSP (For) F _c | | |
| 19.00-19.10 | G + BSP (For) F _c /F _p | $T_{IF} = 16,2^{\circ}C$ $T_{F_{in}} = 16,1^{\circ}C$ | TDI(M) chews on venet carcass. |
| 19.10-19.20 | G + BSP (For) F _c | | |
| 19.20-19.30 | G + BSP (For) F _c | | |
| 19.30-19.40 | G + BSP (For) F _c | | |
| 19.40-19.50 | S (For) F _c ↗ Note! G (For) F _c ↘ BP (For) F _c | JB acting as "land-mark" for P. (Paternal care) | |
| 19.50-20.00 | G + BSP (For) F _c | | |
| 20.00-20.10 | G + BSP (For) F _c /F _p | $T_{IF} = 14,6^{\circ}C$ $T_{F_{in}} = 12,5^{\circ}C$ | → P also "nosing" ground surface. |
| 20.10-20.20 | BSP (For) F _c | | |
| 20.20-20.30 | BSP (For) F _c | | |
| 20.30-20.40 | BSP (For) F _c | | |
| 20.40-20.50 | BSP (For) F _c | | |
| 20.50-21.00 | BSP (For) R G (For) F _c /F _p | | |

Four different states were differentiated:

- F: Feeding (Fp: stationary feeding at a feeding place; Fc: casual feeding: searching and rooting about).
- La: Locomotion: moving about, ambling, without signs of feeding activity; i.e. without focusing attention on the ground surface.
- H: "Hanging" around; stationary and not feeding; probably transient phase to resting, but not lying yet.
- R: Resting; in a lying position of some kind. States F and La were considered "active", whereas H and R were taken as "resting" (*sensu lato*).

States were assigned to full 10-minute recording periods as per observation forms. In cases of mixture of states within 10-minute periods, the dominant, longest applicable, state was recorded as representing the particular 10-minute period. The occurrence of behavioural events was recorded, and included *i.a.* drinking, wallowing, elimination, aggression, marking, nest-building and suckling.

(c) Group association

The individual or group of individuals for which any particular state was applicable was noted with the aid of codes (G: group of boar, sow and juveniles; B: alpha boar; S: alpha sow; J: juvenile(s); Y: yearling(s); P: piglet). Use was also made of the identification numbers of the respective individuals (e.g. TD2).

(d) Locality. Whether in the forest or the fynbos

(e) General notes

These included opportunistic observations on, for example, group coherence (longest axis of group member dispersion) or sounds emitted.

The enclosure study setting was characterized by (I) a relatively small repertoire of behavioural states and low frequency of events, (II) restriction on the movement of the animals within the confines of the enclosure and (III) a reasonable degree of group coherence and synchrony of behavioural states. Observations were thus made according to the "complete record" strategy; i.e. where the observer attempts to record the timing and duration of every occurrence of all the categories of behaviour in which he is interested (Slater 1978). However, in terms of behavioural events generally, *ad libitum* sampling (cf Altmann 1974) is probably a more apt description, since a full record was not achieved. The focus was rather on the recording of relatively rare, but significant events. A complete record was achieved for behavioural states and percent of time, chronological scheduling and durations could therefore be determined. Whenever a full frequency record was required, e.g. for the frequency of suckling events during the study of rearing behaviour, focal animal sampling was used. This refers to any sampling method in which all occurrences of specified actions or interactions of an individual, or specified group of individuals, are recorded during each sampling period of predetermined or known length (Altmann 1974).

5.3.2 Results and Discussion

5.3.2.1 Parturition and early post-parturient phases

Pregnant suid females are reported to farrow in isolation (Martys 1982, Mason 1982). Antagonism towards group members varies greatly in respect of time of onset prior to this event and intensity. Pregnant wild boar females segregate from the sounder 5 to 6 days pre-partum and become intolerant towards other group members (Martys 1982). However, mother-daughter bonds often remain intact and the previous year's litter is allowed to retain close contact (Meynhardt 1978). Pregnant warthog females may become antagonistic towards accompanying juveniles and drive them away as early as six weeks before parturition (Cumming 1975).

After about a week post-partum, the members of the sounder reunite (Hennig 1981), often involving more than one nursing female in both the European wild boar and the warthog (Mason 1982, Briederman 1986). No antagonism towards group members prior to or after farrowing was observed in female bushpigs in the study enclosure. The sow-neonate unit was however mostly alone during the farrowing nest phase, which lasted between one and three days. Excepting the boar, with a clear propensity to be in the vicinity of the unit, group members made infrequent contact visits only and rested separately. After this initial phase the boar was closely involved in the female young unit. With the progress of time, the normal pattern of communal resting took precedence again.

The preparation for parturition in suids typically involves the building of a farrowing nest, which is unique among ungulates (Lent 1974, Leuthold 1977, Walser 1977). These farrowing nests consist of a shallow depression lined with finer shrubbery or grass upon which additional twig material and shrubbery is piled to form a heap, allowing the wild boar sow to be completely covered after entry (Gundlach, 1968, Briedermann 1986). Nest building activity is poorly developed in the warthog and parturition occurs in holes in the ground (Bradley 1968, Cumming 1975, Mason 1982). Gundlach (1968) and Martys (1982) associate the building of farrowing nests with multiparity. In the case of suids nests function primarily to conserve neonate body heat during the first few days when they are believed to have difficulty in stabilising their body temperatures on their own (Alexander, Signoret and Hafez 1980).

Three farrowing events in the study enclosure were detected or observed early enough for the construction of nests to be verified. In only one case was a former farrowing nest actually prepared, and this was not particularly elaborate compared to normal bad weather nests. In the other two cases, farrowing took place in shallow ground hollows. It appeared that if the weather at parturition was favourable, i.e. relatively warm, sows did not prepare farrowing nests. The farrowing season is spring and summer (10.3.5), but bad weather nests are constructed when it is cold and raining (7.3.1.3). During observations of rearing behaviour, four instances of bad weather nest building were recorded. (On 12/13.1.1983: neonates TD8 + TD9, 26 days old;

7/8.3.1983: neonate TD11, 8 days old; 16/17.12.1983: neonate TD12, 7 days old; 24/25.12.1983: also neonate TD12, 15 days old.) In all cases it was raining and ambient temperature varied between 11 and 17°C.

Frädrich (1965) reported on neonate warthogs at the entrance of the birth hole on their second day and a marked loosening of association with the site by the second week. After farrowing, the domestic free ranging sow and her litter studied by Jensen and Recen (1985) remained in, or in the proximity of, the nest for about 9 days.

Frädrich (1965) cites an observation that wild boar mothers remained with their young at the nest for 4 days. The poikilothermic postnatal phase of domestic piglets is reported to last for 2 - 3 days (Frädrich 1967). New-born piglets, with their small body size and sparse pelage, are prone to chill in air temperatures as high as 20°C with a wind of 5 km/h (Mount 1968). Young piglets huddle together or against the sow to minimize heat loss, but feral piglets appear to be more cold resistant than domestic piglets (Alexander, Signoret and Hafez 1980). Studies on maternal behaviour in European wild boar by Gundlach (1968) show that the neonates and also the sow are largely nest-bound during the initial post-partum phase. On the first day after parturition the sow leaves the nest for only short periods, but remains within a few meters of the nest and in auditory contact with the young. On warm sunny days the neonates are allowed to leave the nest for short periods as soon as the second day of their life (Hennig 1981). Largely influenced by weather conditions, the sows remain away from the nest longer and farther on subsequent days. On good weather days the neonates themselves may be away from the nest for considerable periods. The final departure from the farrowing nest usually takes place within 7 to 14 days post partum; largely dependent on weather conditions (Gundlach 1968, Hennig 1981).

The bushpig neonates TD8 and TD9 of sow TD3 had left the farrowing nest by the third day of their life. Neonate TD12 (F) born to sow TD2 on 10.12.1983 between 9:00 h and 10:00 h was walking within the birth hollow and around its mother by 11:00 h; i.e. within two hours post-partum. Between 22:00 h and 23:00 h (within 12 - 15 hours), piglet TD12 followed the sow away from the birth hollow and did not return to it. Although generally very active within the birth hollow, neonates TD13,

TD14 and TD15 of sow TD2 left the birth hollow on day 3 of their lives. From then on they readily followed either sow or boar or made occasional movement bouts away from the resting sites subsequently used. The same applied to the other litters observed in the study enclosure.

Apart from these occasional movement bouts following the mother sow or boar, the piglets remained stationary at the resting sites in the company of either the sow, boar or both.

The initial post-partum phase, while both the sow and the neonates are bound to the site of the farrowing nest or birth hollow, is defined here as the nest phase for bushpigs. From the enclosure observations this phase lasts between 1 and 3 days. It also lasted 3 days in the single case monitored for a free-ranging, radio collared sow (4.3.3.2: sow CT3 with 3 neonates; Fig. 4/10). Subsequent to this phase the distances between shifting resting sites was governed by neonate mobility. One or both parents were bound to the resting sites and the neonates for body contact lying, especially during cold nights, and protection of the young against predators. Although these duties are partially shared with the male, the sow has to return to the resting site at appropriate intervals for nursing. The activity of both parents, but especially of the sow, is therefore substantially restricted during the first 3 weeks post-partum. There is some evidence for preferential day activity of the parent/young unit during this period (Fig 4/10: positions 5 - 6). During the night of 10/11.11.1986 sow CT3 with her 6-day old neonates was monitored and found resting. The minimum ambient temperature then was 8,5°C, whereas the lower critical limit of thermoneutrality for juveniles in the 8 - 15 kg size range is approximately 13°C (7.3.5). Body contact resting in order to conserve body heat, and day-time movement was the most appropriate strategy. Sludskii (1956) reported Russian observations of preferential to compulsory diurnal activity of female European wild boar with juveniles younger than about one month, in contrast to nocturnal activity of individuals or groups without young.

5.3.2.2 Maternal behaviour

Hediger (1955 *op. cit.* Lent 1974) distinguished clearly between the passive and the active types of ungulate mothers in reference to their behaviour in the immediate post-partum period. Maternal passivity of the Suoidea is in contrast to the pattern in other ungulates (Frädrich 1967, Gundlach 1968). Neonates are not licked dry, nor are foetal membranes devoured or umbilical cords severed. Mothers do not assist neonates in their search for the teats or stimulate defecation through abdominal massage. Maternal behaviour is thus largely confined to the provision of nourishment (lactation) and protection of the young against energy loss and predators (Frädrich 1967). Bushpig maternal behaviour was found to agree with the general suid pattern in the present study. In addition to suckling the young, some limited vocal communication, naso-nasal contact and defensive responses to neonate distress calls were observed.

Although little maternal care was observed in wild boar, much nasal contact between piglets and their mothers was evident (Gundlach 1968). The same was found to apply to the bushpig. Frädrich (1974), referring to wild boar during the first three weeks post-partum, noted the young touching the mothers nose with their own after having suckled. He contended that this nasal contact formed a very important link between the female and her offspring.

Bushpig mothers emitted cohesion grunts to stimulate and maintain the "following" reaction. Particularly after leaving the nest the female made the young follow her by making short rhythmical grunts (cf Frädrich 1974). Some grunting by the mother sow also preceded and accompanied suckling during the early post-partum phases (cf Walser 1977). The juveniles often squealed in order to gain access to the teats. The sow immediately responded to the cackling distress squealing of piglets by rushing towards them, emitting typical warning grunts. As also found for other suid species, the younger the litter, the more ready is the mother, (as well as the boar: see next section), to defend them. With increasing age of the young this readiness for defence fades away (Frädrich 1974). Some aggressiveness by the mother sow towards observers was evident within the first few days post-partum.

The nursing bushpig female generally lies on her side while nursing. This position is typical of the Suidae, Hippopotamidae and Tapiridae, but is not found in other ungulate families (Frädrich 1974). With increasing age, bushpig juveniles were also observed suckling from the standing sow, while also standing or sitting on their haunches. Such behaviour, deviating from the general pattern, was also observed in other suids, notably the warthog (Frädrich 1965, Mason 1982).

Mother sows are recorded calling or gathering resting members of their litters together for nursing (Hafez and Signoret 1969). Three phases of suckling were distinguished by Gundlach (1968) in European wild boar: pre-suckling teat massage (nosing); actual suckling and post suckling massage. In the first phase the young vigorously nose the surrounding of the teats. They are then often very excited and the female utters short, rhythmical grunts. Later these grunts become softer and fade away. When the milk flow begins, the young are very calm again (Frädrich 1974). In the domestic pig, Barber *et al.* (1955) observed that during the nosing phase one or two piglets would leave the udder and spend a few moments nosing around the snout of the dam. Donald (1937 *op. cit.* Barber *et al.* 1955) suggested that this behaviour might have some significance in encouraging the dam to eject her milk. On termination of the actual suckling, the young normally nose the belly again for a short while after which they often fall asleep (Frädrich 1974). In bushpig the suckling behaviour closely resembled the general suid pattern as described. The suckling phases were however not always as well-defined; neither did the sows regularly entice or call the young to suckle. She merely lay down and suckling commenced. Whether a definite teat order existed in the bushpig, as reported for wild and domestic *Sus scrofa* and also the warthog (Frädrich 1974), was not established. No teat order was observed in the warthog and in a family group, the piglets often nursed from either sow (Bradley 1968).

Unlike Gundlach (1968) who found nursing time preferences in the European wild boar, suckling bouts in bushpig occurred during all daylight or night hours (over $n = 103$ suckling bouts). The data available on bushpig suckling frequencies and duration are summarized in Table 5/5.

| TABLE 5/5: BUSHPIG SUCKLING FREQUENCIES AND DURATIONS (GOUDVELD STUDY ENCLOSURE) | | | | | |
|--|-------------------|----------------------------------|---------------------------------|----------------------------------|-------------------------------------|
| DATE | PIGLET AGE (days) | SUCKING BOUTS PER 24-HOUR PERIOD | SUCKING DURATION PER BOUT (min) | TOTAL SUCKING TIME PER DAY (min) | AVERAGE SUCKING BOUT INTERVAL (min) |
| 24/25.10.1984 | 2 | 21 | 2,9 | 61 | 68 |
| 21/22.12.1981 | 5 | 17 | 8,0 | 135 | 85 |
| 28/29.12.1981 | 12 | 14 | 4,8 | 68 | 103 |
| 08/09.01.1982 | 23 | 10 | 9,8 | 98 | 144 |
| 09/10.01.1982 | 24 | 9 | 9,7 | 87 | 160 |
| 10/11.01.1982 | 25 | 10 | 10,2 | 102 | 144 |
| 11/12.01.1982 | 26 | 11 | 5,3 | 58 | 131 |
| 12/13.01.1982 | 27 | 11 | 5,1 | 56 | 131 |
| \bar{X} | | | 7,0 | 83 | |
| s | | | 2,8 | 27,7 | |

Bradley (1968) recorded warthog piglets of about 6 weeks old suckling, on average, for 1,8 to 2,4 minutes at intervals of 48 to 93 minutes. The juvenile of a tame free-ranging warthog from 6 to 17 weeks of age suckled between 11 to 18 times per day (Cumming 1975). Suckling bout times recorded for European wild boar were 2,6; 2,8 and 2,0 minutes for 1; 2 and 8 day old young respectively and suckling bout intervals varied between 36 - 40 and 47 - 52 minutes for 1 day and 5 days or older piglets respectively (Gundlach 1968). Comparing these results with those of bushpig (Table 5/5) indicates a pattern of longer suckling bout duration occurring at longer intervals in the latter case. The total suckling times per day are however similar for the two species.

Lactation is reported to last for 3 - 4 months in European wild boar (Hennig 1972 *op. cit.* Schnorrenberg 1979) and may last 5 months in warthog (Cumming 1975, Mason 1982). The lactation period in captive bushpig was observed as 5,5 months (10.3.4). Although lactation may last as long as reported, milk probably becomes much less important to the survival of the juveniles after 3 months of age (Mason 1982). Cumming (1975) recorded a warthog litter surviving after being orphaned at about 13 weeks of age.

5.3.2.3 Paternal and alloparental care

In section 4.3.3.2 the incidence of paternal care is documented with particular reference to the guarding of the young. Paternal care manifested itself in various ways during the course of the study:

- (a) Guarding of and concern for young. The alpha boar maintained close proximity to the young or the sow/piglet unit. The boar/juvenile attachment was particularly prevalent during temporary absence of the sow. When bedded down with the sow/piglet unit the boar was more vigilant than the sow and regularly rose to circle around the group. The boar promptly reacted to any distress call of the young by emitting warning grunts or rushing up towards them. Some nosing (grooming) of the young by the boar was observed and close body contact between the young and the boar was common during resting.
- (b) Overt defensive aggression. Although both the sow and the boar showed aggression towards human observers during the initial stages post partum, this waned rapidly with increasing age of the juvenile in the case of the sow, but not so with the boar. Aggression towards humans handling juveniles emitting distress squeals still occurred with four months old juveniles (4.3.3.2.b.IV).

Bushpig males, especially alpha males, were generally more wary and nervous than sows or subadults. This may be associated with an inherent guarding predisposition resulting from the typical male guarding role.

Whereas the sow may become increasingly intolerant towards the young after weaning, the boar/young bond tends to last until dispersal (4.3.3.2; 4.4.3.4) Post-weaning juveniles and yearlings typically associate with the boar and are presumably only tolerated in the group by the sow because of the boar/young bond. Fissioning of a group into boar/juvenile and sow units after weaning under certain circumstances is suggested by group structures observed. It may serve to reduce intra-group feeding competition, particularly favouring the sow. For example, the boar/sow/juvenile/yearling group with boar CC3 and sow CW5 broke up after weaning, into three units: boar CC3/juveniles; yearling siblings; sow CW5.

Paternal care in the bushpig contrasts with the situation in European wild boar and warthog where multimaternal rearing may occur. The male rearing input in the bushpig appears to be crucial and females may terminate the current reproductive event whenever this input is no longer available. Pregnant females may abort or early lactating females desert their young in such an event. Solitary rearing females were never observed. Just prior to parturition the radio collared bushpig pair TH1 (M) and TH2 (F) from study enclosure B was released in Van Loggerenbos on Goudveld State forest. The boar deserted the female, who left the area within two weeks after having deserted the neonates or losing them due to some unknown cause. This event is open to a variety of interpretations, but further work is indicated on the issue of whether pregnancy or rearing is terminated in the event of a female losing a male.

In addition to male rearing, other group members, notably daughter sows, appear to be involved in alloparental care (4.3.4). Maberly (1967) and Attwell and Bearder (1976) have also reported the occurrence of alloparental care by daughter sows. When juveniles are acutely distressed, all group members, including yearlings of both sexes, show concern both vocally and by moving towards the squealing juveniles. Such behaviour is clearly advantageous as an antipredator strategy.

5.3.2.4 Parental care and juvenile survival

The preceding results and discussions suggest that thermal homeostasis (nests, huddling, preferential day activity) and antipredator behaviour (parental guarding and defence) are crucial to juvenile survival.

Of the 12 young, from 7 litters, born in the study enclosure, four (i.e. 33%) died before weaning (before 5 - 6 months). The deaths of three of these (juvenile TD9 from a litter of 2 of sow TD3 and juveniles TD16 and TD17 of sow TD2) were associated with thermoregulatory stressful periods. Nest building by the mother sows took place in the nights of, or preceding the deaths of the juveniles in all instances. TD9 died on 11.1.1982, when 23 days old, and weighed 2,4 kg. The minimum ambient temperature of the preceding 24 hours was 15°C in the forest part of the enclosure. TD16 and TD17 died on 1.11.1985 and 3.11.1985 respectively,

when approximately 4 weeks old. On 16.10.1985 they weighed 2,1 and 2,5 kg respectively. Available weather parameters (from Diepwalle weather station) for the period when the deaths occurred were as follows:

| Date | Precipitation | Maximum and minimum temperatures | |
|------------|---------------|----------------------------------|--------|
| 29.10.1985 | 25,6 mm | 22,0°C | 9,5°C |
| 30.10.1985 | 6,55 mm | 12,5°C | 8,5°C |
| 31.10.1985 | 0,70 mm | 13,5°C | 8,5°C |
| 1.11.1985 | 0,07 mm | 13,0°C | 9,6°C |
| 2.11.1985 | 0,10 mm | 19,0°C | 9,5°C |
| 3.11.1985 | 2,20 mm | 15,5°C | 11,5°C |

The carcasses were found on the mornings of 11 and 13.11.1985 respectively, weighing only 1,9 kg each. Inspection by dissection revealed a total lack of any fat reserves.

The fourth instance of mortality was a singleton TD10 born to TD2 on 19.9.1982. It died on 22.9.1983, weighing 1,2 kg. Since it was the first young born to sow TD2, maternal care may have been inadequate.

The role of parental defence has already been discussed (5.3.2.3). The possible role of the stripe-spotted coats and "freezing" or "lying prone" behaviour of bushpig juveniles as aids to survival must also be mentioned.

"Freezing" or "lying prone", a posture where the animal stretches its body out, producing the lowest possible profile and remaining entirely motionless, has been associated with hider species (Lent 1974). It is not limited to hidiers, although it has not been described in follower-type bovids, and is expressed weakly or for a shorter period after birth in some follower species (Lent 1974). The waning of the prone behavioural response is associated with the development of a flight response to alarming stimuli. The age of change-over may vary considerably between species, from 12 - 48 hours to 14 days. Among free-ranging peccaries the prone response occurs in juveniles when they are only a few days old, even though they already show a strong following

response (Sowls 1974). The prone response is also recorded for the young of the European wild boar (Gundlach 1968).

"Freezing" of juvenile bushpigs was observed on three occasions in the study enclosure, with ages of up to 12 days, and once under free-ranging conditions with juveniles of 18 days old. In this case it was triggered by a surprise approach towards the radio-collared sow CT3, together with boar CT4 and their litter of three (Fig. 4/10: position 18). Sudden acute threats of uncertain nature and direction appear to induce the prone response in juvenile bushpig, but it is relatively rare. Normally the following-flight response takes precedence. Stripe-spotted juvenile coats, lasting up to 3 months of age in bushpigs (Seydack 1983), appear to be confined to the juveniles of the two suid species typically frequenting habitat providing good cover, namely of the European wild boar and the bushpig. The young of warthog and the giant forest hog do not have such coats. One may speculate that the cryptic effect of the juvenile coat and the prone posture is particularly adaptive during diurnal activity in forest habitat. In conclusion it is proposed that the combination of an early following response, group vigilance, cryptic juvenile coats, prone response, parental guarding and defence together form an effective suite of antipredation devices.

5.3.2.5 Rearing phases and behavioural ontogeny

The eyes of bushpig neonates at birth are open and the body is covered with a hair coat. The neonates stand on their legs shortly after birth. They follow the mother sow away from the birth nest or hollow within the first 1 - 3 days, initially for short distances only. At the age of 4 - 5 days neonates were observed playing, play fighting, and performing rooting movements with their snouts. At that stage they were capable of scratching their shoulders with their hind legs. At the age of 9 days feeding on solids was observed. Similarly, European wild boar juveniles feed on solids from day 12 onwards (Gundlach 1968). Within the first 3 weeks post partum, bushpig juvenile's daily ranging hardly exceeded 200 meters on average (4.3.3.2). Much resting took place, whilst the juveniles were attended by at least one of the parental pair. After this phase, the complete group moved together but ranging distance was

still restricted. Behavioural development is broadly similar to that of the European wild boar (Gundlach 1968, Hennig 1981).

The phase from weaning to dispersal is defined here as the recruitment phase and from birth to weaning the rearing phase. From the perspective of ranging patterns, the rearing phase in the bushpig may be subdivided into 4 subphases:

- (I) Sow and neonates are birth nest or hollow bound (1 - 3 days).
- (II) Juveniles follow one or both parents on relatively short excursions from the resting refuge or whilst undertaking resting refuge shifts. One member of the parental pair may range farther while the other stays with the young (up to 3 weeks).
- (III) Juveniles follow both parents, the group thus ranging as a unit; although still restricted by and influenced by the ranging capabilities of the young (assumed to last up to approximately 6 weeks after birth).
- (IV) Juveniles participate in the unrestricted ranging of the group.

As may be noted in Fig. 4/10, the sow CT3 already exhibited restricted ranging some days before parturition. The full period when parental ranging may be restricted is accordingly estimated to last between 6 to 8 weeks. Ranging restriction, pre- and post-partum, is also recorded for feral sows (Kurz and Marchinton 1972), European wild boar (Sludskii 1956, Frädrieh 1968) and warthog (Cumming 1975, Mason 1982). For the warthog the period lasted from a week before farrowing, until 6 - 7 weeks afterwards (Mason 1982).

Neonates with poor locomotion and uncoordinated movements, but with hair and open eyes at birth, are considered semi-altricial by Walser (1977). However, suid neonates perform coordinated movements and are locomotary fully functional. Feral piglets were thus considered precocious by Graves (1984). Gundlach (1968) considered European wild boar neonates as neither clearly altricial nor precocious. According to anatomical and morphological features they are precocious (pelage, senses, locomotory organs fully functional at birth). Other features are normally associated with the altricial mode: nest building; farrowing

in reclined position of mother; postnatal phase starting in birth nest (Gundlach 1968). Compared with their mother, neonate suids are very small (Frädrich 1974). The birth weights of newborn bushpigs were between 1 - 2 % of that of the mother, but the neonates were morphologically well developed and functional. Bushpig can thus be said to have small-sized, precocious young; the small size apparently having energetic implications relating to thermoregulation and ranging capability.

Although neonate suids spend the first day or days in a nest, burrow or similar protected place, they cannot be classified as true nidicolous mammals in view of their advanced anatomical and physiological development at birth (Frädrich 1974). Suid neonates are already so far developed at birth that Ewer (1976 *op. cit.* Martys 1982) considered them "Fast-Nestflüchter". Small neonate size presumably underlies the thermoregulatory need for a nest phase and results from multiparity.

The hider/follower dichotomy refers to the positional behaviour of the young in relation to the movement of the mother. In hiders the infant selects its own hiding place away from the parturition site, as permitted and aided by the mother. Hiders are typically smaller species able to utilize cover for crypsis (refuge) and occur in forested habitats. In followers both mother and infant show specific behaviours which tend to promote an early and close following response. Followers are prevalent in grassland and tundra habitat (Lent 1974). Some followers have hiding periods and in this sense a continuum exists with regard to the relative emphasis placed upon hiding behaviour. Lent (1974) interprets the observations of Frädrich (1965, 1967) and others as that period in which the piglets remain in the nest analogous to the hiding phase. This period is short, after which the nest is left and the mother followed. Occupying and being bound to nests or other refuges is even less developed in bushpigs compared to the European wild boar or warthog juveniles and it is concluded that bushpig may safely be classed as a follower species.

6. HABITAT UTILIZATION

6.1 Introduction and methods

6.1.1 Habitat use in space and time

Habitat utilization can be thought of as a link between aspects of sociobiology, covered in Chapters 4 and 5, and ecophysiological topics like temperature regulation (7), nutrition (8) and condition (9). It also leads on to reproduction (10) and population dynamics (11).

In this chapter the focus is placed on the spatial and temporal dimensions of habitat use, i.e. the way in which the individual animal adapts to a spatially and temporally heterogenous environment, whilst attempting to secure the energetic requirements for maintenance, growth and reproduction. The spatial habitat components relate to food, water, cover and microclimate and the nature and spatial arrangement of these are of importance. Changes in these components over time and their predictability in time form the temporal component and decisively influence habitat use strategies. In the section on home range analysis (6.2) aspects of spatial extent and concentration of habitat use are addressed, whereas the activity rhythm analysis (6.4) deals with the temporal component. The analysis of movement patterns (6.3) links these two sections.

6.1.2 Methods

All aspects of habitat utilization, be they home range size, space use and preference, movement or activity patterns, involved locating animals in time and space. Nearly all the data were therefore obtained by radio-tracking (1.3.3), supplemented by capture localities (1.3.1). Radio-tracking involved either the determination of discrete animal locations from an aircraft or vehicle or their tracking over one or more 24-hour periods. During continuous tracking an attempt was made to produce an uninterrupted series of half-hourly fixes over the full diel periods involved.

Observations on captive bushpigs in the study enclosure provided valuable supplementary data on activity rhythms (1.3.4) and their relation to weather variables (7.3.1). Details of technique not covered in the general description of methods (1.3), are mentioned in the text of the relevant subsections.

6.2 Home range analysis

6.2.1 Results

6.2.1.1 Home range size

All positions obtained from captures or radio tracking were assigned coordinates from a grid system in order to facilitate estimation of home range size. Positional data from radio tracking consisted of either single or sequential points.

Frequent successive observations tend to be positively correlated and sample variances of locations would thus be underestimates of the true values. Statistical estimates of home range size will then underestimate the true size of the home range by an amount related to the covariance between successive observations (Swihart and Slade 1985). Independence of successive observations is an implicit assumption in the statistical analysis of home range size and shape (e.g. methods based on the bivariate probability density function), but is not required for non-statistical home range measures (e.g. minimum convex polygon method). Independence between successive observations results when an animal's position in its home range at time $t + k$ is not a function of its position at time t . Dependence between observations was minimized by excluding all those observations that occurred within 3 hours of a previous observation of the same animal (Three hours is a time span within which a bushpig could traverse its home range).

Home range size approximations were considered feasible for animals with 8-30 independent positions ($n = 5$) and with 30 or more observations home range size determination was attempted ($n = 7$). Only animals with a positional data base applicable over periods of known home range

fidelity (see below), were selected for home range analysis. Nomadic animals, or those exhibiting obvious shifts in home range or changes in social status, were excluded from the analysis.

Home range size analysis may be undertaken with non-statistical (minimum convex polygon and grid methods) or statistical methods (parametric or non-parametric) (Table 6/1).

| | |
|---|---|
| 1. <u>Minimum convex polygon method</u> (MCP) | |
| 2. <u>Grid methods</u> | Mac Donald <i>et al.</i> (1980) Trevor-Deutsch and Hackett (1980) Voigt and Tinline (1980) |
| 3. <u>Parametric methods</u> Bivariate normal models and variations | Jennrich and Turner (1969) Samuel and Garton (1985) Don and Rennolds (1983) Dunn and Gibson (1977) |
| 4. <u>Non-parametric methods</u> (I) Histogram method (HGM) (II) Fourier transform method (III) Harmonic mean method (HMM) (IV) Exponential kernel method (EKM) (V) Normal kernel method (NKM) | refer to Anderson (1982) Anderson (1982) Dixon and Chapman (1980) Button (1986), Worton (1989) Button (1986), Worton (1989) |

Five of the methods in Table 6/1 were applied to the 12 cases selected for home range analysis. These were the non-statistical minimum convex polygon method and 4 non-parametric statistical methods.

The minimum convex polygon is the smallest convex polygon containing all the observed positions and the area within this polygon is the estimated home range size. This is an easily applied method, but has two main disadvantages:

- (I) Sample size bias, pointed out by Jennrich and Turner (1969): usually the estimated size of the home range increases with the number of observations; and

(II) Shape constrained to a convex polygon: considered an unreasonable assumption by Anderson (1982), especially when the habitat is heterogenous.

Thus, when the home range shape is convex, the MCP estimate approaches asymptotically the total area used by the animal as sample size increases. When the home range is not convex, it can easily produce an overestimate (Anderson 1982).

The statistical methods of home range estimation are based on the "utilization distribution" (UD). The bivariate probability density function gives the probability of finding an animal at a particular location on a plane. This density function is commonly called "utilization distribution" (Jennrich and Turner 1969, Van Winkle 1975, Ford and Krumme 1979, Anderson 1982). The home range estimate is calculated by drawing equal height contours around the UD. The home range is specified by the contour such that the volume under the distribution and within the contour is 95% (or some other fixed percentage) of the total volume under the distribution. The UD is accordingly defined as the two-dimensional relative frequency distribution for the points of location for an animal over a period of time (Fig. 6/1).

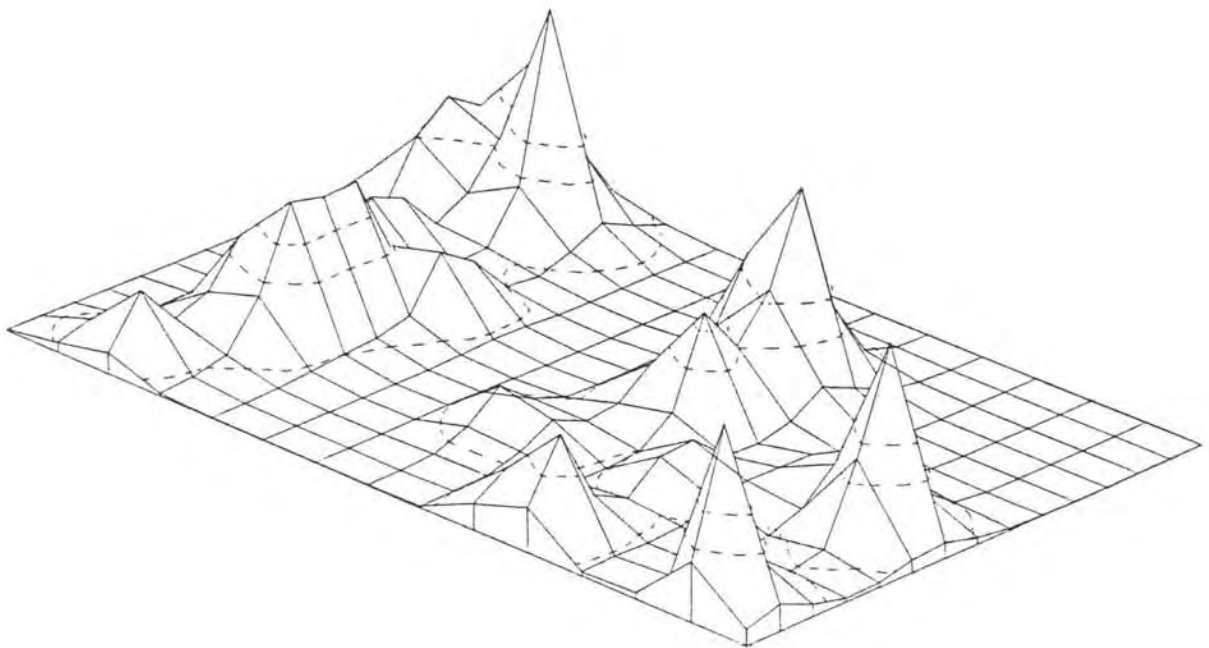


FIG.6/1 :EXPONENTIAL KERNEL ESTIMATE OF THE UTILIZATION DISTRIBUTION FOR BUSHPIG CVI(M)

Four different non-parametric approaches in estimating the UD were applied to the data (with acknowledgement to Mr P. Button, UCT)

Histogram method (HGM)

Imagine the plane on which an animal moves divided in a checkerboard pattern. For each observation a checker is placed on the square which contains that observation. The centre of the top checker in each stack, or square if no checker is present, is connected with a line to nondiagonal adjacent stacks of checkers, or squares. The resulting "net" then represents a two-dimensional surface approximating the UD (Anderson 1982).

The properties of the histogram as an estimator depend strongly on the sample size and number of intervals used in its construction (cf Anderson 1982). Once the appropriate number of intervals has been chosen (Linhart and Zucchini 1986), the estimation of the probability density function simply involves calculating the proportion of observations in each cell.

Harmonic mean method (HMM)

This method of calculating areas of animal activity is based on the harmonic mean of an areal distribution. The resulting isopleths of animal activity (i.e. contours of equal density of the UD) are based on the reciprocal mean distance deviations between grid points and observed animal positions and are thus related directly to the intensity of activity (Dixon and Chapman 1980; Spencer and Barrett 1984).

The harmonic mean method used followed Button (1986):

Given locations L_1, L_2, \dots, L_n where $L_i = (x_i, y_i)$ is the location of the i th observation of the animal with reference to a fixed X, Y coordinate system. A rectangular grid was superimposed over the set of locations and at each point of the grid the "density" was estimated by

"height" at grid point $(x, y) = \frac{1}{n} \sum_{i=1}^n (1/\max(\alpha_i \cdot d_i))$

where d_i is the distance between grid point (x, y) and location i .

Button (1986) applied two kernel based density estimators to define the UD for the purposes of home range analysis.

Exponential kernel method (EKM)

With this method the density at a point (x, y) is given by

$$f(x, y) = \frac{\mu^2}{2\pi} \cdot \frac{1}{n} \sum_{i=1}^n e^{-\mu d_i}$$

where $d_i = (x_1 - x)^2 + (y_1 - y)^2$ and μ is the smoothing parameter (Button 1986).

Normal kernel method (NKM)

The density at point (x, y) and:

$$f(x, y) = \frac{1}{2\pi\tau^2} \cdot \frac{1}{n} \sum_{i=1}^n e^{-d_i^2/2\tau^2}$$

where $d_i^2 = (x_i - x)^2 + (y_i - y)^2$ and:

τ is regarded as the smoothing parameter (Button 1986).

The five selected methods produced divergent results (Table 6/2). The question arose as to which method resulted in the most appropriate home range size estimates and to what extent the results were comparable.

| TABLE 6/2: HOME RANGE ESTIMATES (ha) | | | | | | |
|---|-----|-------|-----|-------|-----|-------|
| Identifi- cation No. | n | MCP | HGM | HMM | EKM | NKM |
| CC3(M) | 17 | 463 | 65 | 1 038 | 380 | 603 |
| CC9(F) | 109 | 750 | 414 | 1 238 | 663 | 806 |
| CE3(F) | 23 | 279 | 87 | 704 | 296 | 481 |
| CE6(M) | 34 | 909 | 129 | 2 005 | 718 | 1 137 |
| CH1(M) | 41 | 556 | 156 | 945 | 535 | 642 |
| CL5(M) | 16 | 440 | 61 | 961 | 328 | 633 |
| CT2(F) | 23 | 1 011 | 87 | 3 201 | 523 | 570 |
| CU5(F) | 50 | 376 | 190 | 1 536 | 578 | 706 |
| CU8(M) | 88 | 980 | 334 | 4 165 | 518 | 561 |
| CV1(M) | 21 | 418 | | 780 | 394 | 500 |
| CW5(F) | 49 | 873 | 186 | 3 747 | 576 | 1 018 |
| CZ1(F) | 40 | 574 | | 2 020 | 541 | 729 |
| \bar{X} | | 635 | | 1 861 | 495 | 698 |
| MCP: Minimum convex polygon method HGM: Histogram method (95% isopleth) HMM: Harmonic mean method (95% isopleth) EKM: Exponential kernel method (95% isopleth) NKM: Normal kernel method (95% isopleth) | | | | | | |

The selection of the method which give the biologically most appropriate results is partially dependent on the home range definition underlying the particular methods. A popular definition of home range, albeit somewhat unspecific, is "that area traversed by the individual in its normal activities of food gathering, mating and caring for young" (Burt 1943 ex Anderson 1982). The statistical UD-based methods have a fixed and specific underlying definition of home range; it is the smallest area which accounts for 95% of the animal's space utilization. With this definition it is possible to calculate a home range of two or more disjoint areas. This happens when the plane, containing the contour that defines the home range (95% in this study), completely slices through two or more peaks in the UD (cf Anderson 1982).

With the MCP method the home range cannot consist of two disjunct areas. The MCP method results in the maximum revealed home range and unless the accessibility to portions of the indicated range is obstructed, gives a minimum estimate of the area available to its occupant. For purposes of biological interpretation in the context of this study a home range definition which centres on availability of space is favoured. Home range is correspondingly defined as the area available to its occupant for routine use. The area available is then constrained by social factors or by foraging profitability, or both.

In order to estimate home range size as an indication of area available to the occupant, high percentage isopleths (90%+) have to be used when applying UD-based methods. Under such circumstances the "boundary problem" is prevalent. This dilemma is described by Anderson (1982) as resulting from small errors in the estimate of the height of the UD in the tails which most likely produces large errors in home range estimates. This is because 90% or higher contours lie in the tails of the UD and at this point the tails are nearly horizontal. Any small fluctuation of the tails up or down results in the contours moving in or out by large amounts. The precise form of the tails is also difficult to predict accurately since there is hardly any data in the tails of the UD. Non-parametric density estimation procedures therefore have difficulties in accurately estimating the tails of a distribution, leading to bias with small sample sizes. Also, the way in which the various methods deal with the tail of the probability density function differs, leading to grossly divergent and non-comparable results.

There are no indications that any portions of the MCP home ranges are inaccessible to the respective occupants. The MCP home range size estimates (Table 6/2) are therefore considered comparatively reliable minimum estimates. Taking the MCP estimates as a basis, the HGM and HMM home range size estimates are judged grossly unrealistic under- and overestimates respectively (Table 6/2). These discrepancies result from the problems described above and also apply to the EKM and NKM home range size estimates, although not manifested to the same extent. It is concluded that, for the sample sizes normally available, UD-based methods either over- or underestimate the area available to the home range occupant. The utility of these methods lies more with internal

space use analysis (e.g. identification of core areas) and the minimum convex polygon method will be used for home range size estimation in this study.

The standard way to assess sample adequacy is by constructing an area observation curve (AO-curve) (e.g. Laundré and Keller 1984). In order to determine whether any particular animal had a definable home range, an index of area used (cumulative MCP areas) was plotted against the number of localizations employed to determine these cumulative areas. This relationship, the AO-curve, was expressed as percentage change in area with successive additions of locations (Table 6/3). When the AO-curve approaches an asymptote, it is assumed that an adequate sample has been obtained to calculate reliable estimates of home range size.

| TABLE 6/3: AREA-OBSERVATION CURVE ANALYSIS PERCENTAGES OF HOME RANGE SIZE CHANGE WITH CUMULATIVE NUMBER OF LOCATIONS (*) | | | | | | | | | | | |
|---|-----------------|---------------|----------------|---------------|--------------|---------------|----------------|---------------|---------------|---------------|---------------|
| CC3 | CC9 | CE3 | CE6 | CF1 | CL5 | CT2 | CU5 | CU8 | CV1 | CW5 | CZ1 |
| 220 (5-8) | 913 (10-20) | 130 (5-10) | 153 (5-10) | 99 (5-10) | 151 (5-8) | 9 (5-10) | 125 (10-20) | 78 (10-20) | 40 (5-10) | 136 (5-10) | 300 (5-10) |
| 7 (8-11) | 15 (20-30) | 8 (10-15) | 133 (10-15) | 28 (10-15) | | 73 (10-15) | 55 (20-30) | 25 (20-30) | 16 (10-15) | 0 (10-15) | 11 (10-15) |
| | 15 (30-40) | 27 (15-22) | 55 (15-20) | 67 (15-20) | | 12 (15-20) | 17 (30-40) | 19 (30-40) | 29 (15-21) | 0 (15-20) | 1 (15-20) |
| | 1 (40-50) | | 0 (20-25) | 6 (20-25) | | 0 (20-23) | 0 (40-49) | 8 (40-50) | | 0 (20-25) | 0 (20-25) |
| | 5 (50-60) | | 44 (25-30) | 8 (25-30) | | | | 2 (50-60) | | 8 (25-30) | 4 (25-30) |
| | 0 (60-70) | | 37 (30-34) | 28 (30-37) | | | | 23 (60-70) | | 0 (30-35) | 0 (30-35) |
| | 0 (70-80) | | | | | | | 76 (70-73) | | 0 (35-40) | 1 (35-40) |
| | 0 (80-90) | | | | | | | | | 0 (40-45) | |
| | 8 (90-100) | | | | | | | | | <1 (45-49) | |
| | 12 (100-105) | | | | | | | | | | |
| * (increase in number of locations leading to percentage home range size change) | | | | | | | | | | | |

Messier and Barette (1982) assumed for coyotes that the estimate adequately represented the size of a home range when 20 additional daily

Locations resulted in an increase of less than 10% of the area used. Asymptotic home range estimates were achieved by Bowen (1982), when area increases were $\leq 2,5\%$ for a period of 1 month or 30 locations, whichever was less. The number of independent locations needed to adequately delineate home ranges generally ranged between 35 and 100: Bowen (1982): ca 42; Messier and Barette (1982): 50; Messier (1985b) 40-80; Laundré and Keller (1984): 100. With multiple asymptotes up to 200 locations may be required.

In this study adequate home range estimation was assumed to be achieved whenever area estimates changed $\leq 5\%$ over 10 additional independent locations (obtained over a minimum period of 10 days). The cases of home range estimation in Table 6/3 may accordingly be classified as follows:

- (I) The data base is obviously inadequate for reliable home range estimation (sample sizes in brackets): CC3(11), CE3(22); CL5(8) and CV1(21).
- (II) Asymptotic home range estimates approached: CU5(49); CW5(49) and CZ1(40).
- (III) Area estimate changes fluctuate in a non-monotonic fashion, suggesting multiple asymptotes: CC9(105); CE6(34); CH1(37); CT2(23) and CU8(73). Multiple asymptotes may arise from temporal core area use, range shifts or expansions and rare visits into "outlying" portions of the range.

Spatially, a home range is a region occupied by an animal. It is however crucial that the temporal pattern of spatial occupation is explicitly defined in order to determine whether an animal wanders at random or actually possesses a home range (Cooper 1978). This is required for differentiating between erratic wanderings or range shifts and rare events of visits to certain portions of the animals home range. Some of the animals had portions within their ranges which were visited comparatively infrequently and such visits were correspondingly located infrequently and sometimes late within the sequence of observations. This then resulted in secondary asymptotes and non-compliance with the sample adequacy rule as laid down. Such cases, otherwise comparatively well-sampled, were however not rejected if it was suspected that random

wanderings or range shifts were not involved. In order to resolve such cases, a rule to guide the temporal interpretation of space use was established. It required that the third of the home range diagonally opposed to the location of the outlying visit had to be visited by the animal within one month after the event. If this was so it was taken to imply that home range shifts or random wanderings had not taken place. On these grounds the home range estimates of CC9, CT2 and CU8 (Tables 6/3 and 6/4) were accepted. The home range of CE6 was identified as a product of range shifting after the death of CE3(F) to which CE6(M) was loosely attached. The adjusted home range estimate of CE6 was then determined as 660 ha, as opposed to the previous estimate of 909 ha. The estimate of CH1(M) (Table 6/4), although not adequately approaching its asymptotic value, was also considered acceptable. It compared well with that of CZ1(F), to which CH1 had a close and stable pair-bond. (Table 6/4).

| TABLE 6/4: BUSHPIG HOME RANGE ESTIMATES (MINIMUM CONVEX POLYGON METHOD) | | | | |
|---|--------------------------|-----|---------------------|--------------------|
| Identification no. | Home range estimate (ha) | n | Sampling time span | Social status |
| CC9(F) | 750 | 105 | 6.01.84 - 10.12.85 | Territorial |
| CE6(M) | 660 | 30 | 7.06.85 - 4.12.85 | Partially solitary |
| CH1(M) | 556 | 37 | 27.06.81 - 30.04.85 | Territorial |
| CT2(F) | 1 011 | 23 | 17.01.85 - 23.07.85 | Territorial |
| CU5(F) | 376 | 49 | 7.01.84 - 27.05.84 | Solitary |
| CU8(M) | 980 | 73 | 12.01.84 - 6.02.85 | Partially solitary |
| CW5(F) | 873 | 49 | 8.01.84 - 20.05.84 | Territorial |
| CZ1(F) | 574 | 40 | 12.10.82 - 22.10.85 | Territorial |
| n = different independent locations | | | | |

The average home range size was estimated as 722 ha ($s = 222,55$; $n = 8$). The average home range estimate for males (732 ha) did not differ significantly from that of females (716 ha). This is in agreement with the expectation for monogamous mammals.

6.2.1.2 Space use patterns and habitat preference

Core areas are areas receiving concentrated use by resident animals (Samuel, Pierce and Garton 1985). Such areas were identified for 6 radio-tracked and repeatedly captured animals. Only independent observations were used. For this analysis, a core area was defined as that portion of the home range accounting for 50% of sightings of the respective resident. These core areas, expressed as percentages of home range size, were taken as indices of space use concentration.

The core areas were established by superimposing a grid over the individual dot diagrams, designating the independent locations, and formed by the smallest number of grid cells accounting for 50% of all observations. In order to maintain comparability between animals with divergent sampling intensities, grid cell size was determined for each case individually by dividing the home range area by the number of sightings. For example, the home range of CC9(F) was determined as 750 ha and contained 105 independent animal locations (Table 6/4). The grid cell size used for this animal accordingly was 7,1 ha. The lowest number of cells containing 50% of the locations was graphically established as 14. The area covered by these cells amounted to 13% of the home range.

With no space use concentration, the core area, as defined, would thus cover 50% of the home range. The lower the core area percentage, the greater the concentration of space use:

| | |
|--------|-----|
| CU8(M) | 11% |
| CC9(F) | 13% |
| CW5(F) | 14% |
| CZ1(F) | 18% |
| CH1(M) | 19% |
| CU5(F) | 22% |

Male CU8 is the only animal whose home range includes a substantial proportion of open, agricultural land (pastures). The low core area percentage is largely attributed to a spatiotemporal avoidance of the open land, resulting in a relatively high concentration of observations (Figure 6/2).

In Table 6/5 the space use concentration pattern of the six animals are compared with the ratio of indigenous forest to plantation habitat available within the home ranges. A trend of lower use concentration is evident for those animals with relatively large proportions of plantation area (CZ1, CH1, CU5). Possible habitat preferences are explored further below.

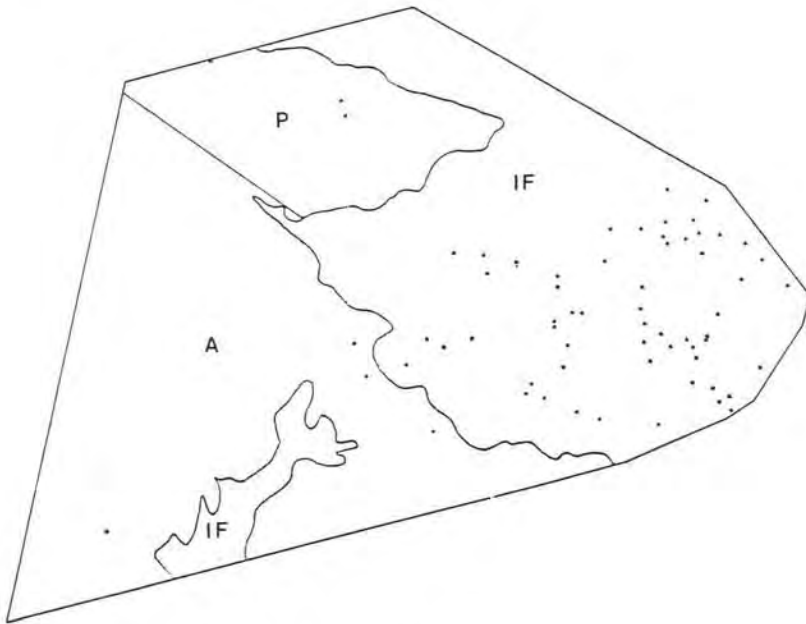


FIG.6/2 :DIAGRAM OF HOME RANGE AND INDEPENDENT LOCATIONS OF CU8(M)

(IF:Indigenous Forest P:Pine plantations A:Agricultural land)

For 5 individual bushpigs sufficient data were available to test the relative preference between indigenous forest (Afromontane forest: 2.4.2.1) and exotic timber plantations. The latter consisted primarily of *Pinus* spp. which occupied fynbos sites. Habitat preferences were determined by use/availability analysis (cf Neu et al. 1974). Using the proportion of indigenous forest versus pine plantation, within the individual home ranges the observed number of locations was compared with the expected number to test the null hypothesis that bushpig used either vegetation category in proportion to its occurrence (Table 6/5).

The preference pattern depicted in Table 6/5 was corroborated by testing habitat use in proportion to habitat availability involving all capture

data. Of the 378 captures of individual bushpigs, 215 occurred in the indigenous forest and 163 in pine plantations. However, according to the capture-days spent in each vegetation category, 203 captures were expected in the pine plantations and only 175 in the indigenous forest.

| TABLE 6/5: HABITAT PREFERENCE ANALYSIS | | | | | |
|---|------------------------------------|-----|--------------------------------------|---------------------------|-----------------------------|
| | Preference ratio * ₁ | n | Availability ratio * ₂ | G-Value * ₃ | Statistical significance |
| CC9(F) | 15,83 | 101 | 4,98 | 9,61 | P < 0,005 |
| CH1(M) | 1,40 | 36 | 0,52 | 7,78 | P < 0,01 |
| CU5(F) | 4,83 | 47 | 1,83 | 6,81 | P < 0,01 |
| CU8(M) | 9,43 | 73 | 3,97 | 5,17 | P < 0,05 |
| CZ1(F) | 2,27 | 36 | 0,61 | 13,50 | P < 0,005 |
| * ₁ Preference Ratio: Locations in indigenous forest to those in pine plantations | | | | | |
| * ₂ Availability ratio: Area of indigenous forest in home range to area of pine plantation | | | | | |
| * ₃ G-test with Yates' correction factor (Sokal and Rohlf 1969) | | | | | |

The capture success in the indigenous forest was thus significantly higher ($\chi^2 = 17,02$; $P < 0,005$). Applying the same test to three forest type categories within the indigenous forests (dry high forest vs medium-moist high forest vs moist/wet high forest) did not indicate that any of the forest types tested were used disproportionately to their availability.

However, two of the home ranges with a reasonable sampling base included a clear forest type moisture gradient. Fifty-nine percent of the indigenous forest within the home range of CC9(F) was either wet, moist or medium moist high forest, but this area contained 84 of the 97 locations (Fig. 6/3). A G-test with Yate's correction yielded a highly significant preference indication for the moister forest types ($G = 38,13$; $df = 1$; $P < 0,005$). For CW5(F) a disproportionate use of moist high forest in comparison to medium moist high forest was evident ($G = 27,78$; $df = 1$; $P < 0,005$).

In order to throw more light onto the possible reasons for the apparent preference for indigenous forest as compared to pine plantations, an analysis was carried out only incorporating data from the peak foraging period, i.e. from 18h00 to 24h00 (6.4). The independent locations of the 5 animals, as in Table 6/5, were pooled for this purpose. The test failed to indicate any preference for the indigenous forest during this period ($\chi^2 = 0,61$; $n = 77$ NS).

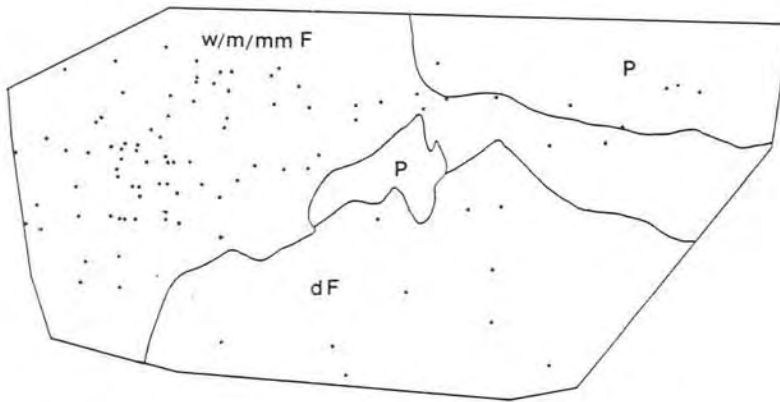


FIG.6/3 : DIAGRAM OF HOME RANGE AND INDEPENDENT LOCATIONS OF CC9(F)

(w/m/mm F : wet/moist/medium moist Forest P: Pine plantations
dF: dry Forest)

From reports and observations over the study area as a whole, bushpigs primarily occurred in Afromontane Forest, Subtropical Transitional Thickets (such as Kaffrarian Dune Thicket, Valley Bushveld, Alexandria Forest, Noorsveld) and Bushclump Savanna (2.4.2). Their presence was also reported and observed in parts of the Cape Fynbos Shrublands, Dune

Fynbos, Renosterveld and Karroid Shrublands, where these vegetation types adjoined forest, thicket or agricultural food sources.

6.2.2 Discussion

6.2.2.1 Home range size

As against an average home range size estimate of 7,2 km² in this study, Kingdon (1979) reports bushpig home range sizes up to 10 km². The largest home range determined by Cumming (1975) for warthog (*Phacochoerus aethiopicus*) was 3,3 km². Home range estimates for European wild boar males (*Sus scrofa*) were 3,8 km² and 3,5 km² for females. These home ranges were however extended to as much as 14 km² during winters with mast failures (Singer *et al.* 1981). The estimates of Mauget (1980) were somewhat higher: 2,4 - 4,3 km² for female wild boar and up to 7,0 km² for males. He cited estimates up to 20 km² in open country. Provisional home range estimates of between 1,8 and 7,8 km² were determined in Western Germany (Kalbhenn *et al.* 1985). Home range sizes of European wild boar in Europe generally do not exceed 5 km² (Briedermann 1986). Feral pig range estimates, averaged over four studies in North America and Hawaii, amounted to 2,7 and 1,4 km² for males and females respectively (*op. cit.* Baber and Coblentz 1986). Considerably larger home ranges were estimated for feral pigs in presumably marginal habitat: 50 km² (males) and 10 - 25 km² (females) in the arid Sierra foothills of California (Barrett 1978). In New South Wales, Australia, range sizes of 10-50 km² for males and 5-20 km² for females were reported (Giles 1978 *op. cit.* Baber and Coblentz 1986). Wild pigs only have home ranges when not forced to wander about due to marginal conditions of food availability (Frädriich 1968). Large-scale wanderings in search of food and water are implicated to explain these large home ranges (Baber and Coblentz 1986).

McNab (1963) was one of the earliest to demonstrate a relationship between home range size, body size and diet. More recent studies have confirmed this relationship in a variety of mammalian groups (Mace *et al.* 1983). The average adult body sizes of European wild boar (males 80 kg; females 65 kg; Briedermann 1986), warthog (males 80 kg; females 57 kg; Mason 1982) and bushpig (males 74 kg; females 69 kg;

Seydack 1983) are similar. Yet their normal home ranges differ substantially in size. Bushpig home ranges tend to be twice as large as those of warthogs and also to be larger than those of the European wild boar. However, the individual home range area characteristic of a species is not only a function of the nature and distribution of the food resources, but also the way in which the local population and not merely an individual, exploits those resources (Damuth 1981b). This brings population density into play, as expressed through group size and home range overlap. These factors cannot explain smaller home ranges in wild boar and warthog since group sizes and home range overlap tend to exceed those of bushpig. (4.3.1.1 and 11.1). Home range size is widely found to be inversely related to food resource density (e.g. Schoener 1971, Diong 1973, Altmann 1974, Verner 1977, Clutton-Brock and Harvey 1977 and 1978, Harestad and Bunnell 1979, Hixon 1980, Singer *et al.* 1981, Mace *et al.* 1983, Lima 1984, Voigt and MacDonald 1984, Baber and Coblentz 1986). The differences in home range sizes between the three suid species may accordingly be explained by the relative density of preferred food items encountered by these.

Apart from depending on minerals, water and other environmental factors, plant survival depends on the limitation of herbivore population growth. Herbivore regulation can ultimately only be achieved through limitations on the access to food, i.e. plant substance. Plants have basically two options in limiting food availability to herbivores: escape or defense. Escape may be either in space or time. Escape in space entails being rare or cryptic and escape in time involves, for example, deciduousity or long fruiting intervals. Defense may entail structural deterrents (e.g. spinescence), nutrient dilution (e.g. sclerophylly) and chemical deterrents (toxic substances, digestibility-reducing substances). Which defensive strategy is most appropriate depends on a variety of inter-linked factors, like climate and soil fertility, and its influence on the nature of food resource availability for herbivores is discussed in greater detail and fully referenced in chapter 8.2.

Here it is hypothesized that escape in space predominates as plant defensive strategy of potential food plants or organs in bushpig habitats. This leads to a dispersed food resource base, requiring relatively large home ranges. All plant defensive strategies effect the

dilution of plant food availability either in space or time, or both in cases of complete unpalatability (structural or chemical deterrents). In environments with strong seasonality, like temperate regions and tropical savannas, escape in time overrides escape in space and chemical defence. Seasonality favours the creation of bottlenecks of food availability through phenological changes of plants during cold or arid winters. These bottlenecks constitute escape in time. They result in regulation of herbivores and reduce pressure by them in subsequent relatively short periods of active growth and reproduction of the plants in spring and summer. A prerequisite for this strategy of escape in time is a sufficiency of nutrient, moisture and energy (temperature) resources during the limited periods of fast growth. If one of these is limiting, as for example in nutrient poor environments, sclerophylly or chemical defence becomes the predominating plant defensive strategy. Thus, escape in time as the predominating plant defensive strategy is associated with a lowered incidence of escape in space (i.e. being "rare") or chemical defence (i.e. being "unavailable"). Food resource under such conditions, as for the European wild boar as a temperate omnivore and the warthog as a savanna grazer, are relatively concentrated in space, thereby favouring relatively small home ranges.

In essentially non-seasonal environments plants or plant organs must defend themselves by escape in space, i.e. by becoming difficult to find or reach. If that is not possible, as in the case of perennial structures of ubiquitous plant species (evergreen leaves, subterranean organs), sclerophylly or chemical deterrents reduce the availability of these plant structures. The diet of bushpigs consists basically of plant reproductive organs, underground storage organs and soft, herbaceous plant parts (8.1). Reproductive organs, like fruit and seeds, are either rare or only infrequently available during fruiting years with polyannual intervals. Soft herbaceous plant parts (juvenile tissues, annuals) are also rare in bushpig habitats or only temporarily available. The underground storage organs of commonly occurring plant species are largely unavailable to bushpigs because of chemical defense or because they are out of reach of profitable rooting. Palatable subterranean plant tissues are rare (8.1; 8.2). For the bushpig as an omnivore in non-seasonal, mostly dystrophic habitats, suitable food items are dispersed over space and time. The relatively large home

ranges associated with the dispersed food resource base found in this study do not however, necessarily apply to home range sizes of bushpigs in more eutrophic environments (like the Valley Bushveld of the Eastern Cape or tropical forest on more nutrient-rich substrates in Central and West Africa).

6.2.2.2 Habitat factors

All suids, with the exception of warthogs, occur in habitats with good cover (Frädriich 1974). Habitat selection generally appears to be related to the availability of food, cover and water (Diong 1973, Hennig 1981). Habitats providing a combination of food and cover are ideal for the European wild boar, whereas large areas without cover are avoided (Hennig 1981). Surface water and moist areas are considered essential throughout the year (Pine and Gerdes 1973). Hasselbach (1970) considers opportunities for wallowing an important habitat factor for European wild boar. Similar habitat requirements are reported for bushpig. Habitat with sufficient moisture to support dense vegetation throughout the year and thus with moderately soft ground, is suitable (Kingdon 1979). All forests and most riverine environments form suitable habitat for bushpig. Important habitat features for the giant forest hog (*Hylochoerus meinertzhageni*) are cover, the presence of water and access to savanna (D'Huart 1978). Requiring relatively large quantities of soft herbaceous plant material, mainly grass as food, the giant forest hog typically occupies the forest savanna ecotone. The warthog is essentially a grazer (Mason 1982, Owen-Smith 1982) and the most important habitat factor is thus the presence of short grass communities (Cumming 1975, Mason 1982, Rodgers 1984). Holes as retreats for the night are also important (Cumming 1975, Mason 1982). For the three African suid species, the bushpig, giant forest hog and warthog, there is a declining dependence on cover and an increasing dependence on grass as a source of food. The associated habitat gradient is one from spatiotemporally stable, dense vegetation types, like forest, to the forest/savanna ecotone and open grasslands.

The habitat/species interrelationships discussed suggest that food is the primary habitat factor and that cover is of secondary importance. The niche differentiation of warthog involves the adaptation to utilize

primarily grasses and the species is secondarily adapted to cope with a general lack of good cover. The bushpig on the other hand, occupies well-covered habitat because its omnivorous food requirements can only be met in such environments (8.2.2) and not because the species critically depends on cover. However, the bushpig adapts behaviourally to a well-covered habitat in terms of predator avoidance (6.4.2.5). The suid species must satisfy their food requirements from the stratum of ca 0,5 m above and below ground. Within this layer sufficient vegetable matter, which is also digestible, must be available. For the omnivorous suids this entails the availability of plant reproductive organs (fruit, seeds), plant storage organs (roots, rhizomes, tubers) and soft herbage (herbs). For the warthog as a grazer, palatable grasses (mainly short grasses) have to be available. Food availability in the layer accessible to suids may be categorized into three classes:

- (I) density of vegetable matter inadequate (arid environments, desert, steppe);
- (II) dominated by grasses, at the expense of other ground vegetation, and dependent on adequate solar radiation, requiring any canopy to be sparse or absent (savanna, grasslands).
- (III) dominated by vegetation reducing sunlight reaching the ground layer and thereby limiting the incidence of heliophile herbaceous ground vegetation (forest, thickets).

The interaction between environment and vegetation characteristics and their implications in determining the nature of herbivore food resources will be discussed in detail in later chapters (8.2; 8.3). Here it suffices to note that the non-overlapping distribution patterns of bushpig and warthog are consistent with the hypothesis that food is being the decisive habitat component. Conditions favouring vegetation capable of supporting one species exclude that suitable for the other. Cover is merely a corollary of nutritionally adequate bushpig habitat. The same is valid for the availability of water for all suid species. Water-courses often support vegetation on which the omnivorous suids, in particular, feed (cf Dardaillon 1985). This clarification is necessary in view of the fact that cover and water are emphasized as habitat factors in the bushpig (Dorst and Dandelot 1970, Smithers 1971, Kingdon 1979,

Haltenorth and Diller 1980, Jones 1984), without much mention of the nature of the food resources as critical factor.

Within the constraints of adequate food resources, suids exhibit great flexibility and adaptability to a wide range of habitat conditions (cf Santiapillai and Chambers 1980, Dardaillon 1985). This is also true of bushpig. Tinley (1977), for example, describes the species as abundant throughout the Gorongosa system, from mountain summits to mangrove marshes; it is only absent from the most extensive grasslands. The fact that agricultural cultivation often leads to regional extensions in the distribution of certain suid species is consistent with the view that food is the primary habitat factor (Frädriich 1964, Diong 1973); a phenomenon also noted for the bushpig (Smithers 1971, this study).

A clear preference for indigenous forest over pine plantations was shown above (6.2.1.2). However this was not maintained at night during the main foraging period from 18:00 to 24:00. Pine plantations offer comparatively little shelter, but apparently have some food value (*Pteridium* patches, *Rhizopogon* sp: 8.1). The poorly sheltered environments are evidently frequented at night, while day foraging and resting are concentrated in the indigenous forest, which offers more cover and a cooler micro-climate. Many of the non-sequential tracking localities were determined during the day, thereby somewhat biasing the results as far as habitat preference in terms of food resource availability is concerned. The results do however, indicate the importance of cover for day-time activities.

The habitat preference gradients within the home ranges of CC9 (w/m/mmHF > dHF Fig. 6/3), CW5 (mHF > mmHF) and CU8 (indigenous forest > pine plantations > pasture; Fig. 6/2) explain the greater use concentration (6.2.1.2) of these animals compared to CH1, CU5 and CZ1. Portions of indigenous forest and pine plantations are interspersed within the home ranges of the latter three animals and there are no mappable forest type differences. The preference for the moister portions of the indigenous forests is in agreement with the observations of Phillips (1926a). A fully convincing explanations for this preference could not be identified.

Von Boetticher (1933) and Kingdon (1979) are among the authors who describe the distribution of bushpigs as following that of forest. In savannas they are found only in association with forest or bush patches, mostly of riverine origin. Much importance is placed on the moisture factor, particularly in relation to ground softness for rooting (Jones 1984). In the Cape Province bushpigs occur primarily in vegetation types which are dominated by woody elements (6.2.1.2), but some of these are comparatively arid (Valley Bushveld, Noorsveld). There is evidence that Valley Bushveld maintains the densest bushpig populations (11.1). The primary importance of availability of food as a habitat factor is further supported by the fact that bushpigs occur in Fynbos and Karroid Shrublands only when these are associated with woody vegetation or cultivation.

6.3 Movement patterns

6.3.1 Results

6.3.1.1 Daily range

The average diel distance ranged was 3 034 m ($n = 44$; $s = 1269$; varying between 480 and 5 840 m). The range distances were determined from straight-line connections of half-hourly positions and thus constitute minimum estimates. No difference between the sexes was evident ($t = 0,80$ $df = 42$; NS). Distances moved differed significantly between successive 3-hour periods ($F = 10,02$; $df = 7$; $P < 0,001$; Table 6/6). There were no significant differences between the winter and summer months in total daily distances moved ($F = 0,66$; $df = 1$; NS).

The average rate of movement was 238 m/h active ($n = 43$; $s = 111$). The maximum recorded rate, maintained over a period of 30 minutes, was 1 660 m/h. Winter and summer averages were similar ($t = 0,32$; $df = 41$; NS). In the context of territorial maintenance, mobility about the home range is considered important. Mitani and Rodman (1979) suggested a measure of home range defendability based on the frequency with which an individual can encounter the boundary of its range, given its normal day range and the size of the home range. Their index of defendability (D)

| TABLE 6/6: AVERAGE RANGING DISTANCES (IN METER) | | | | | | | | | |
|---|----------------|---------|---------|-------|-------|-------|--------|---------|------------------------|
| | 3-Hour periods | | | | | | | | Totals for diel period |
| | 15-18 h | 18-21 h | 21-24 h | 0-3 h | 3-6 h | 6-9 h | 9-12 h | 12-15 h | |
| <u>Summer</u> | | | | | | | | | |
| \bar{X} | 303 | 658 | 513 | 458 | 246 | 395 | 305 | 77 | 2 904 |
| n | 26 | 26 | 26 | 26 | 26 | 22 | 22 | 21 | 21 |
| s | 386 | 456 | 415 | 581 | 370 | 403 | 567 | 165 | 1 416 |
| <u>Winter</u> | | | | | | | | | |
| \bar{X} | 439 | 808 | 678 | 241 | 248 | 459 | 270 | 81 | 3 153 |
| n | 25 | 25 | 25 | 24 | 24 | 24 | 24 | 23 | 23 |
| s | 343 | 605 | 584 | 393 | 335 | 547 | 440 | 159 | 1 137 |
| Pooled over seasons | | | | | | | | | |
| \bar{X} | 370 | 731 | 594 | 354 | 247 | 428 | 286 | 79 | 3 034 |
| n | 51 | 51 | 51 | 50 | 50 | 46 | 46 | 44 | 44 |
| s | 368 | 534 | 507 | 507 | 350 | 479 | 499 | 160 | 1 269 |

Significant differences in average ranging distances between 3-hour periods are shown in Table 6/7.

| TABLE 6/7: TIME PERIOD COMPARISONS* <i>VIDE</i> TABLE 6/6 | | | | | | | | | |
|---|-------|-------|-------|-------|-----|-----|-----|------|-------|
| 3-Hour Periods | | 15-18 | 18-21 | 21-24 | 0-3 | 3-6 | 6-9 | 9-12 | 12-15 |
| In decreasing order of average ranging distances | 18-21 | + | | | + | + | + | + | + |
| | 21-24 | + | | | + | + | | + | + |
| | 6-9 | | - | | | | | | + |
| | 15-18 | | - | - | | | | | + |
| | 0-3 | | - | - | | | | | + |
| | 9-12 | | - | - | | | | | + |
| | 3-6 | | - | - | | | | | |
| | 12-15 | - | - | - | - | | - | - | |
| * Ranging distance of row period significantly higher than column period: +; if significantly lower:- ($\alpha = 0,05$) | | | | | | | | | |
| Data pooled over SEASON | | | | | | | | | |

was quantified by the ratio of the average day range to the diameter of a circle (d') with an equal area to the observed home range (A and $d' = 4A/\pi$). For bushpig in the present study

$$D = \frac{d}{d'} = \frac{3\,034\text{ m}}{3\,030\text{ m}} \approx 1$$

For data of primate species by Mitani and Rodman (1979) territorial species had defendability indices of 1 or higher. It is accordingly suggested that bushpig mobility is of a magnitude allowing territoriality in spite of their relatively large home ranges.

In Figure 6/4 (a-q) selected ranging paths of successive diel periods are shown in relation to the respective home range boundary configurations. The diagrams reveal large-scale day-to-day variation in ranging path lengths. Large portions of the home ranges may be traversed within periods of one to four days. There is a tendency for distances travelled on successive days to be inversely related, i.e. relatively long day ranging distances are followed by shorter ones and vice versa. On average, successive day range lengths differ by a factor of 2,04. This factor just fails to differ significantly from the equivalent factor for non-consecutive day range lengths ($U = 61$; $n_1 = 9$; $n_2 = 9$; NS).

6.3.1.2 Factors underlying movement patterns

Animal movement is influenced mainly by foraging requirements and social factors. Increased ranging activity is generally associated with reduced food availability (Barrett 1978, Clutton-Brock and Harvey 1977, Groot-Bruinderink 1977, Owen-Smith 1982, Singer *et al.* 1981). Larger groups, with larger total food requirements, often range further than smaller groups (Clutton-Brock and Harvey 1977, Van Schaik *et al.* 1983).

Radio-tracking of bushpig took place during 1984 and 1985, primarily during the former year. A good yellowwood fruit year (*Podocarpus latifolius*) is presumed to have increased food availability from April to August 1984. The seasonally differentiated day range distances (Table 6/8) were however not found to differ significantly over the seasons ($F = 0,35$; $df = 3$; NS).

FIG.6/4 :SELECTED DAY RANGING ROUTES OF RADIO-TRACKED BUSHPIGS

Ranging routes for

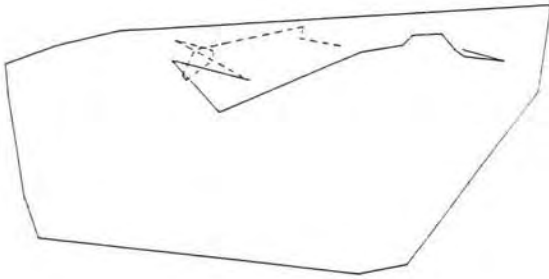
1st _____

3rd.....

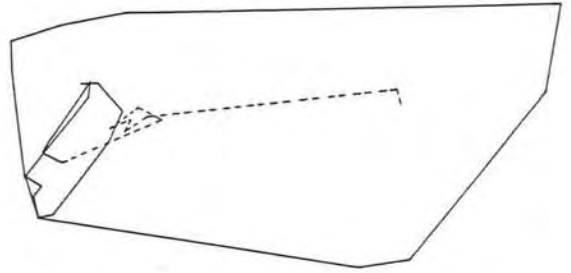
consecutive diel periods from 15.00"-15.00"

2nd - - - - -

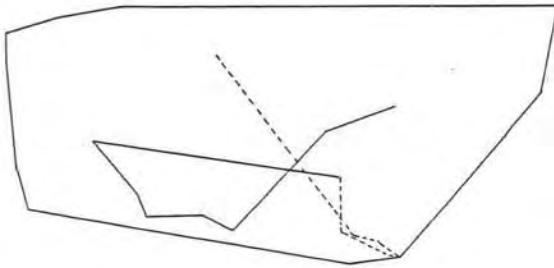
4th - . - . - .



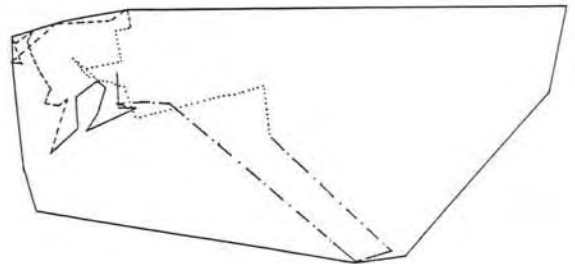
a) CC9(F)
16/17-17/18.1.1984



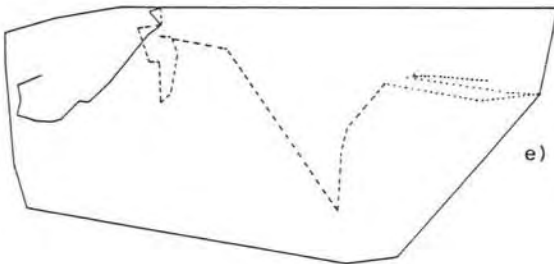
b) CC9(F)
16/17-17/18.7.1984



c) CC9(F)
18/19-19/20.7.1984

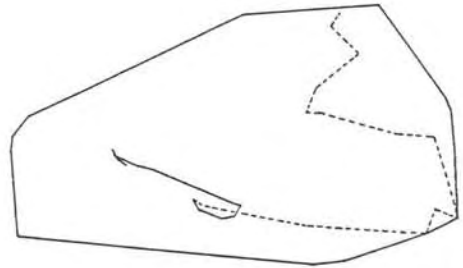


d) CC9(F)
26/27-29/30.8.1984

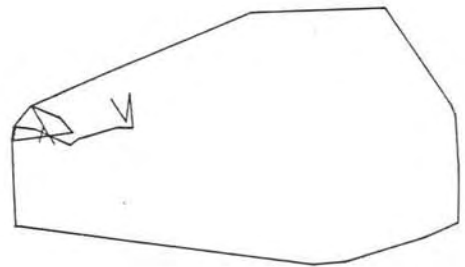


e) CC9(F)
9/10-11/12.12.1984

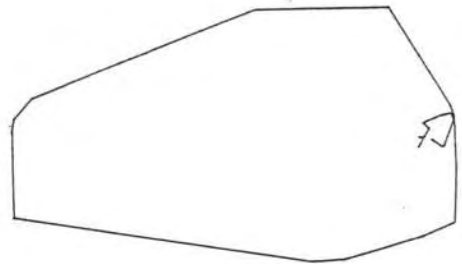
f) CH1(M)
9/10-10/11.1.1985



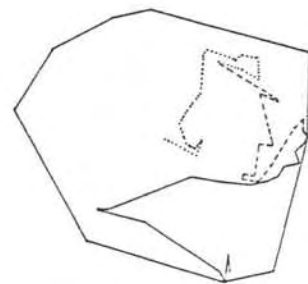
g) CH1(M)
13/14.1.1985

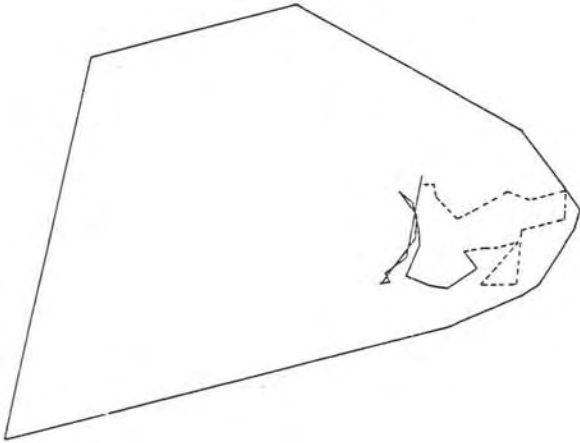


h) CH1(M)
21/22.1.1985

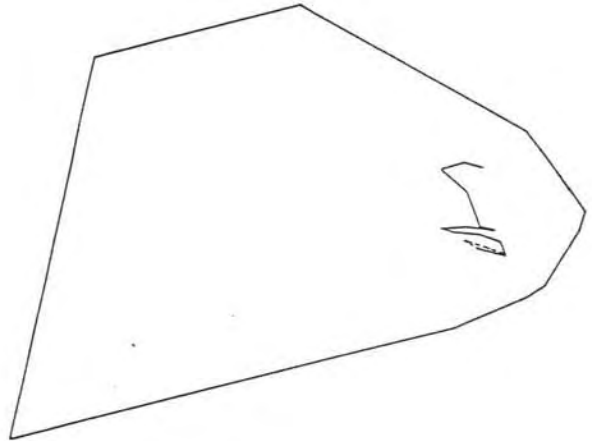


i) CU5(F)
9/10-11/12.4.1984

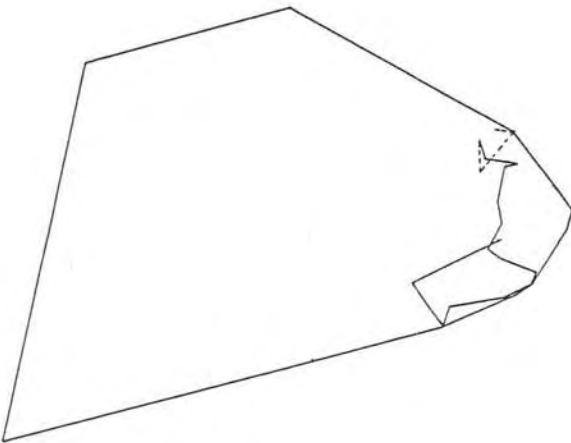




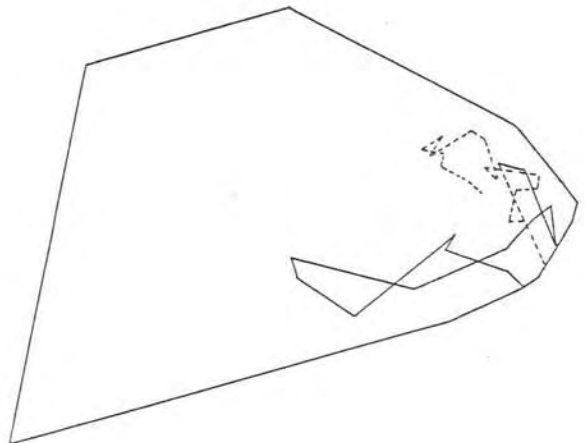
j) CUB(M)
30/1-1/2.10.1984



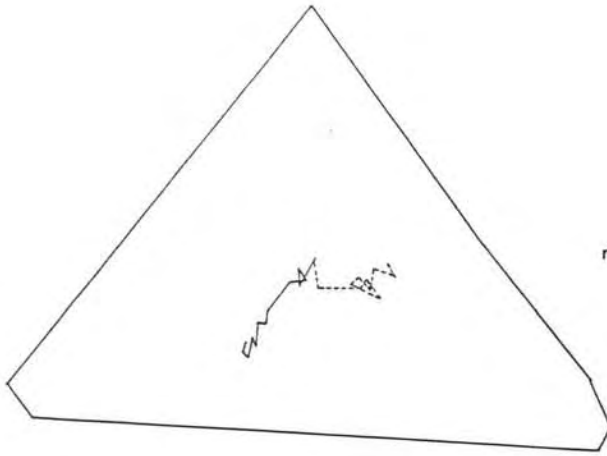
k) CUB(M)
3/4-4/5.10.1984



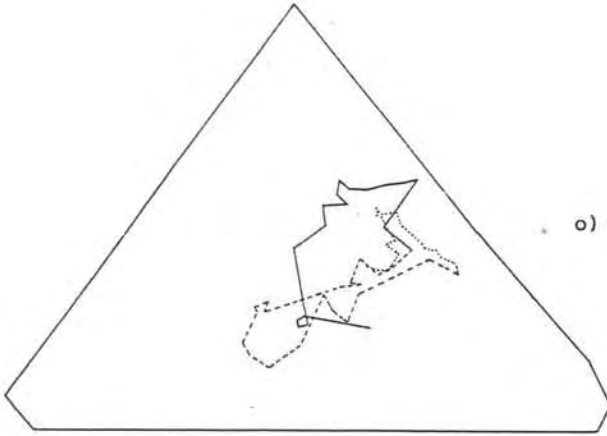
l) CUB(M)
16/17-17/18.10.1984



m) CUB(M)
28/29-29/30.10.1984

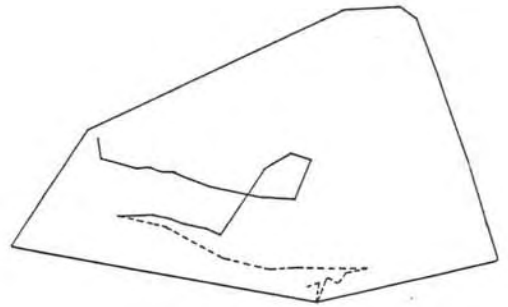


n) CW5(F)
18/19-19/20.3.1984

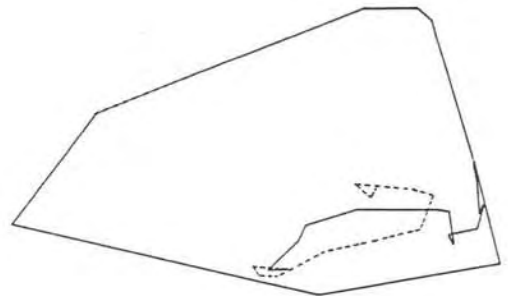


o) CW5(F)
30/1-2/3.5.1984

p) CZ1(F)
3/4-4/5.6.1985



q) CZ1(F)
15/16-16/17.7.1985



| Season | Months | \bar{X} (m) | n | s |
|--------|-----------|---------------|----|-------|
| Summer | Dec-Feb | 3 080 | 10 | 1 337 |
| Autumn | March-May | 2 606 | 7 | 1 112 |
| Winter | June-Aug | 3 056 | 16 | 1 134 |
| Spring | Sept-Nov | 3 234 | 11 | 1 571 |

Day range distances of animals CH1, CU5 and CZ1 (\bar{X} = 2830 m) which had large proportions of pine plantation in their home ranges did not differ significantly from those of animals CC9, CU8 and CW5 (\bar{X} = 3097) with more indigenous forest than pine (t = 0,63; df = 39; NS). Mauget (1980) found that European wild boar moved at a faster rate under conditions of suboptimal food availability (Mauget 1980). The mean rates of bushpig movement in pine plantations were 338 and 247 m/h for the periods 18:00 - 21:00 and 21:00 - 24:00 respectively. The equivalent rates in indigenous forest were 222 and 200 m/h. This is in accordance with the expectation that the animals would move more slowly in the presumably more productive indigenous forest environment during the main foraging periods. The differences in the rates of movement between the two habitat types were however not significant (t = 1,38; df = 41; NS and t = 0,71; df = 42; NS). The interpretation of the possible relationship between ranging behaviour and food availability was hampered because of the sizes of the groups to which the tracked animals belonged (4.3.1.3).

One or more of the following factors may explain why significant relationships between food availability and movement could not be established:

- (I) There were no substantial differences in food availability over space or time during the tracking programme.
- (II) The level of sampling was inadequate to identify statistically significant differences, given the large day-to-day variability.
- (III) Confounding social factors. The influence of reproductive behaviour, territorial patrolling (4.3.2.2.c) and rearing

(4.3.3.2; cf Thomas and Kolbe 1942) on movement patterns may have overridden and blurred any relationship between food availability and ranging extent.

6.3.2 Discussion

A mean daily ranging distance of 3,0 km was determined for the bushpig during this study. Of this movement, 44% on average took place between 18:00 and 24:00. In comparison, a mean daily ranging distance of 4,2 km was determined for the European wild boar in France (Mauget and Sempère 1978). Rates of movement for European wild boar in the United States of America were 80 m/h during a winter with abundant mast; 150 m/h during the summers and 400 m/h during a winter with mast failure (Singer *et al.* 1981). Mean locomotion speed for the same species in France was 1 260 m/h, ranging between 430 and 3 120 m/h (Mauget and Sempère 1978). The average rate of movement for bushpig was 238 m/h, with a recorded maximum of 1 660 m/h, maintained over a period of 30 minutes (6.3.1.1).

Diong (1973) reported on feral hogs in Malayan forests with stomachs filled with sugar cane from fields 8 - 16 km away. Feral hogs were recorded to move 5 and 7,5 km to sorghum fields (Springer 1977 *op. cit.* Wood and Brenneman 1980). The maximum distance moved by wild boar in the Netherlands was determined to be ca 9 km, but reports of up to 15 km were mentioned (Groot-Bruinderink 1977). There are more reports of long distance journeys in the literature, but it is usually difficult to determine whether migratory movements or larger home ranges are involved (Briedermann 1986). Bushpig are also believed to make long-distance forays to agricultural fields but no evidence was obtained in the present study. The maximum diel ranging distance recorded was 5,8 km (6.3.1.1).

Wild boar often moved across an entire seasonal range in a 24-hour period (Singer *et al.* 1980). Males were often found to explore their complete home ranges within a few days, but this was seldom the case with feral sows (Wood and Brenneman 1980). For the bushpig, the average day ranging distance is approximately equivalent to the diameter of the average home range. Bushpig home ranges are regularly traversed within one to 4 days (Figures 6/4 a-q). Both sexes are equally involved and

territorial patrolling is considered to be an important factor underlying this behaviour (4.4.2.3). Only during times of farrowing and early lactation "does the bushpig restrict itself for any length of time to a portion of its extensive range" (Thomas and Kolbe 1942; this study 4.3.3.2). Restriction of movement during the early rearing phase is universally reported for various suid species (Sludskii 1956, Frädrieh 1968, Cumming 1976, Kurz and Marchinton 1972, Jezierski 1977, Barrett 1978, Young 1981, Singer *et al.* 1981).

Frädrieh (1971 *op. cit.* Breytenbach 1977) states that bushpig movements are generally irregular, although cases of regular movement have been described. For example, Breytenbach (1977) found that when animals were seen feeding on an abundant food source at a certain time of the day, they could in most cases be found in the same vicinity on consecutive days. According to the observations of Jobaert (1958), bushpig normally do not frequent the same area or use the same resting sites on consecutive days. The same was found in this study, indicating that shelter is not a limiting habitat factor as suggested by Kingdon (1979).

Two important factors often determining ranging parameters could not be clarified (6.3.1.2), namely food availability and group size. These await future study. Ranging behaviour during ironwood (*Olea capensis* ssp. *macrocarpa*) fruit years should be compared with that during periods of food shortage. It is likely that results similar to those of Smythe, Glanz and Leigh (1982) for the agouti (*Dasyprocta punctata*) and the paca (*Cuniculus paca*) on Barro Colorado Island would be obtained. Both species forage longer and range farther during food shortages. Concerning group size, Van Schaik *et al.* (1983) found a clear increase in day journey length with group size during their study of omnivorous long-tailed macaques (*Macaca fascicularis*). In their search for dispersed food items long-tailed macaques tended to avoid the close proximity of others during foraging. The authors suggest that avoidance of neighbours during searching may indicate that an individual's foraging success will be lower when it has to search in patches covered by others. This implies that foraging efficiency decreases when other individuals are allowed to join at the foraging site or when the searching individual is getting behind, which would happen if it allows others to overtake. This "pushing forward" effect may be interpreted as the

behavioural expression of competition through local depression of food availability and is the most likely mechanism underlying the longer day journeys of larger groups (Van Schaik et al. 1983). Bushpig groups also tend to forage in "extended formation" and a similar mechanism may apply.

6.4 Activity

6.4.1 Results

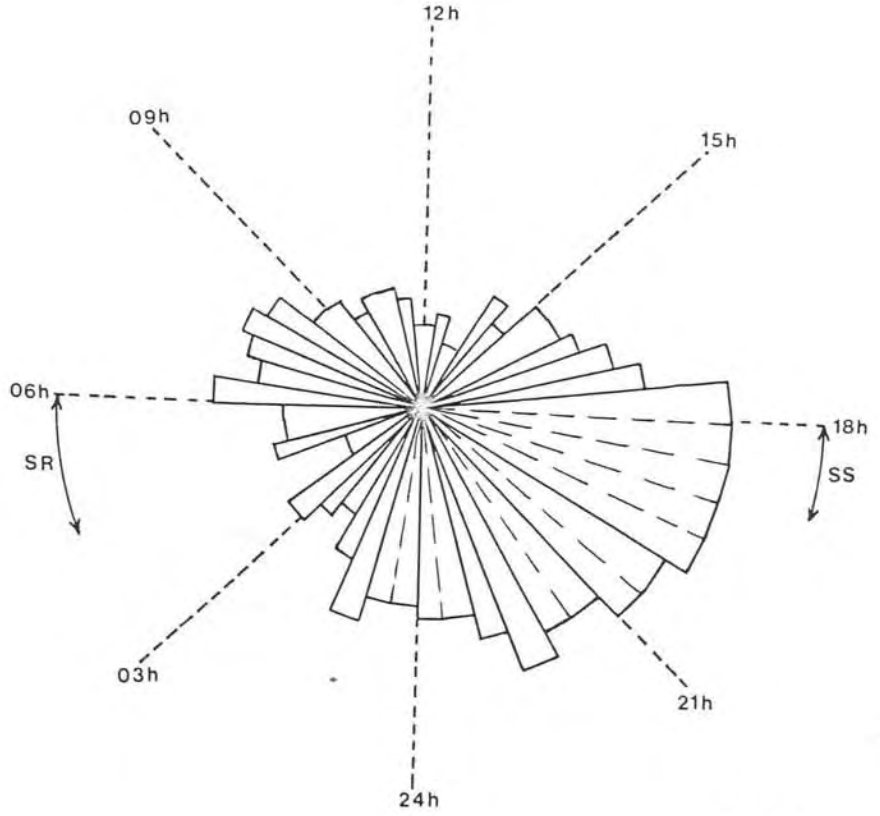
6.4.1.1 Basic activity pattern

Chronological half-hourly activity sums from individual bushpigs tracked for full 24-hour periods are presented to scale in Figures 6/5a and 6/5b (n = 22 each for summer and winter). A biphasic activity pattern is evident in both seasons. The primary activity period usually started sometime before sunset and extended somewhat beyond midnight in summer. During winter it was often terminated at or before midnight. A secondary activity period occurred during the morning hours, mainly between 6 h and 9 h. Such a double-peaked activity pattern, where the first peak exceeds the second one, has been termed a "bigeminus" pattern (Aschoff 1966). The bushpig must accordingly be considered primarily nocturnal, although not exclusively so.

The implication that foraging takes place mainly at night is supported by stomach fill analyses. The stomach fill masses of animals shot during the morning were taken as indices of night foraging, those from animals shot in the evening as indices of day foraging. All stomach fills from animals ≥ 50 kg were used (Table 6/9).

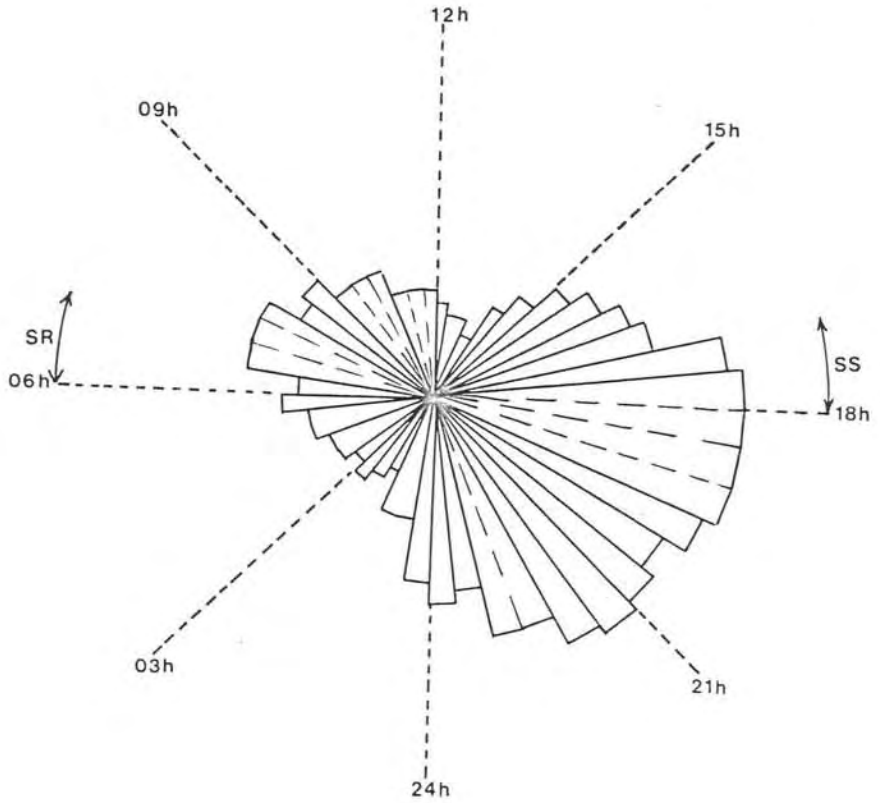
FIG.6/5 : OVERT SEASONAL ACTIVITY PATTERNS OF BUSHPIG

a) SUMMER
(Oct-March)



SR and SS
Ranges of
Sunrise and
Sunset

b) WINTER
(April-Sept)



| TABLE 6/9: AVERAGE BUSHPIG STOMACH FILL MASSES IN KG (n) | | |
|--|-----------------------|---------------------|
| | Index: night foraging | Index: day foraging |
| Summer | 3,85 (22) | 2,08 (11) |
| Winter | 3,27 (22) | 2,86 (18) |

A two-way analysis of variance, adjusted for unequal sample sizes (Steel and Torrie 1960), was applied to the data. The indices of night foraging were significantly higher than those for day foraging ($F = 6,61$; df 1 and 69; $P < 0,05$). Inspection suggested a season/foraging period interaction, implying relatively more day foraging during winter. Statistical significance of the interaction component was approached, but not reached ($F = 2,57$; df 1 and 69, NS).

6.4.1.2 Day-to-day variability in activity

Whereas Figures 6/5a and b provide an indication of the average, overt activity rhythm, Figures 6/6 to 6/12 show the wide day-to-day variability. These actograms were compiled with data from half-hourly activity determinations from 7 bushpigs tracked over full 24-hour periods. A temporally rather opportunistic pattern of daily activity is exhibited. Substantial variability was found in both chronological allocation of activity and activity period lengths for individual days and also on successive days by the same individuals. Some of the possible underlying factors are explored in the subsequent sections.

6.4.1.3 Analysis of variability

Analysis of activity was carried out on data from 8 radio-monitored free-ranging animals and systematic observations on captive bushpigs in the study enclosure (Tables 6/10 and 6/11).

Average daily activity times were 14,6 hours for males and 13,1 hours for females. They did not differ significantly ($t = 1,50$ $df = 41$, NS).

| TABLE 6/10: TOTAL TIME ACTIVE PER DAY (IN HOURS) | | | | |
|--|-----------------------|------------|------------------|------------|
| | Free-ranging Bushpigs | | Captive Bushpigs | |
| | Summer | Winter | Summer | Winter |
| | \bar{X} | 13,6 | 13,8 | 9,4 |
| s | 3,99 | 2,73 | 2,28 | 3,22 |
| Range | 6,5 - 20,0 | 6,5 - 19,0 | 6,5 - 14,5 | 7,0 - 17,0 |
| n | 20 | 23 | 10 | 9 |

n = number of 24-hour periods monitored

Total time active per day was significantly higher for free-ranging than for captive animals in summer ($t = 3,07$ $df = 28$; $P < 0,01$), but not in winter ($t = 1,81$; $df = 30$; NS) (Table 6/10).

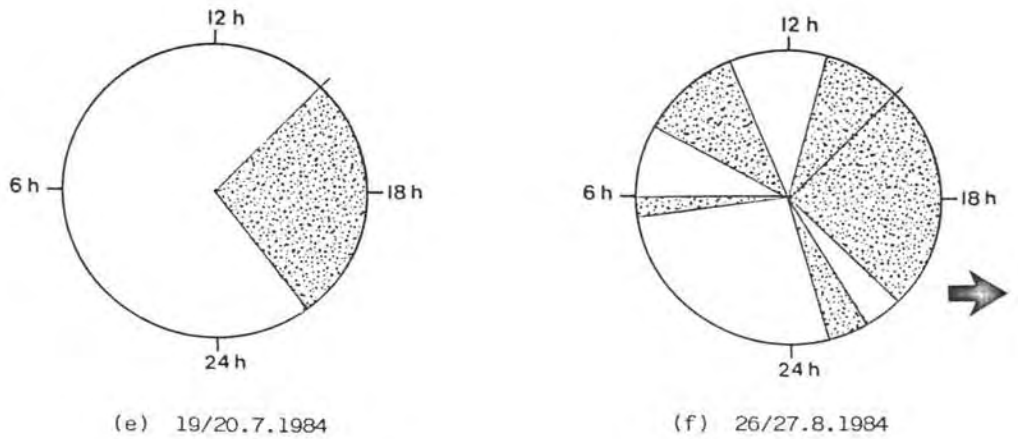
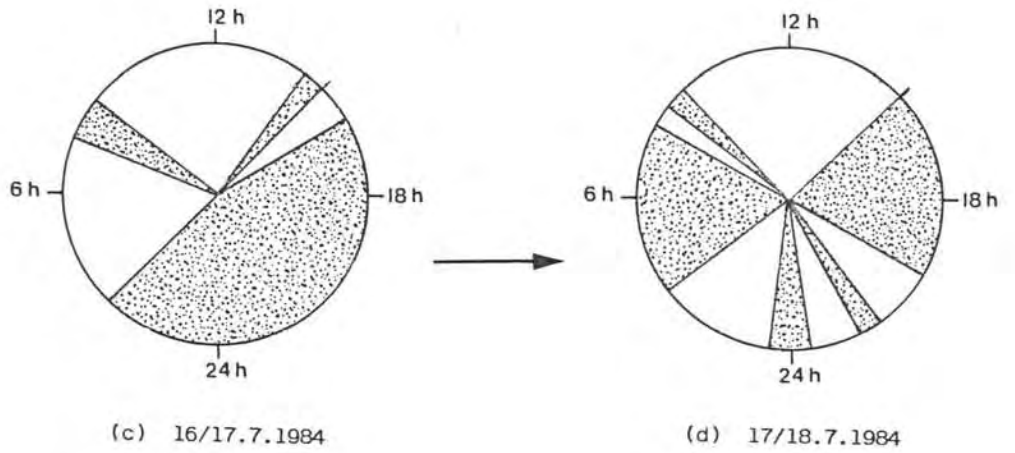
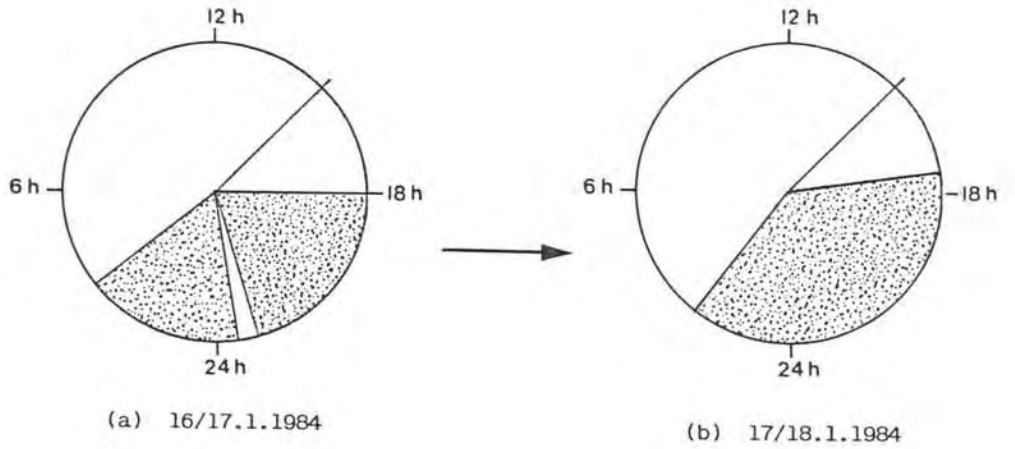
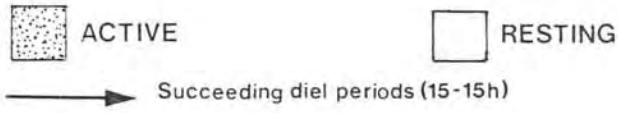
The analysis of variance for Table 6/11 produced two significant sources of variation: time of day and free-ranging versus captive animals activity.

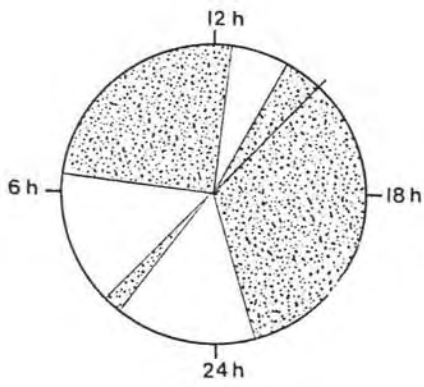
| TABLE 6/11: AVERAGE PERCENTAGE TIME ACTIVE/3h PERIODS | | | | | | | | | |
|---|--------|----------------|------------|------------|----------|----------|----------|-----------|------------|
| | | 3-HOUR PERIODS | | | | | | | |
| | | 15-18 h | 18-21 h | 21-24 h | 0-3 h | 3-6 h | 6-9 h | 9-12 h | 12-15 h |
| Free-ranging bushpigs | Summer | 54 | 95 | 78 | 57 | 39 | 60 | 43 | 29 |
| | Winter | 75 | 96 | 80 | 40 | 42 | 55 | 40 | 36 |
| Captive bushpigs | Summer | 18 | 80 | 52 | 45 | 53 | 53 | 5 | 7 |
| | Winter | 54 | 93 | 65 | 33 | 30 | 59 | 50 | 11 |
| ASSOCIATED SAMPLE SIZES (n) | | | | | | | | | |
| Free-ranging bushpigs | Summer | 26 | 26 | 26 | 26 | 26 | 21 | 21 | 20 |
| | Winter | 25 | 25 | 25 | 24 | 24 | 24 | 24 | 23 |
| Captive bushpigs | Summer | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 10 |
| | Winter | 9 | 9 | 9 | 9 | 9 | 9 | 9 | 9 |

n = number of 24-hour monitoring periods

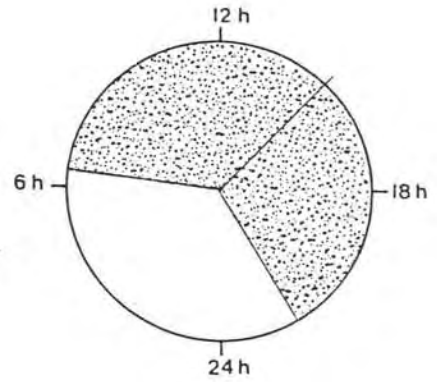
See page 297 for ANOVA table.

FIG.6/6 : ACTOGRAMS OF BUSHPIG CC9 (F)

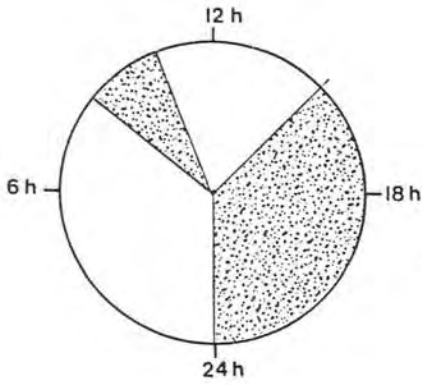




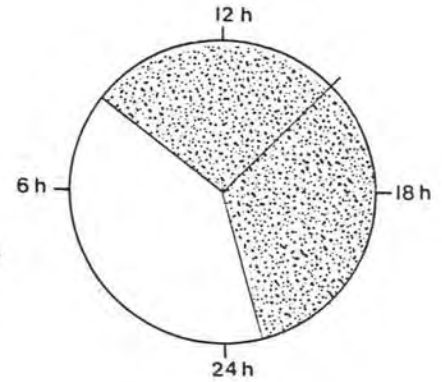
(g) 27/28.8.1984



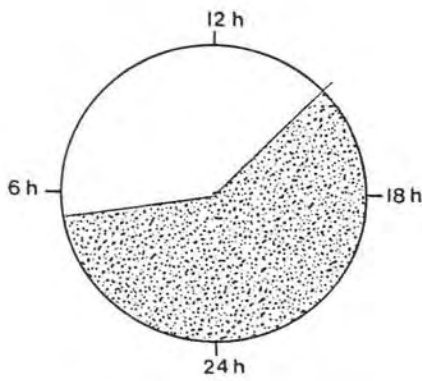
(h) 28/29.8.1984



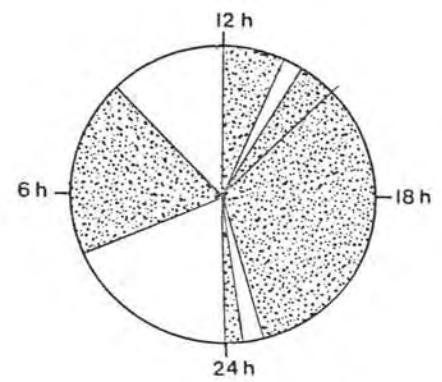
(i) 29/30.8.1984



(j) 30/31.8.1984



(k) 12/13.11.1984



(l) 9/10.12.1984

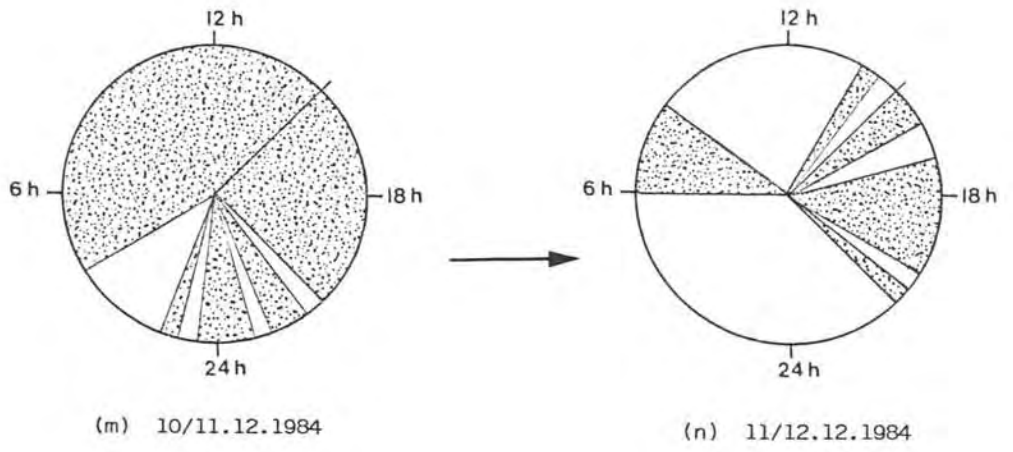


FIG.6/7 : ACTOGRAMS OF BUSHPIG CE6 (M)

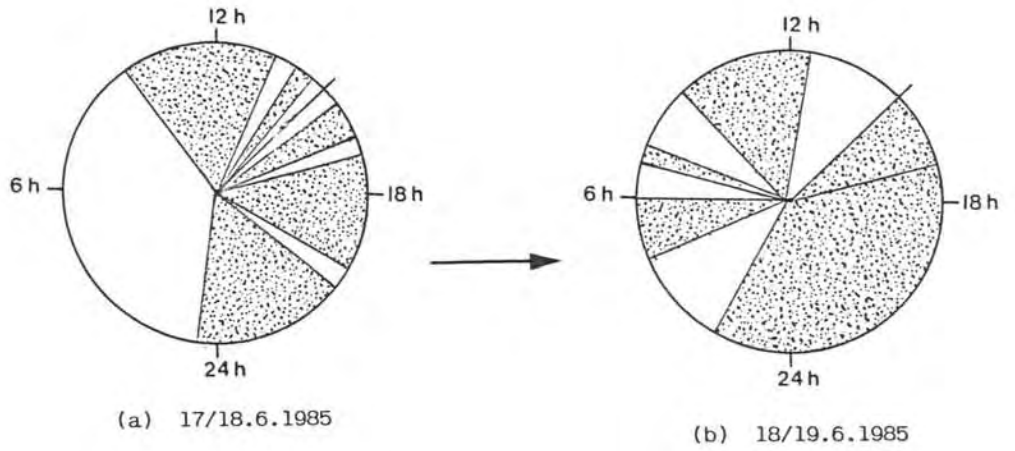
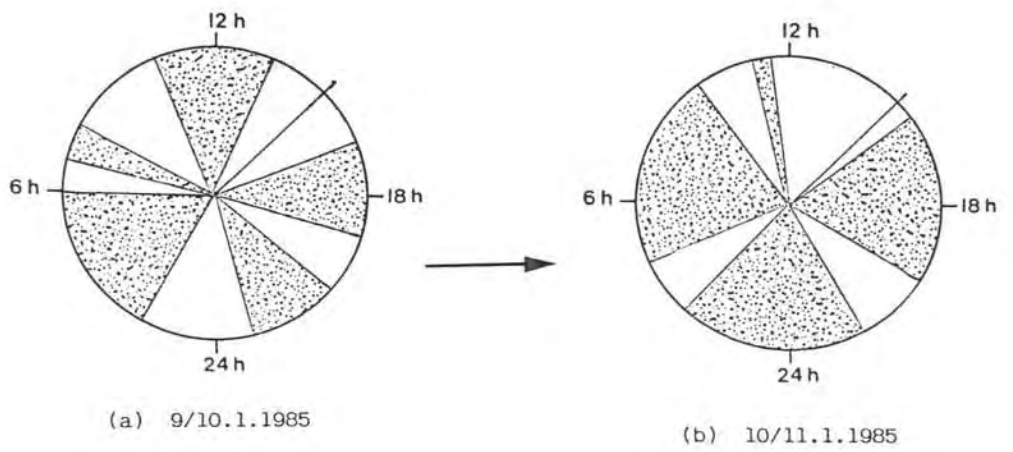
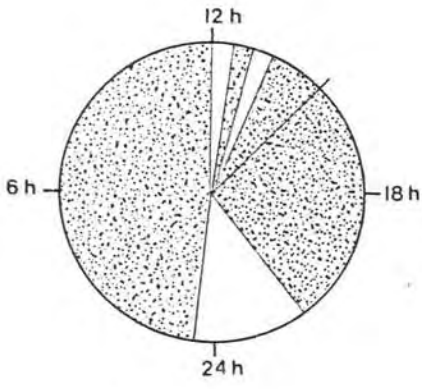
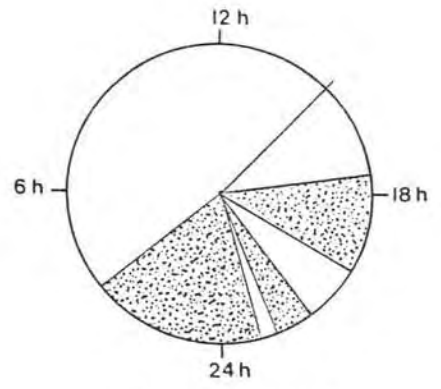


FIG.6/8 : ACTOGRAMS OF BUSHPIG CH1(M)



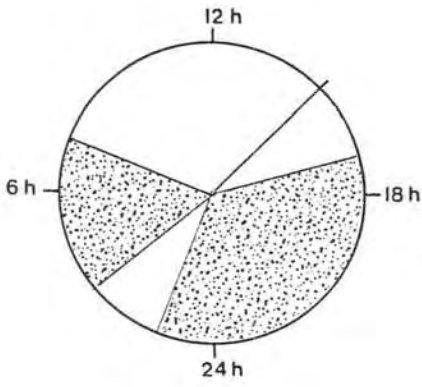


(c) 13/14.1.1985

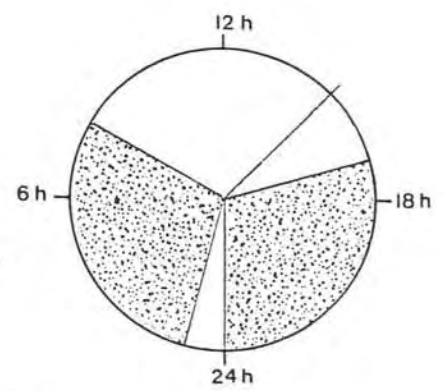


(d) 21/22.1.1985

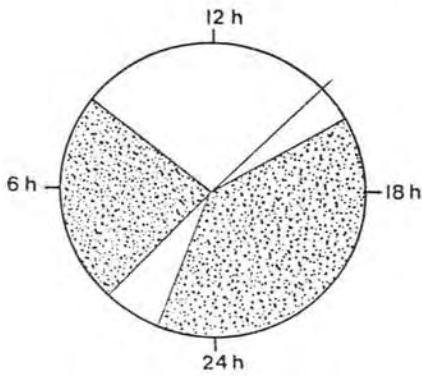
FIG.6/9 : ACTOGRAMS OF BUSHPIG CU5(F)



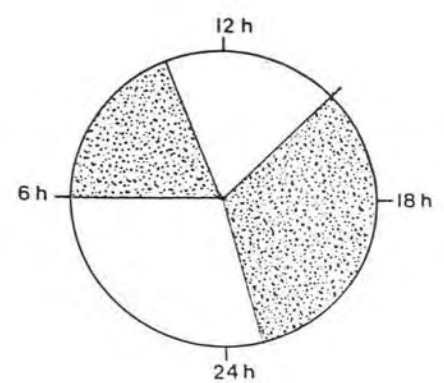
(a) 9/10.4.1984



(b) 10/11.4.1984

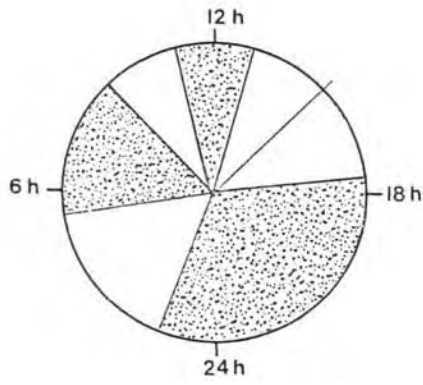


(c) 11/12.4.1984

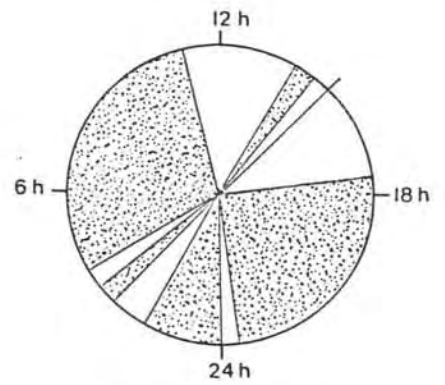


(d) 3/4.7.1984

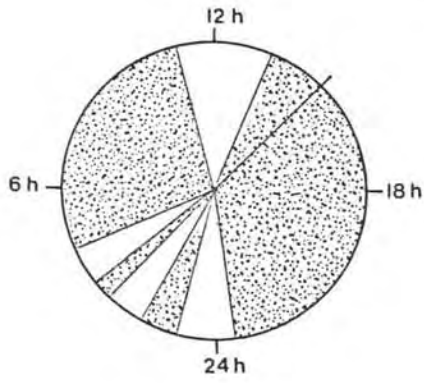
FIG.6/10: ACTOGRAMS OF BUSHPIG CUB (M)



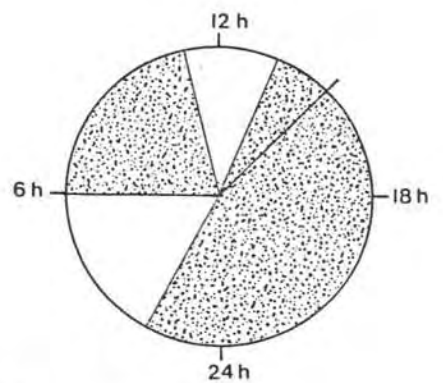
(a) 17/18.9.1984



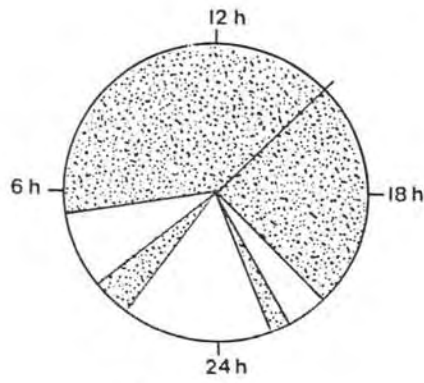
(b) 30/1.10.1984



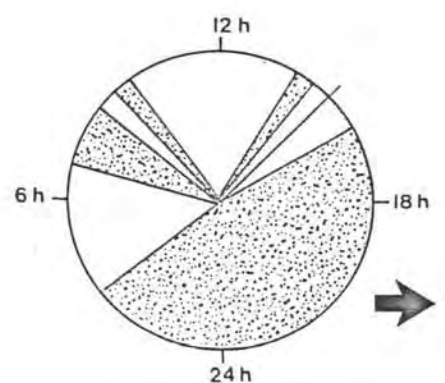
(c) 1/2.10.1984



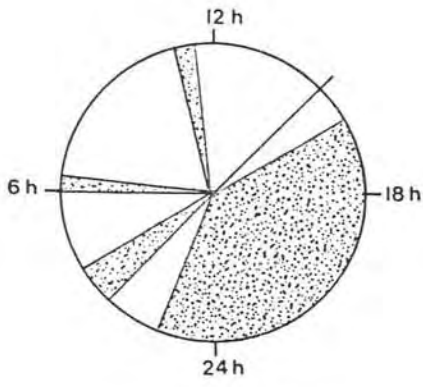
(d) 3/4.10.1984



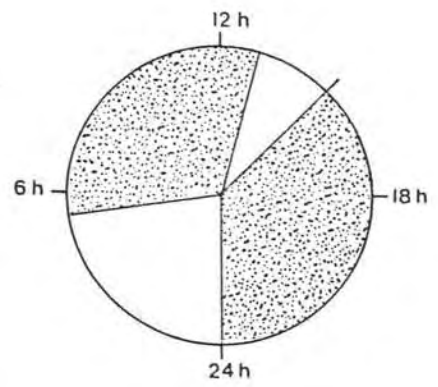
(e) 4/5.10.1984



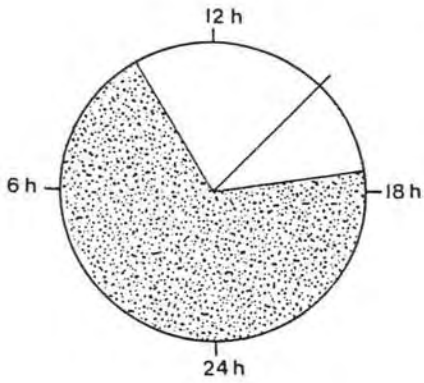
(f) 16/17.10.1984



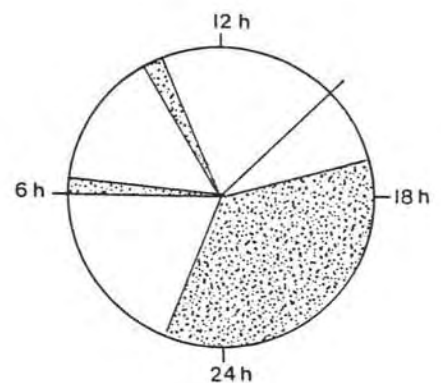
(g) 17/18.10.1984



(h) 28/29.10.1984

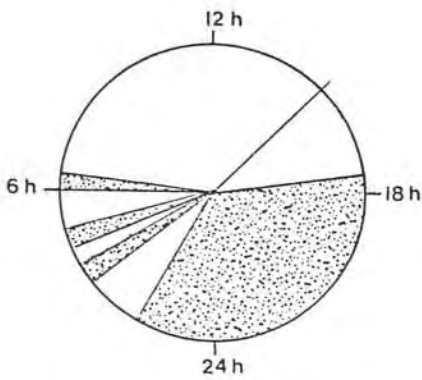


(i) 29/30.10.1984

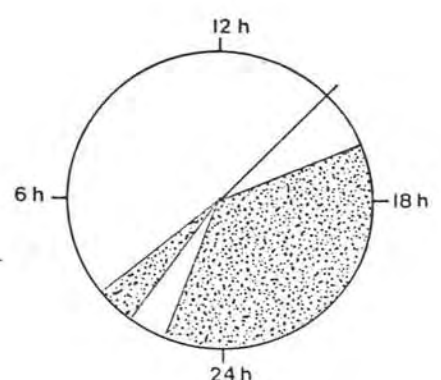


(j) 5/6.11.1984

FIG.6/11: ACTOGRAMS OF BUSHPIG CW5(F)



(a) 18/19.3.1984



(b) 19/20.3.1984

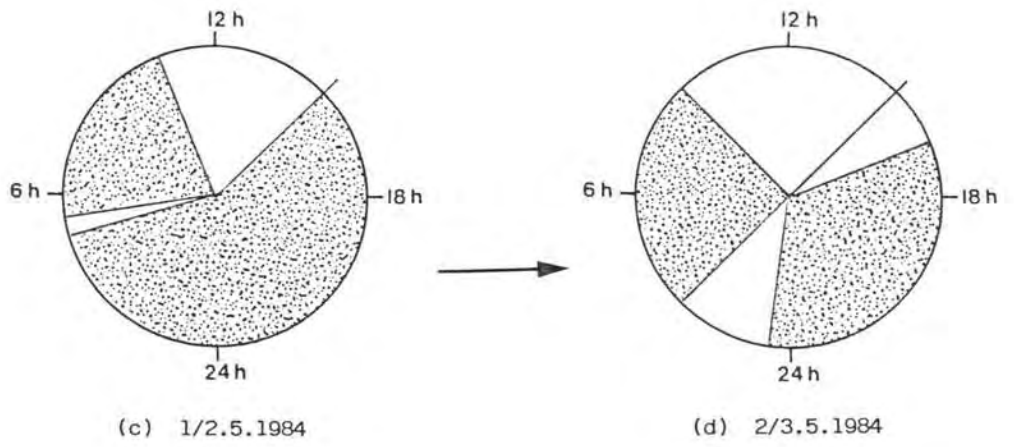
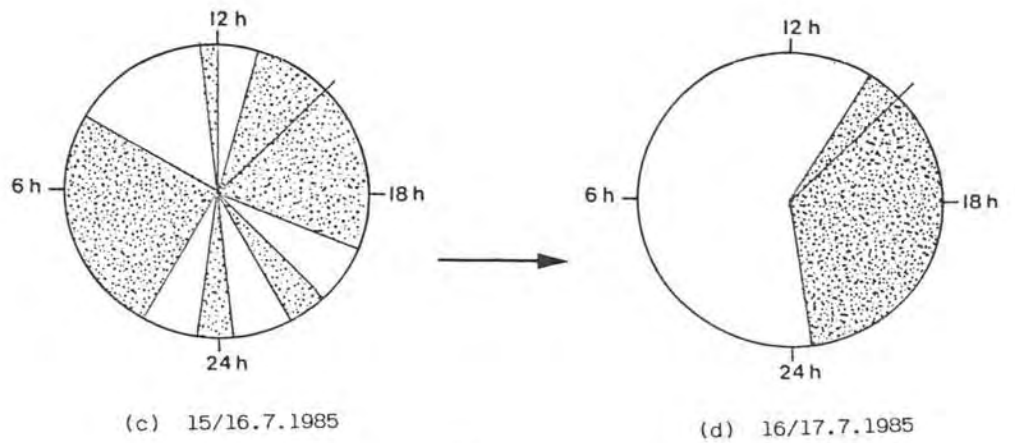
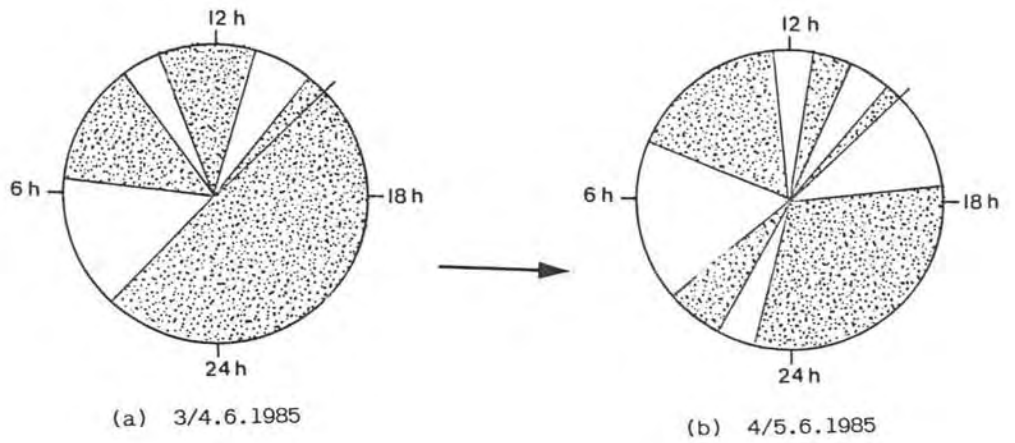


FIG.6/12: ACTOGRAMS OF BUSHPIG CZ1(F)



| <u>SOURCE</u> | <u>DF</u> | <u>F-VALUE</u> | |
|--------------------------------|-----------|----------------|---------|
| A Season | 1 | 2,67 | NS |
| B Time of day (3-hour periods) | 7 | 22,52 | P<0,001 |
| C Free-ranging vs captivity | 1 | 17,74 | P<0,001 |
| A x B | 7 | 1,93 | NS |
| A x C | 1 | 1,91 | NS |
| B x C | 7 | 1,01 | NS |
| A x B x C | 7 | 1,53 | NS |

In Table 6/12 the time periods are arranged in order of declining activity percentages (Table 6/11).

| TABLE 6/12: TIME PERIOD COMPARISONS* <i>VIDE</i> TABLE 6/11 | | | | | | | | | |
|--|-------|------------|------------|------------|----------|----------|----------|-----------|------------|
| 3-Hour Periods | | 15-18 h | 18-21 h | 21-24 h | 0-3 h | 3-6 h | 6-9 h | 9-12 h | 12-15 h |
| Primary activity phase | 18-21 | + | - | + | + | + | + | + | + |
| | 21-24 | + | - | - | + | + | + | + | + |
| | 15-18 | | - | - | | + | | + | + |
| Secondary phase | 6-9 | | - | - | | + | | + | + |
| | 0- 3 | - | - | - | - | - | - | - | + |
| | 3- 6 | - | - | - | - | - | - | - | + |
| | 9-12 | - | - | - | - | - | - | - | |
| | 12-15 | - | - | - | - | - | - | - | |
| * Activity % of row period significantly higher than column period: + ; if significantly lower:- ($\alpha = 0,05$) | | | | | | | | | |
| Data pooled over SEASON and FREE-RANGING/CAPTIVE categories | | | | | | | | | |

The basic characteristics of the activity rhythm quantified and displayed in Table 6/11 and Figure 6/13 are:

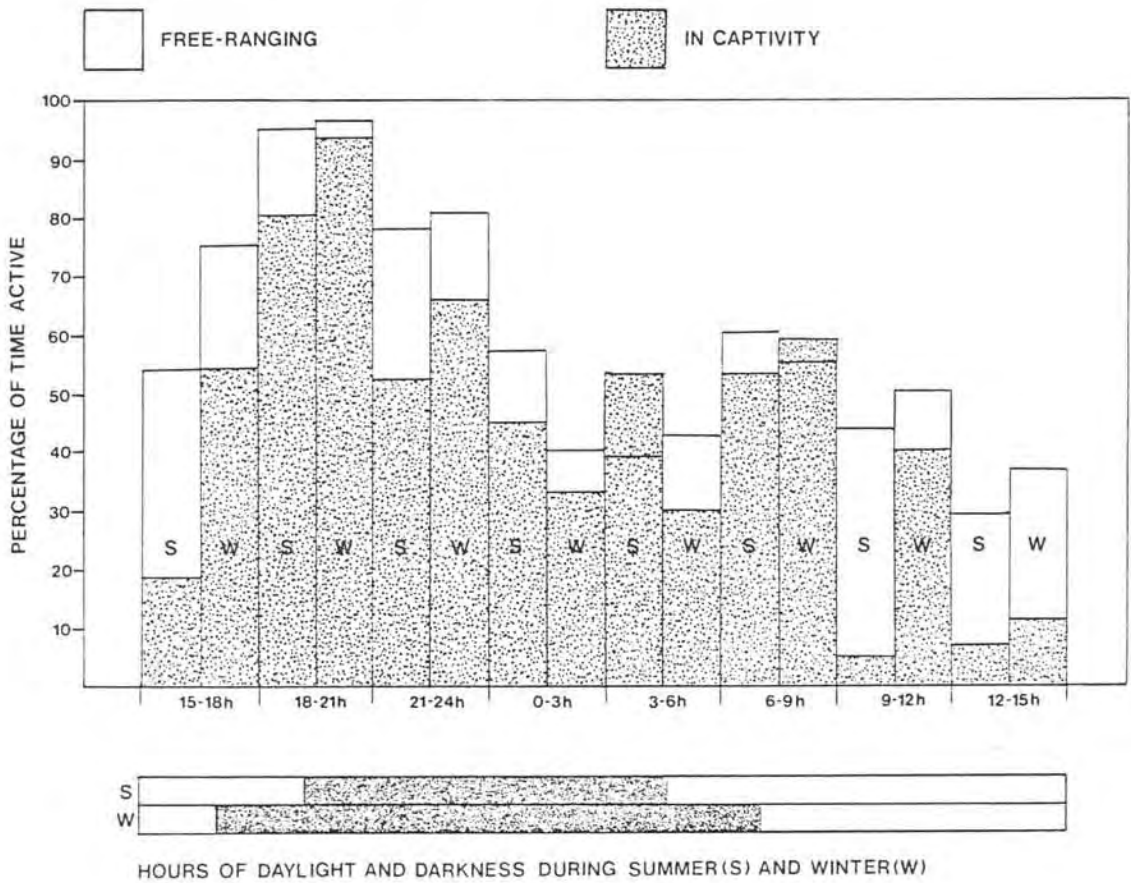
- (I) There are two activity phases: the primary phase from before sunset to approximately midnight and the secondary phase during the morning hours.
- (II) In summer the primary activity phase starts later than in winter (not statistically significant due to high interday variability), but the secondary phases occur in similar periods.

(III) No seasonal differences in the lengths of the activity phases are apparent.

(IV) There is a pronounced resting interval between the primary and secondary activity phases during winter. In summer these intervals are shorter or even absent.

The activity rhythm of captive bushpigs in the study enclosure was similar to that of free-ranging animals. However, captives exhibited a lower total activity which manifested itself in reduced activity during daylight hours compared to free-ranging animals. This was especially marked during the summer months (Table 6/11).

FIG 6/13:ACTIVITY PERCENTAGES FOR BUSHPIG (GOUDVELD)



6.4.1.4 Underlying correlates

Photoperiod and average temperatures change concurrently with season. The earlier onset of activity in winter could therefore be associated either with the earlier onset of cooler temperatures or earlier sunset. This covariance was largely corrected for by classifying activity onset times and associated ambient temperatures in relation to the respective periodic medians (Table 6/13). The 3-month periods used (December-February, March-May, June-August, September-November) were selected in such a way as to minimize within-period temperature differences.

| FREQUENCIES | | ACTIVITY ONSET TIMES | |
|-------------|-----------------------|-----------------------|-----------------------|
| | | Below Periodic Median | Above Periodic Median |
| Temperature | Below periodic median | 19 | 5 |
| | Above periodic median | 11 | 11 |
| n = 46 | | 30 | 16 |

A statistically significant dependency was found between ambient temperature and activity onset (Table 6/13; $G = 4,378$; $p < 0,05$). The data suggests a tendency towards earlier onset of activity when lower temperatures prevail. Activity does however, commence some time before sunset even at ambient temperatures above the periodic median, i.e. the restrictive effect of high ambient temperature only operates up to a point and is thereafter over-ruled by other factors.

Activity recording from radio-telemetric signals did not allow the differentiation of activity according to type and intensity. Although animals may have started to be active at relatively high temperatures, high intensity activity (foraging, especially when rooting) may have been restricted to, or concentrated in periods of relatively low ambient temperatures. This seems to be indicated by the foraging indices from stomach fills (Table 6/9), showing higher night foraging and also suggesting relatively higher day foraging in winter. In comparison,

territorial patrolling often took place during daylight hours (eg. sow CC9).

A phase of depressed activity after midnight in the winter months is noteworthy (Fig. 6/13). It is associated with low ambient temperatures during the period 0 - 3h (Table 6/14).

| TABLE 6/14: FREQUENCY DISTRIBUTION - ACTIVITY DURING PERIOD 0 - 3 HOURS VERSUS MINIMUM AMBIENT TEMPERATURE | | | |
|---|-----------|-----------------------------------|-------|
| Associated daily minimum temperature | | Activity (A) to Resting (R) ratio | |
| | | A ≥ R | R > A |
| °C | 6,0 - 9,9 | 2 | 9 |
| | 10,0 + | 7 | 3 |
| n = 21 | | 9 | 12 |
| Fisher-Yates exact test for independence: P _c = 0,024 H ₀ of independence rejected | | | |

While one might expect that the animals could be sheltering or huddling in response to cold, this cannot automatically be assumed. On those winter days when activity was depressed between 0 - 3h, an earlier onset of the preceding activity phase was evident (Mann-Whitney U test: U = 45,5; n₁ = 6; n₂ = 8; P < 0,01). The low incidence of 0 - 3h activity in winter may thus be due to sheltering behaviour or merely a consequence of the earlier onset of the preceding activity phase. Conversely, during summer, sheltering against cold between 0 - 3h would either not be required or would be in conflict with the time constraints set by shorter summer nights.

The incidence of activity during the main peak period between sunset and midnight is virtually unaffected by the weather variables rain, temperature or wind. Activity around noon in summer is seemingly enhanced by rainy weather (Figures 6/6e; 6/7a and c; 6/10n). Activity may also be temporarily restricted by cold and rainy weather (Fig. 6/6e). These patterns are however by no means consistent. Any existing correlations between weather and activity may also be blurred by interdependence of the activity on successive days. For example, a day

with extensive total activity may be followed by one where this is limited (Figure 6/6: m and n; 6.3.1.1).

The observed activity pattern is broadly consistent with the requirement for behavioural temperature regulation. The day-to-day variability is high, but is not merely a response to changes in the weather. A general double-peaked activity rhythm with the two peaks shifting apart during winter, was documented (6.4.1.3). This resembles activity patterns of other mammals regulated by endogenous rhythms (Aschoff 1960 and 1966). It is accordingly not altogether clear whether bushpig activity should be interpreted as the direct response to environmental stimuli or as an environmentally entrained endogenous circadian rhythm. Elements of both appear to be present.

6.4.2 Discussion

6.4.2.1 Suid activity patterns

Excepting the warthog, which is strictly diurnal (Frädrich 1974, Cumming 1975, Mason 1982) and the giant forest hog, which is largely diurnal (Dönhoff 1942, D'Huart 1978, Cumming 1984, but refer to Kingdon 1979 for a somewhat conflicting report), suids are generally considered primarily nocturnal (Frädrich 1968).

The European wild boar is typically nocturnal, becoming active late in the afternoon and remaining so, deep into the night (Briedermann 1971, Mauget 1980; for the feral pig: Pavlov and Hone 1982). There are strong seasonal differences, the activity being largely nocturnal in summer and more diurnal in winter (Sludskii 1956, Eisenberg and Lockhart 1972, Singer *et al.* 1981, Martys 1982, Krosniunas 1985). In addition, resting after midnight and a secondary foraging period in the morning have been recorded (Heptner, Nasimovic and Bannikov 1966 *op. cit.* Briederman 1971, Iff 1975, Briederman 1977). Feral pigs (Barrett 1978) and domestic swine (Mount 1968) are subject to similar seasonal changes in their activity patterns. In temperate climates swine are active at night during the hottest weather and are otherwise largely diurnal, especially in the cooler months. In tropical and subtropical environments they are largely nocturnal (Hafez and Signoret 1969). A

very pronounced switching from summer night to winter day activity is reported for the collared peccary (Eddy 1961, Ellisor and Harwell 1969, Zervanos and Hadley 1973, Bigler 1974, Sowls 1974, Bissonette 1976).

The predominantly nocturnal activity is considered by many writers to be a result of human disturbance, mainly through hunting. It is reported that European wild boar are less nocturnal or even fully diurnal where undisturbed (Frädrich 1967 and 1974, Gundlach 1968, Briedermann 1971). Bromlei 1964 (*op. cit.* Briedermann 1971) found wild boar in parts of Russia to be mainly diurnal, except during the hottest part of the summer, when inactivity was attributed to harassment by flies and mosquitoes. Foraging on fields however, took place at night. Feral pigs in parts of the USA are reported diurnal by some authors (Kurz and Marchinton 1972, Wood and Brenneman 1977). Whether disturbance is the decisive factor in nocturnal activity remains doubtful in view of the general occurrence of night activity also in areas without significant hunting pressure (Sludskii 1956, Andrzejewski and Jezierski 1978, Mauget 1980, Singer *et al.* 1981).

Bushpigs, although also partly active during the day, are reported to be primarily nocturnal (Lydekker 1908, Von Boetticher 1933, Dönhoff 1942, Thomas and Kolbe 1942, Copley 1949, Roberts 1951, Jobaert 1958, Ansell 1960, Mohr 1960, Frädrich 1968, Sowls and Phelps 1966, Smithers 1971, Kingdon 1979). Diurnal activity was often associated with cool wet conditions or winter periods (Maberly 1967, Breytenbach 1977 and 1979, Kingdon 1979, Breytenbach and Skinner 1982). All the observations of diurnal feeding by Scotcher (1973) were in the winter months. As with the European wild boar, extended daytime activity of bushpigs has been attributed to the absence of disturbance (Maberly 1950, Ansell 1960, Scotcher 1973, Attwell and Bearder 1976). On the other hand long winter day feeding periods were linked to low seasonal food availability and the absence of disturbance by flies (Breytenbach 1977 and 1979, Breytenbach and Skinner 1982).

From the literature review a basic activity pattern emerges which is similar for both the European wild boar and the bushpig. The main activity peak, starting in the afternoon and extending far into the night, with depressed activity during the afternight, is followed by a

secondary morning peak. Activity starts earlier in the afternoon and extends further into the day in winter or generally when cooler. This basic pattern is largely in accordance with the results of this study. The detailed interpretation of the activity patterns observed and their possible adaptive value is dealt with in section 6.4.2.3.

6.4.2.2 Time budgets

The time spent feeding by animals is determined by the balance between food requirements and food availability and dispersion. Food requirements relate to maintenance, growth and energy needs for reproduction. Pregnancy, lactation (Lewis 1977, Moen 1983) and rutting are particularly demanding. Whenever ambient temperatures fall below a critical limit homeotherms require additional energy to maintain body temperature (Kleiber 1961 *op. cit.*, Iwamoto and Dunbar 1983). This may be reflected in either reduced activity or increased food consumption (Whittow 1971). The richness of the food source, its spatial proximity and processing time may all profoundly influence activity budgets (Altmann 1974). Total activity time does not have to be directly related to these factors, since social time requirements also contribute to the total and social time often constitutes a time reservoir when increased foraging time requirements exist.

Two main types of time use strategies are commonly employed: time minimization and energy maximization (Belovsky 1981, Schoener 1983). Time minimizers spend the minimum amount of time foraging needed to fulfil current nutritional requirements. Such an approach is expected when much social time is required, when predator avoidance is critical (and the predation risk higher during foraging) and when food availability is predictable. If the animal is maximizing its intake of nutritional components, it should attempt to maximize its daily feeding time (Belovsky 1981). The energy maximization feeding strategy allows for energy storage when excess food is obtainable and is thus advantageous whenever food shortages are unpredictable in time. Schoener (1983) recognizes two types of energy maximizers: (I) the energy intake is limited by the total time available for feeding and (II) the energy intake is limited by food satiation, as when food processing capabilities are saturated. An example of an energy

maximizer in which both types of constraints operate is the Isle Royale moose *Alces alces* (Belovsky 1978).

European wild boar are reported to be active on average 42% (Dietrich 1984) and 58% (Mauget 1984 *op. cit.* Briedermann 1986) of each 24-hour period. Jezierski and Myrcha (1975) report 14 hours of activity during winter and 10 hours during summer, which compares well with 13 and 11 hours respectively recorded by Janeau and Spitz (1984 *op. cit.* Briedermann 1986). The warthog, on the other hand, appears to spend less time foraging: 6 hours or 25% of the diel period (Owen-Smith 1982). No seasonal difference in activity time budget was found for the bushpig (6.4.1.3). On average, animals were active for 57% of the diel period. During the summer months 56% of the activity occurred during daylight hours. The equivalent percentage for winter was 40%. This can be explained by the relatively short summer nights compared to the total activity time required. With such activity time requirements it is hardly possible for the bushpig to be either exclusively day or night active. Most of the activity of free-ranging bushpig is related to foraging, i.e. either intensive foraging, involving a considerable amount of rooting, or casual, low intensity searching with occasional ingestion events. These findings corroborate the observations of Breytenbach (1977) on bushpig in the St Lucia area (Zululand) which spent nearly all activity time on feeding. The bushpigs in the study enclosure were active for 39 and 49% of the diel period for summer and winter respectively (Table 6/10).

Bushpig are active for a considerably greater proportion of the diel period than warthog (57% vs 25%). This probably results from a more dispersed food resource with an associated high search element during foraging in the case of the bushpig. Bushpigs appear to follow an energy maximizing feeding strategy. For them food resource shortages are rather unpredictable in time (8.2.5), favouring the transformation of food surpluses into energy stores (fat depots). The continued foraging in the study enclosure, albeit at a low intensity, with *ad lib* feeding, supports this interpretation.

The total activity of bushpigs may be subdivided as follows:

- (I) high intensity foraging (relatively little movement and much handling effort, e.g. rooting; high rate of ingestion).
- (II) low intensity foraging (relatively low rate of ingestion per unit of distance moved).
- (III) social activity.

The total time available for activity appears to be constrained by rest requirements and subject to optimization with regard to the maintenance of thermal balance. This implies that if the energetic cost of thermoregulation is higher than the marginal social or energetic foraging gain during any particular period, activity should cease. The generally reduced summer day activity of captive compared to free-ranging animals is interpreted in this light (Table 6/11).

The total daily activity as determined by radio-tracking is unlikely to reflect the balance between energetic requirements and the current status of food availability in bushpig because:

- (I) One component of activity, as defined, may be substituted by another (e.g. more low intensity foraging and social activity by captives replacing the extended periods required for high intensity foraging by free-ranging animals). Such substitution, in conjunction with II below is taken to explain the disproportionately small reduction in the total activity of captives compared to free-ranging animals (Table 6/10).
- (II) A decrease in feeding time with an increase in food availability is only expected for time minimizers (Schoener 1983). Energy maximizers would continue to forage, thereby building up energy stores. The energy maximization feeding strategy may also be the reason for the lack of trends discernable between movement and resource availability (6.3.1.2).

6.4.2.3 Night activity: a result of human disturbance?

From observations and stomach fills, Briedermann (1971) deduced a predominantly nocturnal, double-peaked activity rhythm for free-ranging European wild boar. The primary activity phase started before dusk and peaked some time thereafter, with a secondary peak shortly before sunrise. Resting occurred during the second half of the night, especially in winter, and during the day. This activity pattern largely resembles that for the bushpigs verified during this study and deduced earlier by a number of authors (6.4.2.1).

However, Briedermann (1971, 1986) maintained that the predominantly nocturnal activity is a result of hunting pressure and sought verification under controlled conditions of observation in a study enclosure (1 ha in size). The telemetric option was not available to him. In the enclosure he found a primarily diurnal activity pattern. The activity rhythm again had two peaks, but the main peak started during the afternoon and ended shortly after dusk, while the secondary peak occurred after sunrise. Bright moonlight and warm day temperatures shifted the activity more into the night. Similar results were obtained by Gundlach (1968) and Martinez-Rica (1980) also for enclosed European wild boar. The results obtained led Briedermann (1971) to conclude that European wild boar are inherently diurnal in the absence of human disturbance.

This conclusion can however be challenged since the apparently diurnal activity pattern can be explained by factors associated with captivity.

- (I) Since food is provided in a limited area, the captive animals only require a relatively short time for foraging. If they start foraging in the afternoon, by dusk their food requirements can be satisfied.
- (II) They may also be subject to less thermoregulatory stress on summer days because foraging requires less work. Little difficult rooting is involved and intensive foraging is not extended over long periods since there are no searching intervals. Thermoregulation is still partially operative however, since activity shifts into the night on warm days.

(III) Captive animals do not need to use darkness as substitute for cover when undertaking forays into unfamiliar, open areas, like agricultural fields.

Good evidence exists that the primarily nocturnal activity patterns of free-ranging wild boar and bushpigs are not induced by human disturbance, but related to other factors.

- (I) The well-documented seasonal switch between increased night activity in the summer and more day activity in winter (6.4.2.1) suggests a strong thermoregulatory influence. Why should the animals consider human disturbance less threatening on winter days?
- (II) When cover is sufficient, as in large, continuous forests or dense stands of agricultural crops (cf Hennig 1981), diurnal foraging is not uncommon. It is suggested that day activity goes unnoticed in these situations leading to the assumption that the animals are only active at night.
- (III) Areas poorly endowed with cover are indeed only visited at night. Where there is a low forest to field area ratio the impression of disturbance-induced night activity would result. Such an impression would be partly correct, since open areas are presumably shunned by day to avoid predators. The restriction of day activity to well-covered habitats is however normal behaviour and not necessarily associated with the link between open areas and human disturbance. Daytime activity in open areas by feral pigs on Santa Cruz Island was generally lower than in closed, forested areas (Krosniunas 1985). Diurnal activity of bushpigs in dense cover is not unusual (this study, Ghiglieri *et al.* 1982) and may be partly linked to thermoregulatory factors.
- (IV) The tame, free-ranging bushpig of Cumming (1975) was nocturnal or crepuscular, in clear contrast to the diurnal activity of his similarly tame free-ranging warthogs.

It is concluded that the predominantly nocturnal activity of European wild boar and bushpig is not primarily induced by human disturbance, but is a normal adaptation to factors of thermal comfort, minimum foraging

duration and anti-predator behaviour. Activity during both day and night occurs in variable proportion depending on season, habitat characteristics such as the disposition of cover and food, weather and threat perception (hunting pressure; whether solitary or in group).

6.4.2.4 Adaptive significance of activity rhythms

Optimal activity periods in mammals, i.e. the distribution of activity over the diel period, are probably controlled primarily by the requirements of thermoregulation or predator avoidance, or both (cf Owen-Smith 1982). Climate appears to be overwhelmingly important in determining optimal feeding periods (Schoener 1971). Seasonal changes in activity pattern can provide clues as to the underlying factors of selective importance. Photoperiod and ambient temperature typically change with season. The increased incidence of daytime activity when temperatures decline, particularly during winter, has been noted above for both European wild boar and bushpig (6.4.2.1). If the animals were primarily confining their activity to the hours of darkness for predator avoidance, the opposite result would have been expected. They would have made full use of the long winter nights.

Evidence from this study on bushpigs suggests temperature regulation to be the main factor controlling the basic pattern of activity.

- (I) Periods of active foraging are selected to avoid the warmest periods of the day, i.e. the main activity phase occurs from 18h00 - 24h00 and the secondary phase during 6h00 - 9h00 (6.4.1.1).
- (II) There is an earlier onset of activity at lower temperatures (6.4.1.4).
- (III) Stomach fills indicate primarily night foraging and this is more pronounced during the summer months (Table 6/9: 6.4.1.1). Stomach fills of European wild boar follow the same trend. Summer night foraging resulted in stomach masses five times heavier than those from day foraging. During winter the mass for night foraging was only twice that during the day foraging (Briedermann 1971).

(IV) The reduced summer activity of captive compared to free-ranging bushpigs is primarily at the expense of day activity (Table 6/10, Fig 6/13: 6.4.1.3).

However, reduced summer to winter day activity is not borne out by the radio-tracking data for free-ranging bushpigs. (Table 6/11). The season X time of day interaction is also not statistically significant (6.4.1.3). The interpretation of radio signals did not allow the differentiation between types of activity. External evidence does however indicate that patrolling, wallowing and restless standing and wandering about contributed to "activity signals" during midday hours. Singer *et al.* (1981) experienced the same for European wild boar, but field observations revealed that most afternoon movements (12-16h) in summer were between day beds and wallows. On particularly hot summer days, bushpig in the enclosure tended to wander around restlessly instead of bedding down, presumably to facilitate heat dissipation from air movement (7.3.1). It is thus not activity *per se*, but intensive foraging which bushpigs generally tend to avoid on warm summer days. Heat loads apparently build up and are not effectively dissipated when animals are active at high ambient temperatures (7.3.1). The seasonal switch from diurnal activity in the cooler months to nocturnal activity during the summer, reported for certain suid and tayassuid species, is generally interpreted as a manifestation of behavioural thermoregulation (Mount 1968, Hafez and Signoret 1969, Kurz and Marchinton 1972, Zervanos and Hadley 1973, Graves 1984).

The inverse correlation of ambient temperature and activity from 0-3h during winter (Table 6/14), suggests behavioural energy conservation. Energy is presumably conserved through huddling or sheltering. The building of nests to shelter under cold and wet conditions is noteworthy in this context (7.3.1.3). The phenomenon of early termination of activity on cold nights and subsequent day foraging activity has been documented also for other nocturnal mammals (e.g. for coypu *Myocastor coypus*, Gosling *et al.* 1980). This response is correspondingly considered an adaptation to avoid energy loss at low ambient temperatures.

However, as Aschoff (1966) had emphasized, caution should be applied in the interpretation of correlations from field observation between animal

behaviour and concurrent environmental conditions. It is now well established that the daily rhythms in behavioural and physiological activity are not simple passive responses to the prevailing environmental conditions (Aschoff 1960 and 1964a, 1966, 1969, Enright 1966, Daan and Aschoff 1975). In many and perhaps all animal species, evolution has resulted in circadian rhythmicity, i.e. endogenous self-sustained oscillations which are in some phase relationship with the natural frequency of the earth's rotation (Aschoff 1966). These endogenous oscillations are maintained in phase relationships to the 24 hour periodicity by periodic environmental stimuli, like photoperiod or temperature, which operate as entraining agents ("Zeitgeber"). The temporal pattern in animal activity may be characterized by one, two or more peaks within the diel period. The bimodal pattern is by far the most common (Aschoff 1966). Usually a major peak precedes a minor peak, the combination resulting in a "bigeminus" pattern. Under certain conditions, the major peak follows the minor peak and the resulting pattern is then known as the "alternans" type. Experimental studies indicate that the basic bimodal pattern is a persistent property of the circadian oscillating system and is retained under experimental conditions of constant illumination (Aschoff 1966).

From the above it becomes evident that behavioural patterns are controlled by an hierarchical set of factors. Three levels are often involved: ultimate factors, primary proximate factors and modifying, stimulatory or inhibitory, proximate stimuli (Aschoff 1964b, Gwinner 1981a). The ultimate factors are those environmental variables which, in the course of evolution, have exerted selection pressure favouring the gene complexes of those individuals exhibiting the most adaptive behavioural patterns. Primary proximate factors are those which synchronize endogenous rhythms (circannual or circadian) with environmental oscillations in the most adaptive, anticipatory fashion in relation to the ultimate factors (usually photoperiod). Whereas photoperiod as a primary proximate factor synchronizes the endogenous rhythm, which governs the readiness for the particular behavioural event, the temporal fine tuning of the actual occurrence thereof is achieved by proximate environmental stimuli which are more closely related to the ultimate factors (cf Gwinner 1981a).

A hypothetical interpretation of bushpig activity patterns within the framework of this set of controlling factors will be attempted below. Three main postulates form the basis for the interpretation of the observed activity patterns.

- (I) The ultimate factors responsible for moulding the temporal organization of activity within the diel period are taken as those affecting internal homeostasis (thermal balance; energy conservation). They are those factors believed to have exerted significant selective pressure over evolutionary time spans. Factors of significance here are ambient temperature in conjunction with wind, precipitation and humidity (7.3.1).
- (II) The animal is subject to endogenous rhythmicity related to the internal physiology of alternating activity and rest requirements, coupled to rhythms of metabolism (Aschoff 1964b, cf Aschoff and Pohl 1970). This sets the underlying framework of an alternating predisposition to activity and rest within a single 24-hour period (bimodal activity pattern). Photoperiodism is implicated as the entraining agent controlling the seasonal adaptation of the bimodal activity rhythm to changing day/night lengths. Photoperiod accordingly acts as the proximate factor linking the endogenous activity rhythmicity with the seasonally changing manifestation of the ultimate factors.
- (III) The basic endogenous activity rhythm is fine-tuned on an hourly and day-to-day basis by modifying, proximate stimuli (either stimulatory or inhibitory). These proximate stimuli are essentially formed by short-term changes of the ultimate factors.

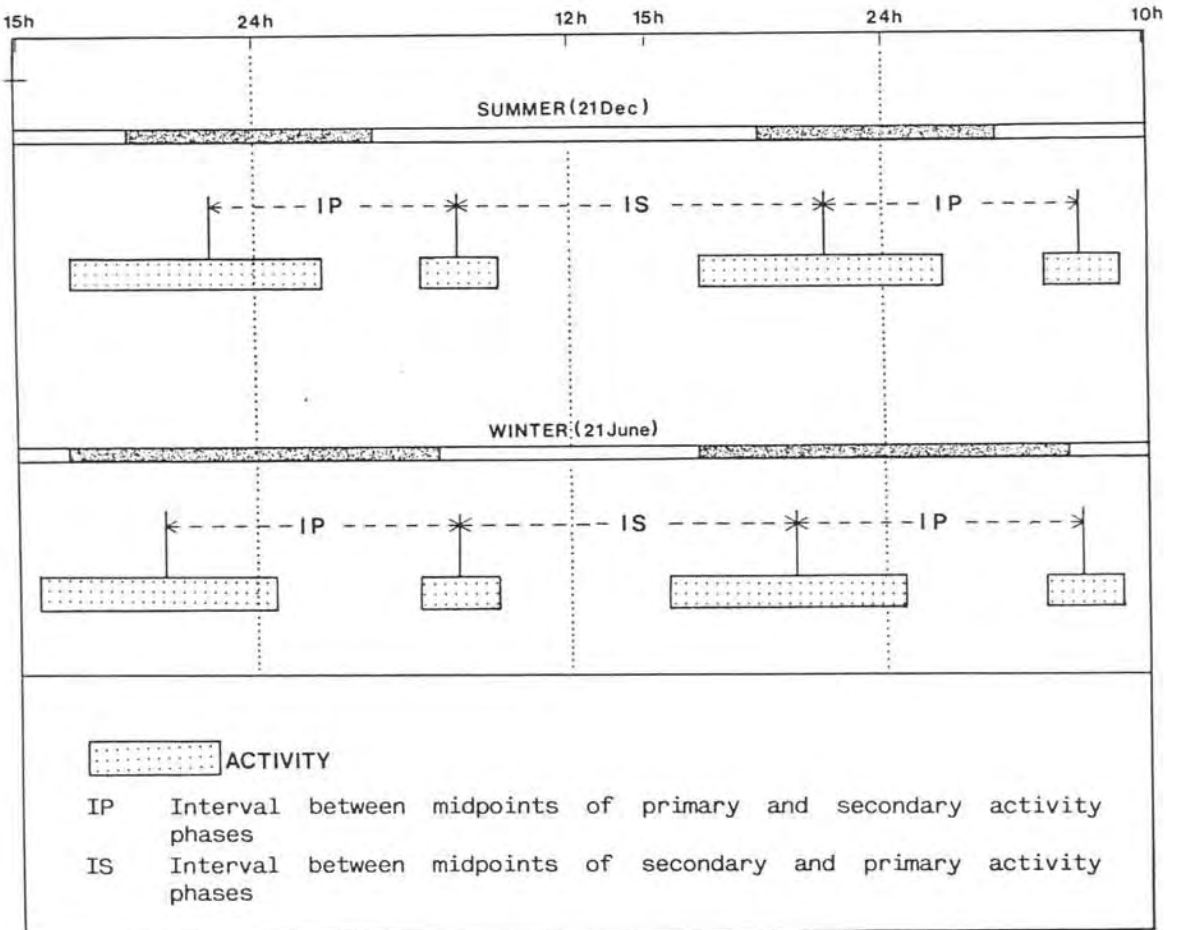
A central question arising immediately pertains to the role of photoperiod as primary proximate factor in entraining the endogenous circadian rhythm according to the requirements of the ultimate factors. Why can the proximate stimuli not fulfil this role just as well, thereby making photoperiod superfluous as an entraining cue? The answer to this question is by no means clear (Enright 1970, Gwinner 1981a).

The hypothesis providing a plausible explanation for the role of photoperiodism as primary proximate factor which will be presented here

pivots around the adjustment of the peak to peak intervals to the seasonally changing day/night ratio. Consider the diagrammatic illustration of bushpig activity below (Fig. 6/14).

The endogenous circadian rhythm with the physiologically optimal IP to IS ratio would remain unchanged were it not for seasonal changes of the day to night ratio and the associated thermal constraints due to diel temperature oscillations. Photoperiod is now postulated to exert an entraining effect on the endogenous rhythm thus adapting the IP to IS ratio to the seasonally changing night to day ratio.

FIG.6/14: TYPICAL PEAK ACTIVITY PERIODS OF BUSHPIG



Oscillation of the interpeak interval of the endogenous rhythm would tend to maintain a fixed phase relationship proportional to the night/day oscillation (photoperiod):

$$\frac{IP}{IS} \approx \frac{N}{D}$$

During summer, when shorter nights prevail, the interval between midpoints of the primary and secondary activity phases (IP) would be correspondingly shorter. This would prevent both activity phases from occurring during periods of the day liable to heat load problems. The existence of a bimodal rhythm suggests it is physiologically advantageous to have a change from activity to rest twice within each diel period. This implies resistance against a breakdown of bimodality, which would occur if IP were to become so short that the two activity phases merged. During winter, with its longer nights, lower temperatures and reduced heat load problems, the IP/IS ratio is probably closer to the physiological optimum in terms of a bimodal alternation between activity and rest. Photoperiod thus operates as a seasonally changing, but otherwise rigid proximate factor. It is not subject to erratic short-term changes from factors like ambient temperature. In the absence of this photoperiodic entrainment an animal might delay the onset of activity on particularly warm summer afternoons and thus experience difficulties in maintaining a bimodal activity pattern of the desired activity phase spans. The secondary phase would shift unduly far into the subsequent days (when it might be already too warm again).

Whereas the photoperiodically entrained endogenous rhythm sets the overt framework of propensity for activity, this basic pattern may be modified on a short-term, i.e. hourly basis, by inhibitory or stimulatory proximate factors.

The individual variability in day-to-day activity patterns (Fig. 6/6 - 6/12) indicates a substantial degree of plasticity, both with regard to the chronological spacing and duration of activity. It has already been shown that activity may commence during relatively warm summer afternoons. In this way two activity peaks of sufficient lengths fit into the comparatively short thermally acceptable proportion of the day. On the other hand, during relatively cool conditions, the onset of activity is often advanced, resulting in the observed daily variability. The one-sided plasticity encountered, i.e. variably modified activity in the absence of thermal constraints through high ambient temperatures but

little deviation from the basic pattern while subject to such, clearly indicates that heat load accumulation and its dissipation during activity is the dominating constraint in moulding bushpig activity patterns (refer to 6.4.1.4, *i.a.* Table 6/13). This is also reflected by reduced summer day activity recorded for captive bushpigs which are not required to forage for extensive periods (Table 6/11).

Unlike the bushpig, where both free-ranging and captive animals maintain similar, largely nocturnal activity rhythms, captive European wild boar in temperate regions exhibit a predominantly diurnal activity pattern (Gundlach 1968, Briedermann 1971, Martinez-Rica 1980). This is in contrast to their free-ranging counterparts (6.4.2.1). This phenomenon may be explained as follows: Since they are provided with food, captive European wild boar do not need to forage intensively for long periods. Both searching and handling times (rooting) are greatly reduced and a larger proportion of the total activity time is filled with social and other relatively low-intensity activity (6.4.2.2). There are indications that social activity takes place mainly during the day (5.1, 5.2, 5.3). Captive wild boar start their foraging activity during the late afternoon, as is normally the case (excepting on particularly hot summer days). Unlike their free-ranging counterparts they have already completed active foraging at dusk. Low-intensity, largely non-foraging, activity occurs mainly during daylight hours. The captive animals then rest from dusk and resume activity at dawn. The long resting period thus shifts into the night and the short resting period is around noon. The result is an "alternans" activity pattern as for diurnal mammals (Aschoff 1966, Briedermann 1971). Such an activity pattern is only possible in the absence of the thermal constraints operative over extended periods of intensive foraging periods to which free-ranging animals are exposed. Use of darkness as a cover substitute when foraging in areas with poor cover (e.g. agricultural fields) for crypsis and for thermal comfort all contribute to the occurrence of nocturnal activity in free-ranging wild boar and bushpig.

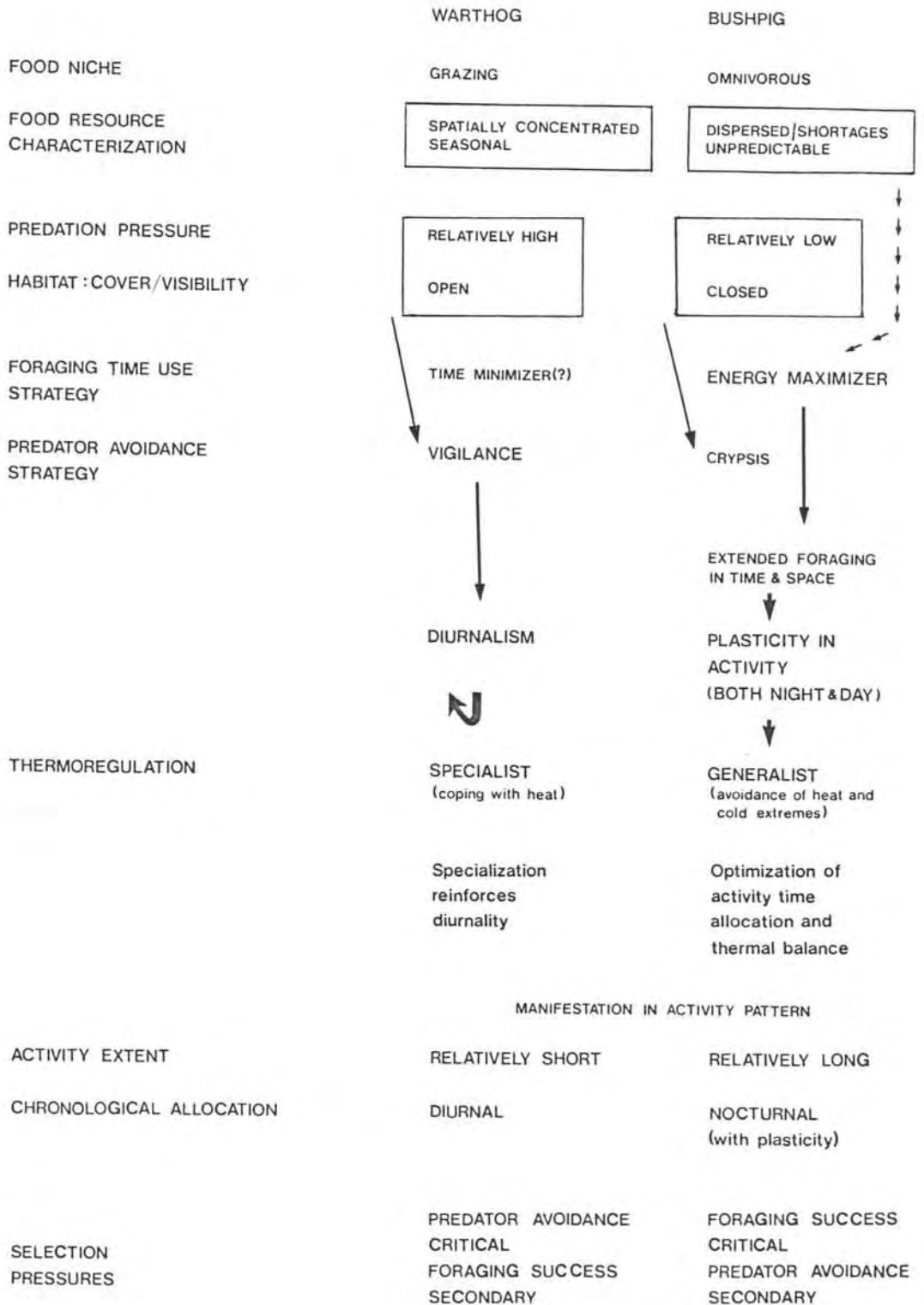
It is concluded that bushpig are primarily nocturnal since the primary activity phase and especially high intensity foraging, occurs at night. A secondary activity phase after dawn is typical and the animals may be fully active by day during winter or in cool shaded environments.

6.4.2.5 Hypothesis on suid activity patterns: an integration

In Figure 6/15 hypothetical interrelationships between the factors moulding activity patterns are contrasted for warthog and bushpig. The food niche is taken to provide the setting for the ultimate environmental factors which determine activity patterns. The warthog as a grazer occupies open habitat with a food resource which tends to be spatiotemporally concentrated and predictable in time. The bushpig on the other hand, typically lives in closed habitat types with a dispersed food resource base, and food shortages which are unpredictable in time. Whereas the warthog is generally subject to relatively high predation pressures (Mason 1982), this factor is of hardly any significance for adult bushpig.

The three sets of environmental factors to which the two suid species have to adapt their patterns of activity are thus degree of cover, nature of the food resource and predation pressure. The two basic antipredator strategies are vigilance and crypsis. The former is postulated to be more effective in open and the latter in closed habitats. Thus, for the warthog, being subject to high predation pressure and living in open habitats, vigilance as an antipredator strategy is of critical importance. The nature of the food resource allows larger group sizes (multimaternal groups), which is also an advantage. In the closed habitat typically occupied by bushpig, crypsis is the appropriate antipredator strategy. In accordance with this strategy bushpig should only visit open areas at night. However, predation pressure is generally comparatively low. Faced with a dispersed food resource and unpredictable periods of food shortage (8.2.5), a time use strategy which maximizes foraging success is of overriding importance. Energy maximization, resulting in extended foraging time, takes precedence over predator avoidance in determining the nature of the activity pattern.

FIG.6/15: POSTULATED INTERACTIONS CONTROLLING ACTIVITY PATTERNS:
 WARTHOG vs BUSHPIG



For animals having to forage in the open, vigilance is considered a more effective anti-predator strategy than using darkness as cover. A predator can also use darkness to its advantage. Vigilance is most effective during daylight and warthog are accordingly diurnal. Crypsis is the appropriate antipredator strategy for animals which forage predominantly in closed habitats. It affects bushpig activity patterns in that open area foraging is usually confined to the hours of darkness. The combination of dispersed food resources and a strategy of energy maximization results in extended foraging in time. Substituting darkness for cover allows extended foraging in space. The result is great versatility in the use of both time and space for foraging. Bushpig activity patterns accordingly show a high degree of plasticity and variability in night and day activity.

In order to cope efficiently with the heat loads and solar radiation associated with diurnal habits and open habitat, the warthog is a thermoregulatory specialist. Specialization to withstand heat has apparently been at the cost of being able to withstand cold. This reinforces diurnality and requires the warthog to spend the night in sheltered localities such as subterranean holes. The bushpigs extended activity requirements preclude it from being active purely by day or by night. It is apparently a thermoregulatory generalist which avoids extremes of both heat and cold (7.4.1). It must optimise allocation of time to activity and thermal balance. This results in the activity pattern described above (6.4.1.1, 6.4.1.2, 6.4.1.3).

These interrelationships (Fig. 6/15) may be viewed as a continuum of selection pressure from critical predator avoidance in open habitat to critical foraging success in closed habitats with warthog and bushpig at the two extremes. Both the giant forest hog and European wild boar fit into this scheme. The giant forest hog as a primarily diurnal bulk feeder on herbaceous material feeding mostly in open environments would be placed closer to the warthog. The omnivorous European wild boar, being primarily nocturnal with some day activity is closer to the bushpig. In accordance with these postulates are the observations of Guiraud (1948 ex Cumming 1975) which suggest a nocturnal activity predominance of warthogs inhabiting densely forested areas in equatorial Africa.

6.5 Synopsis

The average bushpig home range size was 7,2 km², ranging from 3,8 to 10,1 km² (n = 8). These relatively large home range sizes are attributed to a dispersed food resource base. It is suggested that its omnivorous feeding style accounts for the bushpigs habitat preferences and regional distribution patterns over vegetation types. Habitats with poor cover were only visited during the hours of darkness.

Movement data on successive tracking days revealed a high degree of mobility about the home range. Home ranges were often traversed within 1 to 4 days and territorial patrolling is carried out (4.3.2). The average diel ranging distance was 3,03 km (0,48 - 5,84 km), while the average rate of movement was 238 m/h while active.

For its size, the bushpig in the study area was found to be active for relatively long periods. Animals were active for an average of 13,7 hours (57% of diel period) per day. No differences were found relating to sex or season. Bushpig were active during both night and day and exhibited a basic bimodal rhythm. The main phase of intensive foraging occurred from before dusk to midnight (18h00 - 24h00), with a secondary activity phase peaking between 6h00 and 9h00. Great plasticity in the activity pattern is reflected by high day-to-day variability in the extent and time schedule.

The activity patterns were interpreted as being matched to a dispersed food resource base, leading to an energy maximizing time use strategy. The overall activity rhythm was shown to be fitted into the diel period in such a way as to avoid thermoregulatory stress.

7. TEMPERATURE REGULATION AND ENERGY METABOLISM

7.1 Principles of thermal energy exchange: an introduction

Next to nutrition, thermoregulation is the most important component of the energy balance of any animal. Understanding the constraints in this regard is therefore indispensable for the meaningful interpretation of the biology and ecology of a species. Homeothermic animals regulate the balance between heat production and heat loss, both behaviourally and physiologically. The effect of this balance is a relatively constant body core temperature (Moen 1973). The homeotherm thus has developed the ability to maintain, in the face of environmental fluctuations, a relatively stable internal temperature within a range basically determined by

- (I) the animal's maximum capacity to produce heat;
- (II) its maximal thermal insulation; and
- (III) its ability to dissipate heat.

In physiological terms there are three interrelated quantities to be considered: metabolic rate (here equivalent to rate of heat production) and both the temperature gradient and thermal insulation between organism and environment (Mount 1968). In addition, thermal comfort and thus energy economy is facilitated by behavioural means.

The rates of thermal exchange depend on the thermal characteristics of the organism and its environment and the interaction between the different modes of heat transfer between the two (Moen 1973). Thermal energy is exchanged between animal and environment by non-evaporative means (i.e. radiation, conduction, convection) and through evaporation. Non-evaporative heat transfer depends on a temperature difference whereas evaporative heat transfer depends on a difference in water vapour pressure (Mount 1979).

Each of the channels of non-evaporative heat transfer has a particular temperature in the environment with which it is associated. For radiative transfer it is the mean radiant temperature of the

surroundings, for convective transfer it is air temperature and for conductive transfer it is the temperature of the surface that is in contact (Mount 1979). The four channels of heat exchange are defined below (cf Moen 1973).

Radiation

Radiant energy loss occurs from a surface by emitting energy at wavelengths that are dependent on its temperature.

Convection

Convection is the process of heat energy transfer from the surface of an object by air (fluid) flowing over it. Wind velocity is normally the most important factor determining the rate of convective heat loss.

Conduction

The transfer of heat by conduction results from the exchange of energy when oscillating molecules collide, with a higher rate of exchange during more rapid oscillations. Energy dissipation by conduction is from the higher temperatures resulting from more rapidly oscillating molecules to lower temperatures. The thermal conductivity is an expression of the rate of heat flow by conduction along the temperature gradient between two media.

Evaporation

Heat is lost from the surface of an animal by evaporation because energy is absorbed as liquid water is changed to a gaseous state.

When the environmental temperature rises, non-evaporative heat loss is progressively reduced until it becomes zero when the environmental and body temperature are equal. Under hot conditions an animal is thus dependent on evaporative heat loss by either sweating or panting, to regulate its body temperature (Mount 1979).

The physiological response of an animal to the thermal environment can be either heat producing (thermogenic) or heat conserving (Moen 1973). Heat production is an active response involving the metabolism of absorbed nutrients or of body tissue. Heat conservation is accomplished by regulating an aspect of the animal-to-environment gradient, resulting in alterations in the dissipation of heat energy (Moen 1973).

The factors involved in heat balance in the homeotherm may be listed following (Mount 1979):

- Basal metabolism
- Feeding (resulting in heat increment)
- Additional non-shivering thermogenesis
- Shivering
- Muscular activity.

Thermal homeostasis is achieved by:

(a) Decreasing heat loss (heat conservation)

- Peripheral vasoconstriction
- Coat (pilo-erection)
- Subcutaneous fat
- Counter-current heat exchange
- Compact posture

(b) Increasing heat loss (heat dissipation)

- Peripheral vasodilatation
- Sweating
- Panting
- Extended posture

The homeothermic animal maintains a balance between heat production and heat loss by dissipating the heat produced during normal life processes; increasing heat production when the animal is in a critical hypothermal environment and increasing heat loss when in a critical hyperthermal environment (Moen 1973). The upper and lower limits to thermoregulation in the homeotherm are thus determined by heat-production capacity at low

temperature and by heat-dissipating capacity at high temperatures. The zone of thermoneutrality is the environmental temperature range within which the metabolic heat production of an animal is minimal and independent of the environmental temperature (Mount 1979, Schmidt-Nielsen 1979). Below a certain ambient temperature at the lower end of the thermoneutral zone, called the lower critical temperature, the metabolic rate increases linearly with decreasing temperature if the body temperature is to be maintained (Schmidt-Nielsen 1979).

Basal metabolism is defined as the minimal energy cost when an animal is at rest in a thermoneutral environment and in a post-absorptive condition. The energy required to maintain life at the basal metabolic rate (BMR) provides for circulation, excretion, secretion, respiration, anabolic and catabolic processes and the maintenance of muscle tone (Moen 1973). Oxygen consumption can be measured under controlled conditions and is thus generally used as a practical measure of metabolic rate. The reason why this is appropriate is because the amount of heat produced for each litre of oxygen used in metabolism is nearly constant, irrespective of whether fat, carbohydrate or protein is oxidized. An average value of 4,8 kcal/l of oxygen is customarily used as a measure of metabolic rate (Schmidt-Nielsen 1979). The BMR is useful as a base line with which comparisons may be made when the animal is physically active, on different diets, reproductively active, or in some condition that requires expenditure of energy (Moen 1973).

Basal metabolic rate, lower critical temperature and thermal conductance all vary inversely with body size and all are intimately related (Vaughan 1972). The relationship between heat production and body weight has been determined for a variety of species: the so-called Benedict's "mouse-to-elephant" curve. The shape of the curve illustrates that the heat production per unit mass of a small animal is far greater than of a larger animal (Moen 1973). In accordance, small size is thus disadvantageous in terms of heat conservation due to an unfavourable surface to volume ratio (Vaughan 1972).

As a guide, the basal heat production approximates $70W^{0,75}$ kcal/day (W weight in kg). A free-ranging animal has an ecological metabolic rate that is an expression of the energy "cost of living" for the conduction

of daily activities and other life support processes. The ecological metabolic rate is usually about 2 x BMR (Moen 1973). Factors influencing energy metabolism include the following: activity, diet, thermoregulatory functions, sex, reproductive condition, time of day and year, coat characteristics, weather factors, parasites and pathogens and various social and psychological effects (Moen 1973).

Whenever the homeostatic mechanisms of an animal are activated, extra energy is expended in the process. The energy so expended is no longer available for productive processes. Thus, the more the animal spends on temperature regulation, the lower is its capacity for growth and reproduction (Bianca 1976). Through their effect on energy economy, thermoregulatory constraints have an important bearing on thermocomfort behaviour, activity and particularly juvenile survival. Also, adaptations relating to energetic efficiency, such as the nature of the pelage, endogenous metabolic cycles and body size, are codetermined by thermoregulatory requirements.

7.2 Methods

7.2.1 Behavioural temperature regulation

Six 5-day activity observation periods in the study enclosure were involved:

| | <u>Periods</u> | <u>Group composition</u> |
|-----|------------------------|--|
| I | 1/2.6 - 5/6.6.1981 | TD5(adM); TD3(adF); TC2(YM); TD1(YM); TD2(YF); TD7(JM) |
| II | 8/9.1 - 12/13.1.1982 | TD5(adM); TD3(adF); TC2(sadM); TD1(sadM); TD2(sadF); TD7(YM); TD8/9(J) |
| III | 11/12.7 - 15/16.7.1982 | TD5(adM); TD2(sadF); TD1(sadM); TD7(YM) |

| | | | | |
|----|------------------------|------------------------|-----------------------|-----------|
| IV | 6/7.1 - 10/11.1.1983 | TD5(adM); TD7(sadM) | TD2(adF); | TD1(adM); |
| V | 11/12.1 - 15/16.1.1983 | TD5(adM); TD7(sadM) | TD2(adF); | TD1(adM); |
| VI | 4/5.7 - 8/9.7.1983 | TD5(adM); TD7(adM); | TD2(adF); TD11(JF) | TD1(adM); |

(ad = adult; sad = subadult; Y = yearling; J = Juvenile)

The observations were carried out over the full 24 hour periods, with the study enclosure illuminated at night (1.3.4). Focal animal sampling was conducted, but due to behavioural group coherence, general activity recordings were representative for the entire groups. Activity was recorded for 10-minute intervals (5.3.1.2). Behavioural responses including those related to thermocomfort, such as body posture, or whether in forest of fynbos, were noted.

A general subjective characterization of weather was made for 3-hourly periods (degree of cloud cover, warm/cold, wind strength and direction). Ambient temperature was measured in the shade with SABS approved mercury thermometers at \pm 50 cm above ground level. These measurements were taken at two sites, one in the forest and one in the fynbos part of the enclosure. Onset, end and intensity of precipitation was recorded.

During observation periods I and II, the focus was specifically on temperature regulation, including body core temperature telemetry and intensified weather monitoring. In addition to ambient temperature measurements, black bulb temperature, relative humidity and wind speed were recorded hourly. A whirling psychrometer was used to determine relative humidity.

Prior to observation periods I and II, three and four animals respectively (TD5, TD3, TC2 and TD7) were immobilized with M99. Temperature transmitters were implanted into the peritoneal cavities by a veterinary surgeon. Each transmitter had been calibrated against SABS approved mercury thermometers. Body core temperatures were monitored

hourly with a receiver (Lafayette, Mini-Mitter Company, Inc.: Bio-Telemetry Equipment, Indianapolis, USA) and a stopwatch. They were calculated from the average of 3 time periods of 30 bleep-signals for each animal and measuring event.

7.2.2 Thermal insulation

Four 4 x 4 cm (16 cm²) samples were cut from fresh skins of 44 bushpigs, two from each side. A 4 x 4 cm template was placed on the hairless side of the skin and care was taken not to sever any of the hairs while cutting the samples. Samples were located midway between the crest and ventral end of the skin, from just behind the cardiac region and the haunch.

The hairs of the skin samples were cut with a scalpel flush with the skin and placed in numbered envelopes. For each coat sample the lengths of all the hairs were measured, the number of recordings representing the number of hairs per 16 cm² of skin. The hair of the coat samples from each animal was weighed to the nearest mg.

7.2.3 Water use

(a) Water deprivation

Towards the end of observation period V on 10.1.1983 access to all free surface water was removed in the study enclosure. This was maintained throughout observation period VI; i.e. until 16.1.1983. The food consumption of the study animal group was monitored and any behavioural responses noted.

(b) Water consumption

Four animals from the study enclosure were isolated in enclosure B on four separate occasions, two in winter and two during the summer. A drum, 28,4 cm in diameter, was sunk into the ground of enclosure B, the rim protruding about 5 cm above ground level. The daily change in the water level was determined at a standardized time. Water consumption

was calculated and corrected for evaporation with reference to a similar drum to which the study animal had no access.

(c) Urinary water loss

Fresh kidneys from 10 culled bushpig were weighed and the width (B), length (D) and depth (C) were measured. The kidneys were then bisected medially and the widths of the cortex and medulla (A) were measured at 10 intervals along the periphery. The relative medullary thickness (RMT) was calculated according to the method of Sperber (1944).

$$\text{RMT} = \frac{10 \times \text{medullary thickness (A)}}{\sqrt[3]{B \times C \times D}}$$

In addition, the osmolality and the sodium and potassium concentrations of 8 urine samples were determined. Osmolality was measured using a Wescor osmometer (Model 51 008). Sodium and potassium concentrations were determined with a flame photometer.

7.2.4 Energy metabolism

Three male juvenile bushpigs, between 3 - 4 months old, were conditioned to tolerate face masks which were placed over their snouts periodically for progressively longer intervals during the day. After about 2 weeks of daily conditioning, no signs of discomfort were noticed when putting on the masks and the animals generally rested peacefully during the appropriate times.

The study animals were fed the usual pelleted diet once daily in the evening, *ad libitum*. All three animals maintained their masses during the experimental week of 25.1 - 29.1.1982. The oxygen consumption determinations were carried out in the temperature chambers at the University of Port Elizabeth according to the following schedule (Table 7.1):

| TABLE 7/1: EXPERIMENTAL SCHEDULE OF OXYGEN CONSUMPTION DETERMINATIONS | | | |
|---|-----------|-----------------------------------|---|
| DAY | DATE | MEASURING PERIODS | TEMPERATURE CHAMBER SETTINGS |
| MONDAY | 25.1.1982 | 17 - 18 h | $\pm 20^{\circ} \text{C}$ |
| TUESDAY | 26.1.1982 | 17 - 12 h 16 - 18 h 1 - 3 h | $\pm 20^{\circ} \text{C}$ $\pm 25^{\circ} \text{C}$ $\pm 25^{\circ} \text{C}$ |
| WEDNESDAY | 27.1.1982 | 8 - 9 h 9 - 11 h | $\pm 30^{\circ} \text{C}$ $\pm 35^{\circ} \text{C}$ |
| THURSDAY | 28.1.1982 | 9 - 11 h 15 - 16 h | $\pm 15^{\circ} \text{C}$ $\pm 20^{\circ} \text{C}$ |
| FRIDAY | 29.1.1982 | 10 - 13 h | $\pm 5^{\circ} \text{C}$ |

The face masks were placed over the snouts of the animals and fastened with masking tape onto a neck strap at least 2 hours prior to transfer to the temperature chamber. In the chamber, two hours were allowed for acclimation to any specific air temperature before the oxygen consumption was measured.

Oxygen consumption measurements were obtained by drawing laboratory air through the face mask at the rate of between 15-17 l/min before it entered the polarographic oxygen probe (Bioscience OX 140 oxygen transducer in a specifically built cell coupled to an amplifier) coupled to a recorder. The flow rate of air through the system corrected to STP, and the difference in oxygen concentration between the incurrent and excurrent air was used to calculate the oxygen consumption. The oxygen probe was calibrated for the specific flow rates and the expected exhaled air composition against a known mass of air from a gas cylinder with a known gas concentration, drawn through the entire system.

The rate of oxygen consumption had to be approximately constant for at least 5 consecutive minutes before it was accepted as a reading. At least 2 valid readings per animal and treatment were used to calculate the rate of oxygen consumption. Air temperature was measured regularly and the treatment average was taken as the representative temperature reading, rather than the temperature setting of the chamber.

Thermocomfort responses, like panting, shivering and posture, were recorded while an animal was connected to the airflow system. Rectal temperatures were taken at the end of each treatment.

7.3 Results

7.3.1 Behavioural thermoregulation

7.3.1.1 Climatic setting

The regional climate was characterized in section 2.3. Table 7/2 provides a summary of the temperature regime recorded during the various observation periods in the study enclosure.

| | OBSERVATION PERIOD | SEASON | $\bar{T}_a \pm s (^{\circ}\text{C})$ | n | RANGE ($^{\circ}\text{C}$) |
|--------|----------------------|--------|--------------------------------------|-----|------------------------------|
| FOREST | 8/9 - 12/13.1.1982 | SUMMER | 19,6 \pm 3,4 | 116 | 14,5 - 27,0 |
| | 6/7 - 10/11.1.1983 | | 20,5 \pm 4,6 | 120 | 13,2 - 35,5 |
| | 11/12 - 15/16.1.1983 | | 18,7 \pm 5,5 | 120 | 11,5 - 32,9 |
| | 1/2 - 5/6.6.1981 | WINTER | 13,8 \pm 2,8 | 120 | 10,0 - 23,7 |
| | 11/12 - 15/16.7.1982 | | 11,3 \pm 3,4 | 120 | 5,0 - 21,5 |
| | 4/5 - 8/9.7.1983 | | 9,1 \pm 5,1 | 119 | 3,2 - 22,8 |
| FYNBOS | 8/9 - 12/13.1.1982 | SUMMER | 20,1 \pm 5,0 | 119 | 13,5 - 32,0 |
| | 6/7 - 10/11.1.1983 | | 21,5 \pm 6,1 | 120 | 12,3 - 39,3 |
| | 11/12 - 15/16.1.1983 | | 19,3 \pm 6,7 | 120 | 10,5 - 37,5 |
| | 1/2 - 5/6.6.1981 | WINTER | 13,3 \pm 3,3 | 120 | 8,0 - 24,0 |
| | 11/12 - 15/16.7.1982 | | 10,6 \pm 3,6 | 120 | 4,3 - 21,0 |
| | 4/5 - 8/9.7.1983 | | 8,8 \pm 4,8 | 119 | 2,5 - 20,8 |

The average summer and winter temperatures were 19,6 $^{\circ}\text{C}$ and 11,3 $^{\circ}\text{C}$ respectively in the indigenous forest and 20,3 $^{\circ}\text{C}$ and 10,9 $^{\circ}\text{C}$ in the fynbos. The fynbos temperature averages thus were 0,7 $^{\circ}\text{C}$ higher in summer and 0,4 $^{\circ}\text{C}$ lower in winter than the equivalent forest temperatures. Conversely, during the course of any particular day, higher temperatures are experienced during daytime and lower temperatures at night in the fynbos, compared to those in the forest.

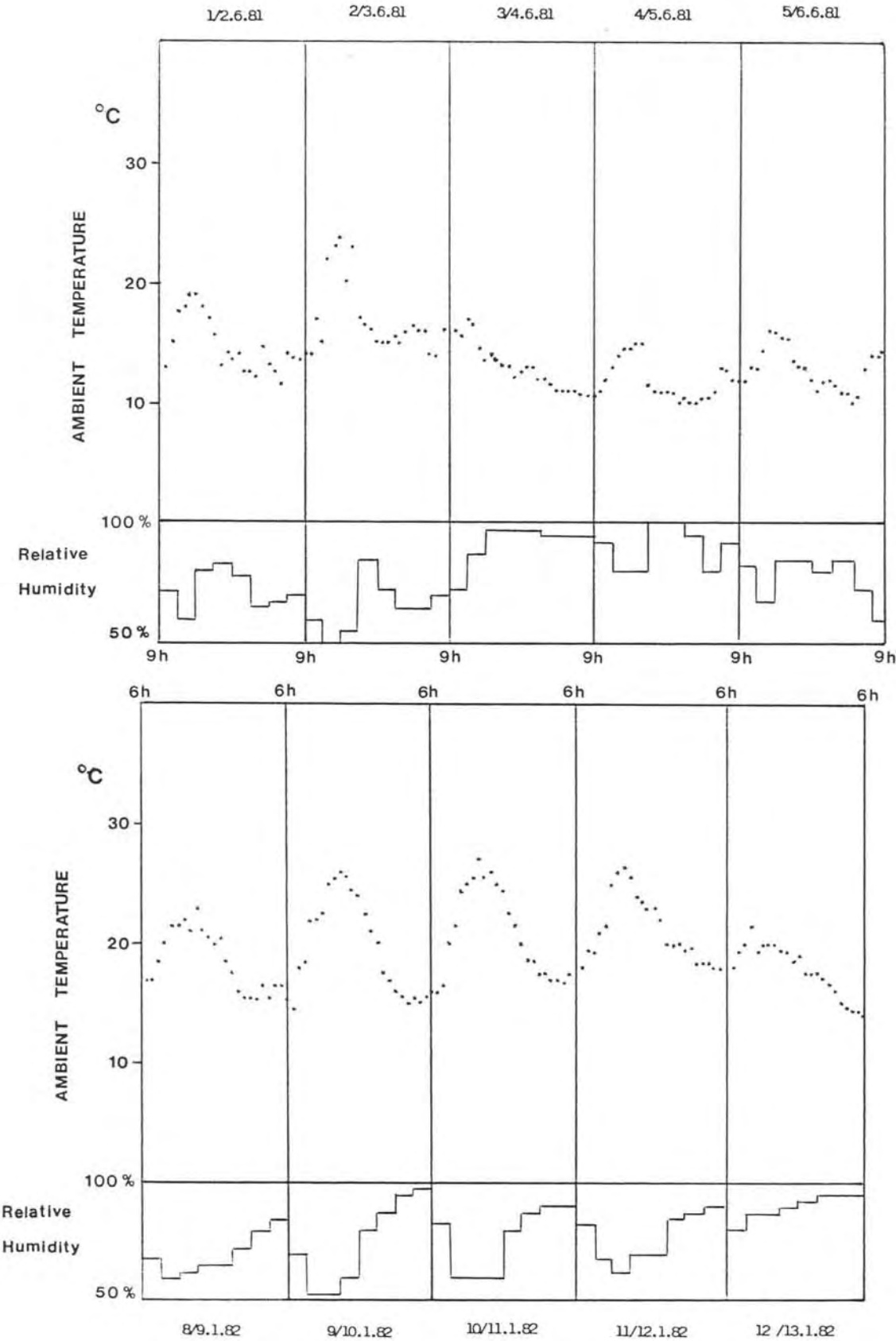
This equalizing effect of the forest canopy on diel temperature extremes is absent on overcast or rainy days. The interplay between diel temperature changes and overcast or rainy conditions, as indicated by relative humidity, is illustrated in Fig. 7/1 for the observational periods when telemetric body core temperature monitoring was undertaken.

7.3.1.2 Activity scheduling

In Tables 7/3 to 7/8 the activity schedules of bushpigs and ambient temperatures in the study enclosure over a total of 30 days are shown. Inspection of the data, in conjunction with additional notes made on the observation forms, revealed that weather which is particularly cold or cold and rainy, tended to suppress activity (Table 7/3; 3/4.6.1981, 2 - 6 h: rainy and wet; 4/5.6.1981; 22 - 6 h: raining and nest building; Table 7/4: 12/13.1.1982; rainy all day and nest building). The total levels of daily activity during observation periods V (Table 7/7) and VI (Table 7/8) are considerably lower than those of the previous periods. This is presumably due to the effect of experimental water deprivation during observation period V and particularly low temperatures during period VI. The basic trends in activity during the day were unchanged during these periods.

There was a significant positive correlation between total daily activity and ambient temperature in winter ($n = 15$, $r = 0,63$ $P < 0,05$), i.e. cooler weather tended to limit activity during the winter. A poorly defined negative correlation between total daily activity and ambient temperature was evident in summer, but not statistically significant ($n = 15$, $r = -0,35$ NS). Direct correlation analysis of this type is however hampered by (I) activity not being independent over time (sequential time period dependence); (II) non-linearity of the relationship of temperature and activity and (III) activity compensation; i.e. high day temperatures in summer may delay the onset of activity, but total activity time is compensated for during the summer nights.

FIG. 7/1: WEATHER CHARACTERIZATION: GOUDVELD ENCLOSURE



| TABLE 7/3: ACTIVITY (A%) VS AMBIENT TEMPERATURE (T°C) | | | | | | | |
|---|--------|-------------|-------------|------------|-------------|-------------|----------------------|
| OBSERVATION PERIOD I (WINTER) | | | | | | | TIME PERIOD AVERAGES |
| DATE | | 1/2.6.81 | 2/3.6.81 | 3/4.6.81 | 4/5.6.81 | 5/6.6.81 | |
| 6 - 10 h | A T | 50 13,5 | 75 14,5 | 25 11,9 | 50 12,0 | 50 13,6 | 50 13,1 |
| 10 - 14 h | A T | 25 17,4 | 0 19,3 | 0 15,9 | 25 13,4 | 0 14,1 | 20 16,0 |
| 14 - 18 h | A T | 50 17,4 | 100 20,9 | 50 10,3 | 25 13,9 | 100 14,9 | 65 15,5 |
| 18 - 22 h | A T | 100 13,6 | 100 15,6 | 75 12,6 | 100 11,0 | 75 12,2 | 90 13,0 |
| 22 - 2 h | A T | 100 12,9 | 50 15,1 | 50 12,1 | 0 10,1 | 0 11,6 | 40 12,4 |
| 2 - 6 h | A T | 100 12,7 | 100 16,1 | 0 11,0 | 0 11,2 | 25 11,2 | 45 12,4 |
| DAILY AVERAGES | A T | 71 14,6 | 71 16,9 | 33 12,3 | 33 11,9 | 50 12,9 | 52 13,7 |

| TABLE 7/4: ACTIVITY (A%) VS AMBIENT TEMPERATURE (T°C) | | | | | | | |
|---|--------|-------------|-------------|------------|-------------|------------|-------------------|
| OBSERVATION PERIOD II (SUMMER) | | | | | | | TIME PERIOD AVER. |
| DATE | | 8/9.1.82 | 9/10.1.82 | 10/11.1.82 | 11/12.1.82 | 12/13.1.82 | |
| 6-10h | A T | 100 18,1 | 50 18,0 | 75 18,5 | 75 19,5 | 25 19,7 | 65 18,8 |
| 10-14h | A T | 0 21,5 | 0 23,7 | 0 25,5 | 0 24,7 | 25 19,9 | 5 23,1 |
| 14-18h | A T | 50 21,5 | 50 25,0 | 25 25,2 | 0 24,0 | 50 18,7 | 35 22,8 |
| 18-22h | A T | 50 18,1 | 25 20,2 | 75 20,6 | 100 21,2 | 50 17,4 | 60 19,5 |
| 22-2h | A T | 100 15,7 | 50 15,9 | 50 17,6 | 50 19,4 | 25 15,5 | 55 16,8 |
| 2-6h | A T | 100 16,0 | 100 15,5 | 25 17,3 | 50 18,2 | 50 14,4 | 65 16,3 |
| DAILY AVER. | A T | 67 18,4 | 46 19,7 | 42 20,8 | 46 21,2 | 37 17,6 | 47 19,5 |

| TABLE 7/5: ACTIVITY (A%) VS AMBIENT TEMPERATURE (T°C) | | | | | | | |
|---|--------|-------------|------------|------------|-------------|------------|-------------------|
| OBSERVATION PERIOD III (WINTER) | | | | | | | TIME PERIOD AVER. |
| DATE | | 11/12.7.82 | 12/13.7.82 | 13/14.7.82 | 14/15.7.82 | 15/16.7.82 | |
| 6-10h | A T | 100 10,9 | 75 7,8 | 75 11,7 | 50 12,2 | 50 6,0 | 70 9,7 |
| 10-14h | A T | 25 10,7 | 0 13,1 | 0 15,6 | 25 10,6 | 50 11,0 | 20 12,2 |
| 14-18h | A T | 50 10,6 | 25 14,5 | 25 19,8 | 75 8,7 | 25 11,6 | 50 13,0 |
| 18-22h | A T | 100 13,0 | 100 9,1 | 100 9,9 | 75 14,9 | 75 7,9 | 90 11,0 |
| 22-2h | A T | 100 12,0 | 75 8,0 | 75 9,5 | 100 17,2 | 25 5,9 | 75 10,5 |
| 2-6h | A T | 75 13,0 | 50 7,6 | 25 11,4 | 0 13,3 | 0 5,5 | 30 10,2 |
| DAILY AVER. | A T | 75 11,7 | 54 10,0 | 50 13,0 | 54 12,8 | 37 8,0 | 56 11,1 |

| TABLE 7/6: ACTIVITY (A%) VS AMBIENT TEMPERATURE (T°C) | | | | | | | |
|---|--------|-------------|-------------|------------|-------------|-------------|-------------------|
| OBSERVATION PERIOD IV (SUMMER) | | | | | | | TIME PERIOD AVER. |
| DATE | | 6/7.1.83 | 7/8.1.83 | 8/9.1.83 | 9/10.1.83 | 10/11.1.83 | |
| 6-10h | A T | 75 15,3 | 50 22,7 | 50 20,5 | 50 18,4 | 50 18,1 | 55 19,0 |
| 10-14h | A T | 0 21,3 | 0 33,0 | 0 25,7 | 0 21,7 | 0 20,4 | 0 24,4 |
| 14-18h | A T | 0 23,4 | 0 34,0 | 0 25,0 | 25 20,7 | 0 20,5 | 5 24,7 |
| 18-22h | A T | 100 18,9 | 100 24,9 | 75 20,5 | 100 19,3 | 100 18,8 | 95 20,5 |
| 22-2h | A T | 100 15,4 | 50 18,9 | 0 18,8 | 50 18,0 | 50 16,8 | 50 17,6 |
| 2-6h | A T | 100 14,8 | 25 14,5 | 50 17,7 | 0 17,6 | 50 17,3 | 45 17,0 |
| DAILY AVER. | A T | 62 18,2 | 37 25,2 | 29 21,4 | 37 19,3 | 42 18,6 | 42 20,5 |

| TABLE 7/7 ACTIVITY (A%) VS AMBIENT TEMPERATURE (T°C) | | | | | | | |
|--|---|------------|------------|------------|------------|------------|-------------------|
| OBSERVATION PERIOD V (SUMMER) | | | | | | | TIME PERIOD AVER. |
| DATE | | 11/12.1.83 | 12/13.1.83 | 13/14.1.83 | 14/15.1.83 | 15/16.1.83 | |
| 6-10h | A | 0 | 50 | 25 | 0 | 50 | 25 17,2 |
| | T | 17,6 | 13,3 | 15,4 | 17,8 | 21,7 | |
| 10-14h | A | 0 | 0 | 0 | 0 | 0 | 0 22,2 |
| | T | 16,8 | 16,1 | 21,2 | 25,2 | 31,9 | |
| 14-18h | A | 50 | 25 | 0 | 0 | 0 | 15 22,3 |
| | T | 16,2 | 16,0 | 21,4 | 25,3 | 32,6 | |
| 18-22h | A | 100 | 100 | 100 | 100 | 25 | 85 19,0 |
| | T | 14,4 | 14,9 | 17,1 | 21,7 | 26,9 | |
| 22-2h | A | 25 | 25 | 25 | 75 | 0 | 30 15,7 |
| | T | 13,3 | 13,7 | 11,7 | 17,5 | 22,5 | |
| 2-6h | A | 25 | 25 | 0 | 25 | 0 | 15 15,0 |
| | T | 12,1 | 11,8 | 14,0 | 17,2 | 19,9 | |
| DAILY AVER. | A | 33 | 37 | 25 | 33 | 12 | 28 18,6 |
| | T | 15,1 | 14,3 | 16,8 | 20,8 | 25,9 | |

| TABLE 7/8: ACTIVITY (A%) VS AMBIENT TEMPERATURE (T°C) | | | | | | | |
|---|---|----------|----------|----------|----------|----------|-------------------|
| OBSERVATION PERIOD VI (WINTER) | | | | | | | TIME PERIOD AVER. |
| DATE | | 4/5.7.83 | 5/6.7.83 | 6/7.7.83 | 7/8.7.83 | 8/9.7.83 | |
| 6-10h | A | 50 | 0 | 75 | 0 | 0 | 25 9,1 |
| | T | 21,4 | 6,8 | 4,9 | 4,0 | 8,2 | |
| 10-14h | A | 0 | 25 | 25 | 25 | 0 | 15 11,0 |
| | T | 22,0 | 5,7 | 7,9 | 9,7 | 9,9 | |
| 14-18h | A | 75 | 100 | 25 | 25 | 50 | 65 11,6 |
| | T | 22,1 | 5,2 | 9,0 | 11,6 | 10,2 | |
| 18-22h | A | 100 | 50 | 50 | 75 | 50 | 65 8,1 |
| | T | 13,9 | 4,3 | 5,8 | 7,9 | 8,7 | |
| 22-2h | A | 25 | 0 | 0 | 0 | 0 | 5 8,1 |
| | T | 14,8 | 4,5 | 5,5 | 8,0 | 7,8 | |
| 2-6h | A | 0 | 0 | 0 | 0 | 0 | 0 6,2 |
| | T | 8,4 | 4,7 | 4,4 | 7,5 | 6,2 | |
| DAILY AVER. | A | 42 | 29 | 29 | 29 | 17 | 29 9,0 |
| | T | 17,1 | 5,2 | 6,2 | 8,1 | 8,5 | |

An analysis of the incidence of full 4-hour resting periods, revealed that these were not independently distributed over the hours of the day or night between winter and summer (Table 7/9)

| TABLE 7/9: INCIDENCE OF 4-HOUR RESTING PERIODS | | |
|--|--------|--------|
| | SUMMER | WINTER |
| DAY (6 - 18h) | 24 | 9 |
| NIGHT (18 - 6h) | 4 | 15 |
| G = 13,55 (P < 0,005) | | |

A pattern of increased summer day and winter night resting was again verified. In order to eliminate the effect of serial correlation, i.e. activity not being independent over the time sequence, only those time periods for which an approximately equal number of activity versus resting periods were observed, were used to investigate the relationship of air temperature to activity. This applied *i.a.* to the time periods 14 - 18 h in summer and 22 - 6 h in winter (Table 7/10)

| TABLE 7/10: INTERACTION: ACTIVITY AND TEMPERATURE °C | | | |
|--|----|-----------|------|
| | n | \bar{X} | s |
| (a) SUMMER DAY TEMPERATURES | | | |
| ACTIVE | 7 | 20,4 | 3,76 |
| RESTING | 8 | 25,8 | 4,94 |
| (b) WINTER NIGHT TEMPERATURES | | | |
| ACTIVE | 15 | 12,0 | 3,20 |
| RESTING | 15 | 8,0 | 2,89 |

The 4-hour periods (14-18h) during which bushpigs were observed to rest on summer days had significantly higher ambient temperatures than those with activity ($t = 2,33$; $P < 0,05$). Conversely, the 4-hour periods (22 - 2 h; 2 - 6 h) during which bushpigs were observed to rest during winter nights had significantly lower ambient temperatures than those with activity ($t = 3,59$; $P < 0,01$).

The emerging activity pattern is one with restricted daytime activity in summer and resting after midnight in winter under conditions of

particularly low ambient temperatures (Table 7/11). Radio-tracking data showed that free-ranging bushpigs exhibited the same activity trends (6.4).

| TABLE 7/11: SEASONAL ACTIVITY SCHEDULING (STUDY ENCLOSURE) | | | | | | |
|---|--------|------------|------------|------------|----------------------|--------------------------|
| WINTER OBSERVATION PERIODS | | | | | TIME PERIOD AVERAGES | WINTER PATTERN |
| | | I | III | IV | | |
| 6-10h | A T | 50 13,1 | 70 9,7 | 25 9,1 | 48 10,6 | MAIN RESTING PERIOD |
| 10-14h | A T | 20 16,0 | 20 12,2 | 15 11,0 | 18 13,1 | |
| 14-18h | A T | 65 15,5 | 50 13,0 | 65 11,6 | 60 13,4 | |
| 18-22h | A T | 90 13,0 | 90 11,0 | 65 8,1 | 82 10,7 | MAIN ACTIVITY PERIOD |
| 22-2h | A T | 40 12,4 | 75 10,5 | 5 8,1 | 40 10,3 | SECONDARY RESTING PERIOD |
| 2-6h | A T | 45 12,4 | 30 10,2 | 0 6,2 | 25 9,6 | |
| SUMMER OBSERVATION PERIODS | | | | | TIME PERIOD AVERAGES | SUMMER PATTERN |
| | | II | IV | V | | |
| 6-10h | A T | 65 18,8 | 55 19,0 | 25 17,2 | 48 18,3 | MAIN RESTING PERIOD |
| 10-14h | A T | 5 23,1 | 0 24,4 | 0 22,2 | 2 23,2 | |
| 14-18h | A T | 35 22,8 | 5 24,7 | 15 22,3 | 18 23,3 | |
| 18-22h | A T | 60 19,5 | 95 20,5 | 85 19,0 | 80 19,7 | MAIN ACTIVITY PERIOD |
| 22-2h | A T | 55 16,8 | 50 17,6 | 30 15,7 | 45 16,7 | |
| 2-6h | A T | 65 16,3 | 45 17,0 | 15 15,0 | 42 16,1 | |
| A: Periodic Activity Percentage T: Periodic Ambient Temperature Average (°C) n: Summarized Data: Tables 7/3 - 7/8 (Total of 30 observation days) | | | | | | |

The observed pattern of activity is interpreted as being geared to avoiding high temperatures during peak activity and adjusted to avoid energy loss through resting during cold and wet periods.

7.3.1.3 Thermocomfort behaviour

Heat loads are counteracted behaviourally by avoiding times of the day with high ambient temperatures for peak activity (previous section) and through the facilitation of heat dissipation from the body. Heat dissipation behaviour was observed to take on the following forms:

- (I) Selecting resting sites subject to air movement.
- (II) Avoidance of body contact during resting and lying in an extended posture, usually on their sides.
- (III) Facilitation of conductive heat loss to the substrate by selecting cool, moist hollows to lie in or by rooting up of the cooler subsoil.
- (IV) Standing and wandering about during very hot weather when there is some air movement. This increases body surface exposure to air movement.
- (V) Wallowing. When chased for extended periods (e.g. during hunts with dogs), bushpigs purposefully sought out pools to wet their body surfaces.

Heat conserving behaviour consisted mainly of sheltering, huddling and nest-building.

- (I) Sheltering involved the selection of resting sites which were protected from air movement and provided a dry substrate. Such sites typically were protected depressions (Plate 9b), hollow and overhanging tree stumps (Plate 9c) and dense vegetation, such as fynbos.
- (II) Huddling while resting was observed to be the rule. The young in particular wedged themselves in between the adults.

(III) Contact to a cold substrate was minimized by adopting a flexed upright posture; resting on the stomach with knees tucked in underneath.

(IV) Nest-building entailed the heaping up of twigs, branches and foliage by the sow. The group members then moved in underneath the sizeable stack of twigs and branches, which presumably retained most of the body heat emitted. Weather conditions on days when nest building was observed in the study enclosure (Table 7/12) were compared with the overall weather conditions during the months concerned (Table 7/13).

| DATE | RAIN (mm) x 0,1 | MIN. TEMP (°C) | ADDITIONAL INFORMATION (w = age in weeks) |
|---------------|-----------------------|----------------------|--|
| 4/5.6.1981 | 9,0 | 8,2 | |
| 12/13.1.1982 | 6,0 | 14,0 | One of 2 juveniles (2w) died during night |
| 7/8.3.1983 | 12,5 | 8,5 | |
| 9/10.5.1983 | 24,0 | 8,2 | TD2(F) with juvenile (8w) |
| 10/11.5.1983 | 15,0 | 5,5 | ditto |
| 22/23.5.1983 | 7,5 | 9,0 | TD2(F) with juvenile (10w) |
| 12/13.6.1983 | 90,5 | 7,0 | |
| 24/25.7.1983 | 40,5 | 2,0 | |
| 26/27.7.1983 | 79,5 | 8,4 | |
| 7/8.10.1984 | 18,0 | 4,4 | TH2(F): no juvenile |
| 28/29.10.1984 | 21,0 | 11,0 | TD2(F) with 5 day old juveniles |
| 29/30.10.1984 | 5,0 | 11,0 | TD2(F) with 6 day old juveniles |
| 6/7.4.1985 | 4,5 | 5,0 | |
| 13/14.10.1985 | 14,6 | 7,4 | TD2(F) with juveniles (2w) |
| 15/16.10.1985 | 55,4 | 8,5 | ditto |
| 31/1.11.1985 | 7,0 | 8,5 | Juvenile death: 1.11 and 3.11.1985 (4w) |
| 20/21.4.1986 | 0,5 | 11,0 | TD2(F) with juveniles (3w) |
| 3/4.7.1986 | 20,0 | 1,0 | TD2(F) broke off <i>i.a.</i> 15mm ironwood sapling |
| 30/31.10.1986 | 28,0 | 9,0 | |
| 31/1.11.1986 | 20,5 | 7,5 | |
| 23/24.1.1987 | 12,5 | 9,5 | |
| 10/11.2.1987 | 19,5 | 9,0 | |
| 14/15.9.1987 | 10,0 | 7,0 | |
| 22/23.9.1987 | 80,6 | 9,0 | |
| 26/27.9.1987 | 12,0 | 6,5 | |

| TABLE 7/13: WEATHER CHARACTERISTICS AND NEST BUILDING | | | | | |
|---|------|------|---------------------------------|------|------|
| FREQUENCY OF DAYS WITH WEATHER COMBINATIONS INDICATED | | | | | |
| WITH NEST BUILDING | | | WITHOUT NEST BUILDING | | |
| RAIN | 1 | 24 | RAIN | 56 | 138 |
| NO RAIN | 0 | 0 | NO RAIN | 116 | 177 |
| | WARM | COLD | | WARM | COLD |
| WARM: > 12°C (DAILY MINIMUM) | | | COLD: < 12°C (DAILY MINIMUM) | | |

Applying a hierarchical log linear model to the three-way frequency data of Table 7/13 showed that nest building was more likely to occur when it was cold ($\chi^2 = 10,61$; $P < 0,01$ $df = 1$) and when it was raining ($\chi^2 = 35,70$ $P < 0,0001$ $df = 1$). In fact, nest-building was virtually confined to periods of rain combined with comparatively low temperatures.

7.3.2 Thermal insulation

Tissue insulation resists heat flow from the body core to the surface (Curtis 1970). Thus, when an animal with a considerable layer of subcutaneous fat is exposed to cold, peripheral vasoconstriction is very effective in producing a high specific insulation (Mount 1968). Fat is particularly effective as insulator, partly because it has a lower thermal conductivity than other tissues (Burton and Edholm 1955 ex Mount 1968). The thickness of the subcutaneous fat layer in the bushpig varied with locality on the body surface, age, condition and reproductive state in the female (9.3.2). The subcutaneous fat layer in bushpig males, measured over three body localities (back, shoulder, thorax: 9.3.2), ranged between 0 and 9 millimeter ($\bar{X} = 2,6\text{mm}$, $n = 89$ animals). The equivalent values for females were 0 to 15mm ($\bar{X} = 5,0\text{mm}$; $n = 91$).

Pelage insulation is the most important component of total thermal insulation in most mammals (Curtis 1970). Characteristics of the

bushpig's coat in respect of hair density, length and mass are set out in Tables 7/14 and 7/16.

| TABLE 7/14: BUSHPIG PELAGE: HAIR DENSITY AND MASS | | | | |
|---|------------------------------------|----|--------|-------------|
| AGE CLASS | \bar{X} Hairs/cm ² | n | s | RANGE |
| JUVENILES | 40,0 | 9 | 22,779 | 22,2 - 96,3 |
| YEARLINGS | 19,7 | 13 | 3,858 | 13,2 - 25,9 |
| SUBADULTS | 17,3 | 7 | 3,938 | 11,5 - 22,4 |
| ADULTS | 16,7 | 15 | 3,523 | 11,9 - 26,3 |
| | mg/cm ² | n | s | RANGE |
| JUVENILES | 35,8 | 9 | 14,819 | 14,8 - 56,7 |
| YEARLINGS | 38,7 | 13 | 9,943 | 21,6 - 54,7 |
| SUBADULTS | 38,0 | 7 | 9,144 | 28,5 - 49,5 |
| ADULTS | 37,4 | 15 | 9,304 | 21,6 - 51,8 |

The hair density of juveniles (J) is significantly higher than that of yearlings (Y), subadults (S) and adults (A) ($t = 3,18$ $P < 0,01$). No other significant differences in hair density or hair mass between the age classes were evident.

No seasonal or regional differences in hair density were evident (data pooled over subadults and adults: Table 7/15)

| TABLE 7/15: HAIR DENSITIES: SEASONAL + REGIONAL BREAKDOWN | | | | |
|---|------------------------------------|----|-------|--------------------------|
| <u>SEASON</u> | \bar{X} (hairs/cm ²) | n | s | STATISTICAL SIGNIFICANCE |
| JAN - APRIL | 16,5 | 8 | 4,303 | t = 0,56 NS |
| MAY - AUG | 17,6 | 9 | 3,819 | |
| SEPT - DEC | 16,2 | 5 | 1,805 | t = 0,76 NS |
| <u>REGION</u> | | | | |
| SOUTHERN CAPE | 16,1 | 11 | 2,361 | t = 1,05 NS |
| EASTERN CAPE | 17,7 | 11 | 4,446 | |

Hair length within the juvenile age class changes as indicated in table 7/16 below. At 7 months of age the hair length attains adult values; compared with the subsequent age class averages (Table 7/16).

| TABLE 7/16: HAIR LENGTHS IN BUSHPIGS | | | |
|--------------------------------------|--------------|---------------------|---|
| IDENTIFICATION | AGE (MONTHS) | AVERAGE HAIR LENGTH | |
| OKC 49 | 2,4 | 16,1 mm | |
| EC 23 | 2,6 | 18,6 mm | |
| TF 4 | 4,6 | 31,0 mm | |
| OKC 41 | 5,3 | 46,7 mm | |
| OKW 10 | 7,0 | 50,1 mm | |
| T 7 | 7,3 | 60,6 mm | |
| CC 5 | 10,5 | 59,8 mm | |
| | \bar{X} | s | n |
| YEARLINGS | 59,1 | 7,42 | 7 |
| SUBADULTS | 61,1 | 14,00 | 5 |
| ADULTS | 59,1 | 7,80 | 9 |

The frequency distribution of adult hair lengths is shown in Table 7/17.

| TABLE 7/17: ADULT HAIR LENGTH FREQUENCY DISTRIBUTION | | | | |
|--|-------------|-----------------------|------|------|
| LENGTH CLASSES mm | FREQUENCIES | FREQUENCY PERCENTAGES | | |
| 0 - 10 | 284 | 2,9 | | |
| 10 - 20 | 923 | 9,3 | 12,7 | |
| 20 - 30 | 1 343 | 13,5 | | |
| 30 - 40 | 1 505 | 15,1 | 28,6 | |
| 40 - 50 | 1 276 | 12,8 | | |
| 50 - 60 | 977 | 9,8 | 22,6 | |
| 60 - 70 | 806 | 8,1 | | |
| 70 - 80 | 670 | 6,7 | 14,8 | 95,1 |
| 80 - 90 | 476 | 4,8 | | |
| 90 - 100 | 376 | 3,8 | 8,6 | |
| 100 - 110 | 300 | 3,0 | | |
| 110 - 120 | 230 | 2,3 | 5,3 | |
| 120 - 130 | 177 | 1,8 | | |
| 130 - 140 | 115 | 1,2 | 3,0 | |
| 140 - 150 | 116 | 1,2 | | |
| 150 - 160 | 76 | 0,8 | 2,0 | |
| 160 - 170 | 58 | 0,6 | | |
| 170 - 180 | 62 | 0,6 | 1,2 | |
| 180 - 190 | 31 | 0,3 | | |
| 190 - 200 | 34 | 0,3 | 0,6 | |
| 200 - 210 | 37 | 0,4 | | |
| 210 - 220 | 14 | 0,1 | | |
| 220 - 230 | 19 | 0,2 | | |
| 230 - 240 | 13 | 0,1 | | |
| 240 - 250 | 15 | 0,1 | | |
| 250 - 260 | 7 | 0,1 | | |
| 260 - 270 | 7 | | | |
| 270 - 280 | 8 | | | |
| 280 - 290 | 3 | 0,1 | | |
| 290 - 300 | 1 | | | |
| 4,9 | | | | |
| DATA FROM 9 ADULT BUSHPIGS | | | | |

It is noteworthy that although juvenile coat length is shorter below the age of approximately 7 months, hair coat density is higher, resulting in similar hair mass over all four age classes.

7.3.3 Aspects of water turnover

Water plays a role in temperature regulation even in mammals which do not sweat profusely. Some information on water consumption, reaction to water deprivation and the ability to control urinary water loss in the bushpig was obtained during the study.

(a) Water consumption

Water consumption of 4 animals was monitored over a total of 26 days. Results are given in Table 7/18. The results indicate a substantially higher consumption of water per unit body mass during the warmer summer monitoring periods.

| ANIMAL IDENT | MASS (kg) | PERIOD | MEAN MONTHLY TEMP. (°C) | n | WATER CONSUMPTION | | |
|--------------|-----------|--------|-------------------------|---|-------------------|-------------|----------------------------|
| | | | | | l/day | ml/kg/day | ml/kg ^{0,75} /day |
| TD7(M) | 75 | 7/85 | 11,5 | 1 | 2,1 | 27,1 | 82,0 |
| TD1(M) | 87 | 7/85 | 11,5 | 9 | 1,9 ± 0,65 | 22,2 ± 7,5 | 67,7 ± 23,0 |
| TD13(M) | 65 | 1/86 | 18,2 | 9 | 3,3 ± 1,24 | 50,1 ± 19,0 | 142,2 ± 54,0 |
| TD14(M) | 56 | 2/86 | 18,0 | 7 | 2,6 ± 0,74 | 45,7 ± 13,3 | 125,0 ± 36,4 |

n: Number of days monitored.

(b) Water deprivation

Four adult sized bushpigs in the study enclosure were denied access to free surface water on the morning of 10.1.1983. On 13.1.1983 the animals dug a seepage hole at the base of a tree from which a little water was obtained.

Water needs were thus partially satisfied during the remainder of the water deprivation experiment which was terminated on 16.1.1983. The dry pellet food consumption of the group (4 bushpigs) declined as shown below:

| | |
|--------------|---------|
| 12/13.1.1983 | 6,65 kg |
| 14/15.1.1983 | 3,80 kg |
| 15/16.1.1983 | 2,20 kg |

On the last day of the experiment, which was also particularly hot (25,9°C on average), the bushpigs were only active for 12,5% of the 24 hour period (i.e. for 3 hours).

(c) Control of urinary water loss

The relative medullary thickness (R.M.T) of the kidney gives an indication of its ability to concentrate urine (Schmidt-Nielsen and O'Dell 1961).

| TABLE 7/19: BUSHPIG KIDNEY PARAMETERS | | | | | | | |
|--|--------------|---------------|---------------|--------------|----------------|---|--------------------------------|
| Sample No | Mass (wet) g | length (D) mm | height (C) mm | width (B) mm | Medulla (A) mm | Kidney size S = $\frac{A \times 10}{\sqrt[3]{D \times C \times B}}$ | R.M.T. $\frac{A \times 10}{s}$ |
| ? | 97,1 | 97 | 50 | 30 | 12 | 52,6 | 2,28 |
| B22 | 142,8 | 119 | 52 | 30 | 14 | 57,0 | 2,46 |
| B25 | 84,9 | 99 | 48 | 26 | 16 | 49,8 | 3,21 |
| CL1 | 100,7 | 113 | 51 | 26 | 17 | 53,1 | 3,20 |
| D9 | 112,5 | 116 | 47 | 24 | 13 | 50,8 | 2,56 |
| D10 | 137,4 | 119 | 55 | 29 | 15 | 57,5 | 2,61 |
| E2 | 157,0 | 112 | 51 | 33 | 16 | 57,3 | 2,79 |
| R4 | 68,6 | 97 | 46 | 23 | 11 | 46,8 | 2,35 |
| R5 | 45,0 | 82 | 34 | 19 | 11 | 37,6 | 2,93 |
| R6 | 80,3 | 91 | 46 | 20 | 12 | 43,7 | 2,75 |
| \bar{X} | 102,6 | | | | | 50,6 | 2,71 |
| s | 35,3 | | | | | 6,5 | 0,33 |
| Measurements according to SPERBER (1944) | | | | | | | |

Although the maximum urine concentration was not measured, the low urine osmolality (Table 7/20) would suggest that the bushpig is dependent on a

regular supply of water. Both sodium and potassium concentrations in the urine were low (Table 7/20).

| URINE SPECIMEN | OSMOLALITY (mOsm/kg) | K ⁺ (mM/l) | Na ⁺ (mM/l) |
|----------------|----------------------|-----------------------|------------------------|
| 050 | 138 | 39 | 7 |
| 051 | 191 | 47 | 10 |
| 052 | 195 | 37 | 7 |
| 053 | 210 | 45 | 4 |
| 054 | 223 | 46 | 11 |
| 055 | 122 | 18 | 9 |
| TD4 | 132 | 16 | 3 |
| TD4 | 137 | 21 | 4 |
| \bar{X} | 168,5 | 33,6 | 6,9 |
| s | 40,2 | 13,2 | 3,0 |
| n | 8 | 8 | 8 |

7.3.4 Body core temperature relations

The body core temperature data which were obtained in two recording sessions of 5 days each in winter (1/2 - 5/6.6.1981) and summer (8/9 - 12/13.1.1982) are presented in Table 7/21.

| IDENTIFICATION | SEX | WINTER(W) SUMMER(S) | AGE CLASS | MASS (kg) | \bar{T}_b | s | n | T _b RANGE | ΔT_b |
|----------------|-----|------------------------|-----------|-----------|-------------|-----|-----|----------------------|--------------|
| TD5 | M | W S | ADULT | 71 | 38,3 | 0,5 | 120 | 37,2 - 39,2 | 2,0 |
| | | | ADULT | 72 | 39,0 | 0,6 | 119 | 37,9 - 40,8 | 2,9 |
| TD3 | F | W S | ADULT | 87 | 37,4 | 0,4 | 120 | 36,6 - 38,3 | 1,7 |
| | | | ADULT | 91 | 38,7 | 0,3 | 118 | 37,8 - 39,4 | 1,6 |
| TC2 | M | W S | Y | 48 | 38,9 | 0,4 | 120 | 37,3 - 39,0 | 1,9 |
| | | | sad | 60 | 38,3 | 0,4 | 95 | 37,3 - 39,0 | 1,7 |
| TD7 | M | S | Y | 46 | 39,9 | 0,4 | 119 | 39,2 - 40,9 | 1,7 |

Both the individual and seasonal variation in body core temperatures was significant ($F = 198,1$ $df = 3,804$ $P < 0,0001$ and $F = 70,8$ $df = 1,804$ $P < 0,0001$). The body core temperatures of TD5 and TC2 did not differ

significantly, but those of TD3 were lower and TD7 higher than of the other two. The winter body core temperature average of 38,0°C is significantly lower than that of the summer (39,0°C). In contrasting to the general trend, male TC2 had a higher body core temperature in winter. This may be explained by his state of excitement due to the stress of being chased around by sow TD3. Yearling TC2 had been introduced into the study enclosure approximately 5,5 months prior to the winter body core temperature monitoring period and was still not fully accepted as a group member.

TABLE 7/22: TIME SERIES ANALYSIS OF BUSHPIG BODY CORE TEMPERATURES

| | SOURCE | F | V1/V2 | P< | AMPLITUDE (°C) | PHASE PEAK (h) | * |
|---|------------------------------------|------------------------|-------------------------|--------------------------|-------------------|----------------------|---|
| TD5 SUMMER | Ta CIRCADIAN RHYTHM ACTIVITY | 23,04 17,86 5,67 | 1/112 2/112 1/112 | 0,0001 0,0001 0,05 | 0,58 | 14,53 | I |
| TD5 WINTER | Ta CIRCADIAN RHYTHM ACTIVITY | 0,76 33,36 0,12 | 1/113 2/113 1/113 | NS 0,0001 NS | 0,45 | 14,88 | I |
| TD3 SUMMER | Ta CIRCADIAN RHYTHM ACTIVITY | 9,53 3,40 0,65 | 1/111 2/111 1/111 | 0,005 NS NS | 0,15 | (2,86) | P |
| TD3 WINTER | Ta CIRCADIAN RHYTHM ACTIVITY | 20,38 0,36 2,24 | 1/113 2/113 1/113 | 0,0001 NS NS | 0,03 | (4,77) | I |
| TC2 SUMMER | Ta CIRCADIAN RHYTHM ACTIVITY | 13,95 13,08 1,48 | 1/87 2/87 1/87 | 0,0005 0,0005 NS | 0,48 | 1,36 | P |
| TC2 WINTER | Ta CIRCADIAN RHYTHM ACTIVITY | 1,88 11,70 2,78 | 1/113 2/113 1/113 | NS 0,001 NS | 0,25 | 13,85 | I |
| TD7 SUMMER | Ta CIRCADIAN RHYTHM ACTIVITY | 10,55 15,37 0,33 | 1/112 2/112 1/112 | 0,005 0,0005 NS | 0,45 | 14,10 | I |
| Ta: AMBIENT TEMPERATURE ACTIVITY: ACTIVE vs RESTING * AVERAGE DAILY Tb PROPORTIONAL (P) OR INVERSE (I) TO AVERAGE DAILY Ta | | | | | | | |

Multiple regression time series analysis applying cosine trend estimation (Cryer 1986), revealed the following (Table 7/22):

- (I) For the given observed activity scheduling over the diel period, body core temperature (Tb) was largely independent of activity.
- (II) Ambient temperature significantly influenced Tb of all four animals during the summer measuring periods, but only that of TD3 during the winter period. (TD3 was also the only animal not exhibiting any nyctemeral rhythm of the body core temperature).
- (III) Statistically highly significant endogenous nyctemeral cyclicality of the body core temperatures was evident in three of the four animals during both winter and summer measuring periods.
- (IV) In 4 of the 5 cases of documented nyctemeral rhythmicity, a phase peak at $14.20h \pm 30$ minutes was found. In the remaining case of TC2 in summer a phase peak shift to 1.20h had apparently occurred.
- (V) An average amplitude in Tb of $0,44 \text{ }^\circ\text{C} \pm 0,12$ emerged. All diel oscillations remained within $1,2 \text{ }^\circ\text{C}$ from the mean Tb.

The effect of locomotory exertion on internal heat building-up, as indicated by Tb, was investigated on 13.1.1982 by chasing the study animals around in the enclosure. The change in body core temperature after periodically running, trotting and walking from 10.40h to 11.10h was as follows:

| | Tb(TD5) | Tb(TD3) | Tb(TD7) |
|--------|---------|---------|---------|
| 10.40h | 39,0°C | 38,2°C | 40,3°C |
| 11.10h | 40,8°C | 39,4°C | 42,3°C |
| 11.15h | 42,0°C | 39,3°C | 42,4°C |

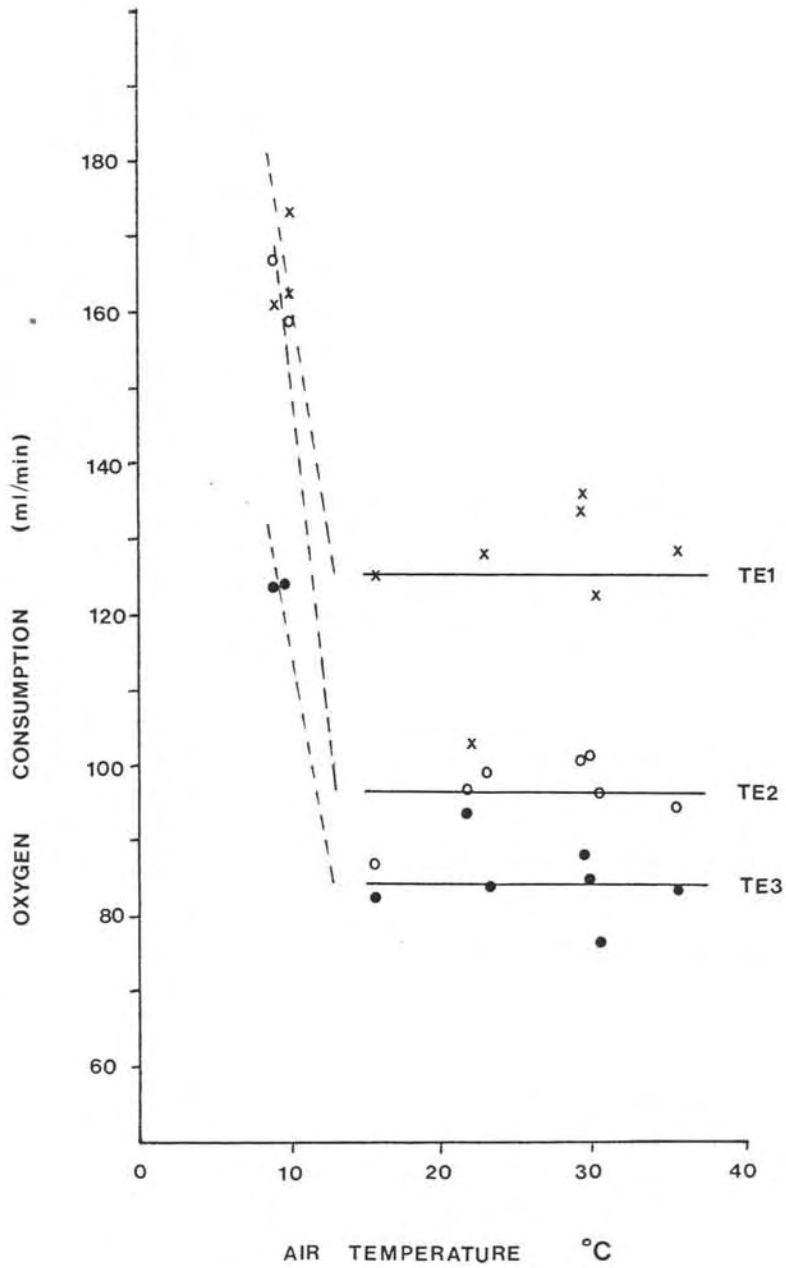
Sow TD3 did not run as much as the others. All however panted and wetted themselves by moving through the watering dam in the enclosure. On another occasion TE1 (M) was subject to acute overheating stress resulting from immobilization with M99 as evidenced by squealing, panting and excessive salivation. The animal was lying on its side and had a rectal temperature of $41,9^\circ\text{C}$, with 150 respirations per minute.

The metabolic responses to environmental temperature changes which emerged from the data in Tables 7/23 - 7/25 are summarized below:

- (I) The average rectal temperature of 37,0°C in the environmental temperature range of 9,0 - 15,6°C is significantly lower than 39,5°C measured at 29,2 to 35,4°C ($t = 9,60$ $df = 12$ $P < 0,001$).
- (II) At temperatures approaching 30°C heat stress was experienced, as indicated by intermittent panting. The apparent absence of heat stress at 30°C, at 8 - 9h may possibly be explained by the influence of circadian endogenous rhythmic variation in energy metabolism (cf Aschoff 1981a). Continuous panting with 150 - 170 respirations per minute indicated acute heat stress at 35°C.
- (III) The onset of shivering occurred between 9 and 16°C, seemingly dependent on body size. Whereas TE1 (13,2 kg) only showed signs of shivering at 9,8°C, TE3 (7,2 kg) already started to shiver at 15,6°C. A postural response to low temperatures was observed with all three animals at 15,6°C or lower.
- (IV) Schmidt-Nielsen (1979) defined the thermoneutral zone as "the temperature range within which the metabolic heat production is unaffected by a temperature change". For bushpig in the given weight range, the lower critical limit of the thermoneutral zone is somewhere between 10 and 15°C. As a best approximation 13°C is taken as the lower critical temperature (Fig 7/2). Thermoneutral oxygen consumption is 125,4; 96,5 and 84,6 ml/min for TE1, TE2 and TE3 respectively. The corresponding accelerated levels in oxygen consumption at $\pm 10^\circ\text{C}$ are 164,4; 163,4 and 123,8 ml/min.

Basal metabolism has been defined as the minimum energy cost when an animal is at rest in a thermoneutral environment and in a post-absorptive condition (Moen 1973). When the post-absorptive state is not achieved, as in this study, resting metabolism is a more appropriate term (cf Moen 1973). Resting metabolic rates (RMR) calculated from oxygen consumption at thermoneutrality, are given in Table 7/26. One liter of oxygen consumed was considered equivalent to 4,8 kcal of energy (Schmidt-Nielsen 1979)

FIG.7/2: METABOLIC RESPONSE TO ENVIRONMENTAL TEMPERATURE IN JUVENILE BUSHPIGS



| UNITS | MASS | TE1 13,2kg | TE2 8,2kg | TE3 7,2kg |
|---|------|---------------|--------------|--------------|
| l O ₂ /day | | 180,6 | 139,0 | 121,8 |
| l O ₂ /kg/day | | 13,7 | 16,9 | 16,9 |
| l O ₂ /kg ^{0,75} /day | | 20,1 | 28,7 | 27,0 |
| kcal/day | | 866,8 | 667,0 | 584,8 |
| kcal/kg/day | | 65,7 | 81,3 | 81,2 |
| kcal/kg ^{0,75} /day | | 125,2 | 137,6 | 133,0 |
| kJ/day | | 3626 | 2791 | 2446 |
| kJ/kg/day | | 247,7 | 340,4 | 339,7 |
| kJ/kg ^{0,75} /day | | 523,6 | 576,0 | 556,5 |

The average metabolic rates at $\pm 10^{\circ}\text{C}$ were 132%, 169% and 146% of those at thermoneutrality for inactive TE1, TE2 and TE3 respectively.

Myrcha and Jezierski (1972) determined resting metabolic rates for European wild boar weighing up to 30 kg (n = 13). Applying a power curve of the form $M = aW^b$ to their data resulted in the function $M = 167,4 W^{0,66}$ (M in kcal/day; W in kg). The RMR predicted from this equation closely resembled those found in the bushpig:

| Identification | Mass (kg) | Resting Metabolic Rate (kcal/day) | |
|----------------|-----------|-----------------------------------|-----------|
| | | Measured (Table 7/26) | Predicted |
| TE3 | 7,2 | 584,8 | 616 |
| TE2 | 8,2 | 667,0 | 671 |
| TE1 | 13,2 | 866,8 | 919 |

The oxygen consumption per unit of body mass of the domestic pig was determined to be about 5 ml/kg/min at a body mass of 100 kg (Mount 1979). The 100 kg equivalent for the European wild boar, extrapolated with the above equation (ex Myrcha and Jezierski 1972) was similarly 5 ml/kg/min. The extrapolated resting metabolic rates in Table 7/27 are also in good agreement with those determined for the domestic pig (Mount, Lister and McCance 1963, Irvin, Peyton and Monson 1965, Mount 1968, Stevens 1971, Whittow 1971, Verstegen et al. 1973). Based on

these findings RMR was extrapolated over the full range of body mass for European wild boar and bushpigs (Table 7/27).

| TABLE 7/27: EXTRAPOLATED RESTING METABOLIC RATES FOR BUSHPIG AND EUROPEAN WILD BOAR | | | |
|---|------------|-------------|------------------------------|
| MASS (kg) | * kcal/day | kcal/kg/day | kcal/kg ^{0,75} /day |
| 5 | 484 | 97 | 145 |
| 10 | 765 | 76 | 136 |
| 20 | 1 209 | 60 | 128 |
| 30 | 1 580 | 53 | 123 |
| 40 | 1 910 | 48 | 120 |
| 50 | 2 181 | 44 | 116 |
| 60 | 2 496 | 42 | 115 |
| 70 | 2 764 | 39 | 114 |
| 80 | 3 018 | 38 | 113 |
| 90 | 3 208 | 37 | 110 |

* $M = 167,4W^{0,66}$ (n = 13) Data from Myrcha and Jezierski (1972)

7.4 Discussion

7.4.1 Behavioural response to the thermal environment

7.4.1.1 Activity scheduling

Bushpig activity exhibits nocturnal peaks in both seasons, i.e. with inherently lower activity during the warmer parts of the 24-hour period. This affects high intensity foraging in particular. The activity pattern also exhibits increased summer day and winter night resting, i.e. there is evidence for adjustment to the seasonally changing thermal regime (6.4.1; 7.3.1.2). Metabolic heat production can easily increase more than 10-fold with activity and unless heat loss is increased proportionately, body temperature will rise rapidly. The conditions for heat loss vary largely with external factors, mainly with air temperature and wind (Schmidt-Nielsen 1979). Temperature was accordingly interpreted as both the ultimate cause and proximate influence determining the activity pattern in the bushpig. It is primarily related to heat avoidance and to a lesser extent the avoidance of cold extremes in winter.

An adjustment of the endogenous activity rhythm to expected seasonal temperature changes is in accordance with the possibility that there may be an endogenous seasonal body core temperature rhythm (7.3.4). The reason for not fully switching to diurnal activity in winter, in spite of higher summer night than winter day air temperatures is interpreted as the effect of seasonal acclimatization. Frequently the range of thermal tolerance is different for the same species in summer and in winter. A winter animal is often less tolerant to high temperature than a summer animal and conversely, a winter animal often tolerates temperatures which are experienced as relatively low by a summer animal. Such changes in temperature tolerance with climatic change are called acclimatization (Schmidt-Nielsen 1979).

If heat generated by activity did not substitute for heat required for thermoregulation, but was quantitatively dissipated, inactivity could be seen as an energetically rewarding strategy (Gates and Hudson 1979). This was shown to be the case in subjects with *i.a.* poor external insulation. In a study of the ecological bioenergetics of wapiti (*Cervus elaphus canadensis*) Gates and Hudson (1979) found that activity in the cold resulted in a thermoregulatory penalty which increased in magnitude with level of activity. When an animal becomes active it exposes a large effective heat exchange area to the environment and increases air movement over its surface. The effect of the latter is accentuated by convective heat loss taking place more readily from small parts, such as limbs, than for the trunk (Mount 1968). In the case of poorly insulated animals such as the bushpig (7.3.2) the lower critical level is expected to be higher during activity. It follows that bushpigs rest during cold winter afternights as a heat conservation strategy. The average ambient temperature of 15 afternight winter resting periods was 8°C (Table 7/10) and although 10°C is hardly below thermoneutrality for the resting adult bushpig, it is conceivably so for an active one.

Animals inhabiting tropical and subtropical regions have to cope with both heat and cold on the same day. They are confronted with the problem of overheating as well as cooling within a short span of time (cf Scholander *et al.* 1950 a and b). Heat or cold must thus either be avoided behaviourally through appropriate activity scheduling or the

animal must adapt physiologically or morphologically (insulation). Under certain conditions emphasizing adaptation to cold is energetically preferable, while behaviourally avoiding heat (bushpig, European wild boar). Under others specialized adaptation to cope with solar radiant heat loads is physiologically imperative (warthog).

The warthog is generally known for its susceptibility to cold (Bradley 1968, Cumming 1975, Mason 1982). Individuals as old as 8 months have been reported to have died on a particularly cold night without access to holes or other shelter (Cumming 1975). Warthogs refrain from activity on rainy or even overcast days and require holes or otherwise well-protected places for resting at night. They are virtually exclusively diurnal (Cumming 1975, Mason 1982). Predation was proposed as the dominant constraint favouring diurnality (6.4.2.5). Specialization to cope with radiant heat loads in an open environment, has apparently been achieved at the cost of cold resistance. The physiology of thermoregulation in the warthog has not yet been studied in any depth. However the lack of a pelage must be presumed to facilitate heat dissipation. Although a pelage would counter radiative heat influx, it would also be an impediment to the dissipation of internal heat generated by activity. Unlike other grazing or browsing herbivores, the foraging mode of the warthog may involve a relatively high work input over extended periods. Internal heat must thus be dissipated along a shallow temperature gradient; without sweating. Panting while feeding would be rather problematic.

7.4.1.2 Thermocomfort behaviour

Animals respond behaviourally to the thermal regime, altering the balance between heat loss and heat production by changes in activity, posture, by seeking cover (Moen 1973) or by special behavioural means such as wallowing, huddling and nest-building.

Due to a lack of sweat glands, feral pigs rely on behavioural thermoregulation to maintain a favourable heat balance under hot conditions (Mount 1968, Signoret *et al.* 1975). Pigs under such conditions are primarily crepuscular and nocturnal during the summer months, minimizing activity during the hotter portions of the day (Baber

and Coblenz 1986). Apart from the avoidance of warm periods through routine activity scheduling, as discussed above (7.4.1), temporary thermocomfort relief behaviour is observed during conditions of thermal extremes.

Like other suid species, bushpigs selected cool, moist bedding sites, utilized the heat dissipating effect of air movement and resorted to wallowing under hot conditions. Wallowing as a heat relief measure has been reported for all well-known suid species: for European wild boar by Sludskii (1956) and Henning (1981), warthog by Cumming (1975) and Mason (1982), giant forest hog by D'Huart (1978) and the domestic pig by Mount (1968) and Hafez and Signoret (1969).

Two to three months old bushpig juveniles were subject to heat stress at $\pm 30^{\circ}\text{C}$, as evidenced by panting (7.3.5). Intermittent panting with 40 - 100 respirations per minute at *ca* 30°C increased to continuous panting with frequencies of between 150 to 170 respirations per minute at *ca* 35°C (7.3.5). For comparison, the respiratory frequency of the domestic pig was recorded as 181/min. at 35°C (Ingram 1964). Heitman *et al.* (1959) reported 130 - 170 respirations per minute at 32°C - 36°C under shade. The respiratory rates of pigs at the same temperatures, but with access to wallowing, were ± 45 - 75 per minute (Heitman *et al.* 1959). As a rule the pig thus compensates for its inability to sweat (Ingram 1964) by wallowing in any available water, including wet surfaces, mud and urine (Mount 1979). Wet mud, by holding water, produces prolonged cooling (Ingram 1965b). The pig tolerates heat poorly when not allowed to wallow, since it is only capable of dissipating a relatively small proportion of its heat production by panting (Ingram 1965a, Ingram and Legge 1969).

A compact posture, sheltering, huddling and nest-building are the principal means of reducing heat loss to the environment (Mount 1979). They are all part of the bushpig's behavioural repertoire (7.3.1.3). These behaviour patterns function by reducing the thermal body-to-environment gradient or by minimizing body-to-environment contact. Calculations of the thermal balance between heat production and heat loss under different thermal regimes indicate that wind is the most important factor at low air temperatures (Moen 1973). Seeking cover and

nest-building minimize the effect of wind, reducing thermal gradients by stabilising the air immediately surrounding the animal. A compact posture, with limbs and chin supporting the trunk, the limbs folded under the body, minimizes the area of the trunk in contact with the floor, thereby lowering conductive heat loss.

Huddling reduces the exposed surface, thus reducing cold stress and the metabolic requirements for heat production (Schmidt-Nielsen 1979). The huddling of pigs under cool conditions effects a considerable saving in metabolic heat production. Mount (1968, 1979) found that body temperature was maintained in the cold by metabolic rates of about 40% less than those which would be required for thermoregulation by a single pig under similar conditions. The saving in energy expenditure became proportionately greater with falling ambient temperature (Mount 1968). Groups huddling below thermoneutrality saved about 70 - 80% of the heat produced by singly housed pigs in the trials by Verstegen (1971). Oxygen consumption of two crab-eating foxes (*Cerdocyon thous*) huddling together was 5 - 18% lower than when they were separated (Hennemann, Thomson and Konecny 1983). Apart from farrowing nests, nest-building to combat heat loss under particularly energy-demanding conditions has been reported for the European wild boar in Russia (Sludskii 1956), the pygmy hog, *Sus salvanius*, in Assam (Oliver 1980) and the warthog (Cumming 1975). This study has verified nest-building in the bushpig in response to combined cold and wet weather conditions (7.3.1.3).

7.4.2 Tissue and pelage adaptations to the thermal environment

7.4.2.1 Tissue insulation

Thermal insulation consists of two components: tissue insulation below the skin surface and external insulation (Mount 1979). External insulation is mainly due to the pelage of an animal. Tissue insulation is the resistance offered to the flow of heat between the heat-producing tissues and the skin surface. It largely depends on the thickness of subcutaneous fat. In addition, peripheral vasoconstriction and vasodilation change the blood flow and lead to increased and decreased tissue insulation respectively (Mount 1979).

Fat deposits in mammals primarily serve to store energy (Pond 1978) and their tissue insulative effect is considered a secondary spin-off. Unlike savanna ruminants (Owen-Smith 1982) suids generally tend to exhibit subcutaneous fat layers. These vary interspecifically as well as intraspecifically, according to age, condition and reproductive status (9.3.2). In the European wild boar, for example, the seasonal accumulation of subcutaneous and other fat deposits is a well-known phenomenon. In regions with cold winters, the subcutaneous fat layer on back and flanks may be 3,5 - 5,0 cm thick (Sludskii 1956).

Vasoconstriction reduces peripheral blood flow and thus the circulatory transfer of heat from body core to surface. Consequently, surface temperature drops, reducing surface-environmental temperature gradients and therefore rate of sensible heat loss (Curtis 1970). Under warm conditions peripheral vasodilation leads to dissipation of heat from the surface in spite of the subcutaneous fat layer, because blood flow through the blood vessels of the fat layer effectively "short-circuits" the insulation of the fat (Mount 1979). When a pig with a considerable layer of subcutaneous fat is exposed to cold, peripheral vasoconstriction is very effective in producing a high specific insulation. When there is no fat layer the increase in insulation with peripheral vasoconstriction is small. This is so because, although the cooled outer layer of tissue acts as an insulator, it is not so effective as fat (due to the lower thermal conductivity of fat compared to other tissues; Miller and Blyth 1958 ex Mount 1968).

According to Bonsma and Pretorius (1943), lean and undersized animals in tropical and subtropical areas often have exceptionally long hair. The same was observed in certain bushpig individuals in particularly poor conditions. Animals which maintain poor condition for prolonged periods would have a relatively high lower critical temperature due to the lack of tissue insulation and energy reserves for thermogenesis. Increased hair length may be a response to improve their thermal insulation.

7.4.2.2 Pelage characteristics and adaptation

The most important physical properties of the pelage are depth (thickness), density and colour (Hofmeyer 1985). The insulative value

of the fur depends on the still layer of air trapped on and within it, which is mainly dependent on effective fur depth (Johnson 1984). The fur acts by maintaining a boundary layer of air at a temperature closer to skin temperature than that of the surrounding air. Thus, the boundary layer is a layer of air which offers convective insulation because it is stable in a direction normal to the surface (Mount 1979).

Thermal insulation is positively correlated with pelage depth (Hofmeyer 1981, 1985). The pelage of mammals not only provides protection against heat loss, but also influences the amount of radiant heat gained from the environment. In warm environments solar radiation increases the heat load on the animal and ultimately evaporative water loss would have to be increased if the animal is to maintain a stable body temperature (cf Hofmeyer 1981). Accordingly, summer coats, are generally thinner than winter coats, thereby facilitating heat loss under hot conditions. The depth of an ungulate pelage therefore appears to reflect an evolutionary compromise and the results of Hofmeyer (1981, 1985) show that under the predominantly hot conditions of the African savanna, natural selection seems to have favoured the facilitation of heat loss rather than the prevention of heat gain or reduction of heat loss.

Apart from pelage depth, wind profoundly influences thermal insulation and the effect of wind varies with hair density. Wind greatly increases heat loss from a skin with a sparse pelage, while having a relatively smaller effect on dense fur (Mount 1979). Tregear (1965) stressed the importance of hair density in determining the resistance against wind penetration into the fur and concluded that the conductivity of fur with a density of less than 1 000 hairs/cm² is greatly affected by forced convection. Whereas the air between the hairs of dense fur is relatively unaffected, the air between sparse hairs appears to be stirred by the wind right down to the skin surface. A density of 1 000 hairs/cm² is rather above what many ungulates have, so that these animals are susceptible to cooling by wind (Mount 1979). In summary, heat loss through very dense hair is convectional and invariant, while that through sparse hair, as in the pig, is both radiative and convectional. The latter is vastly increased by wind, in proportion to the square root of wind velocity (Tregear 1965, Mount 1968, 1979).

Thermal resistance may thus be viewed as proportional to the product of pelage depth and density, i.e. crudely proportional also to pelage weight density. The density of the adult bushpig pelage is particularly low (16 - 17 hairs/cm²). In comparison, average summer and winter hair densities of 42 and 76 hairs/cm² were determined in the collared peccary (Zervanos and Hadley 1973). For the European wild boar in Russia 48 - 96 short bristles/cm² were recorded for the summer and up to 640 downy curly hairs per cm², 7 - 8 cm long, as well as 40 - 80 bristles/cm² of 12 - 15 cm length for winter animals (Sludskii 1956). The average hair lengths in the collared peccary were 4,6 and 6,8 cm in summer and winter animals respectively (Zervanos and Hadley 1973), and thus comparable to the average adult bushpig hair length of ca 6,0 cm (7.3.2). Buys and Keogh (1984) record average hair lengths of 6,6 cm for bushpigs and 2,9 cm for warthog. The bushpig pelage does not have an undercoat typical of the European wild boar (Sludskii 1956, Hennig 1981) nor does hair density or length change with season. In contrast, at all surface locations in the collared peccary, summer animals exhibited a significant decrease in hair density from the winter condition. Bristle length decreased at certain locations in summer animals (Zervanos and Hadley 1973). The low hair density of the bushpig coat is interpreted as an adaptation to facilitate effective endogenous heat dissipation, particularly during intensive activity and under conditions of little or no air movement, which are presumably often encountered in closed habitats. As already mentioned, a sparse pelage allows both radiative as well as convective heat dissipation. The disadvantage of low hair density is heat loss at low ambient temperatures, especially when coupled with wind. This effect is presumably partially counteracted by the relatively long hair, capable of trapping some air. The thermal resistance of such a pelage may also be modified through pilo-erection and orientation in relation to wind direction.

The ratio of surface area to volume decreases with increasing body mass. Smaller animals are therefore potentially subject to higher rates of heat gain or loss. This, coupled with a low thermal inertia due to small volume, results in smaller animals being liable to rapid body temperature increases and decreases. Small animals therefore need to be well insulated and a dense pelage affords protection not only against

heat loss, but also against heat gain (cf Hofmeyer 1981, 1985). Larger animals, on the other hand, have relatively more endogenous heat production per unit of surface area. Larger animals in hot environments thus face the problem of dissipating heat to the environment. Juvenile bushpigs have denser pelages, but with shorter hairs than adults (7.3.2).

All age classes have similar pelage weight densities (Table 7/14). These observed pelage patterns and differences between bushpig size classes make sense in terms of the expected constraints resulting from changing surface area to mass ratios. Juvenile coats are geared to prevent undue heat gain or loss and adult coats allow effective endogenous heat dissipation.

7.4.2.3 On the thermoregulatory significance of coat colour

Bushpig coat colour morphs and their geographic distributions were outlined in section 3.2.2. The two basic coat types in the bushpig coincide with climatically disparate regions: subspecies inhabiting tropical western and central Africa have red-brown, dense, short pelages, those from subtropical southern and eastern Africa darker, sparse and long-haired pelages. Bushpigs subspecies inhabiting lowland savanna areas may be seen as an intermediate category (cf Tookey 1959). They have sparse, long-haired coats which are lighter in colour (e.g. *Potamochoerus choeropotamus mashona*; Von Boetticher 1933). The extremes of the two pelage types are represented by *Potamochoerus porcus porcus* of the tropical lowland rainforests which has a reddish-coloured, dense, soft, short and fatty pelage, and *Potamochoerus choeropotamus daemonis*, of Mount Kilimanjaro, with a black, long-haired coat (cf Von Boetticher 1933). Bushbuck and buffalo exhibit analogous geographic trends in coat colour (Grubb 1972). In the bushbuck coat colour even appears to play a role in habitat selection by subspecies and by the sexes. In the Gorongosa National Park (Mocambique) the dark-coloured southern race (*Tragelaphus scriptus sylvaticus*) is most common in forest areas, whilst the lighter brown coloured western race (*Tragelaphus scriptus scriptus*) is characteristic of palm thickets (Tinley 1977). The latter is the warmer habitat, with greater exposure to solar radiation. In the Southern Cape, dark coloured male bushbuck prefer the

cooler, shaded forest. In contrast the light red-brown coloured females show no preference between forest and plantation areas, where they are exposed to greater levels of solar radiation (Seydack 1977; Table 7/28).

| TABLE 7/28: SEX DIFFERENTIAL HABITAT ASSOCIATION OF BUSHBUCK (GOUDVELD; SOUTHERN CAPE) | | | | |
|---|-------------------------|---------|-----|--------------------|
| HABITAT | OBSERVATION FREQUENCIES | | | G = 7,74 P<0,01 |
| | MALES | FEMALES | | |
| INDIGENOUS FOREST | 168 | 95 | 263 | |
| PINE PLANTATIONS | 90 | 88 | 178 | |
| | 258 | 183 | 441 | |
| SEYDACK (1977) | | | | |

The thermoregulatory significance of coat colour has been the subject of investigation by various authors. Bonsma and Pretorius (1943) found that the amount of light reflected from the skins of cattle of different colours was directly correlated with colour intensity, i.e. the lighter the colour of the coat, the greater the amount of light reflected. During the winter months the hair of various cattle breeds was longer and duller. In the summer months when the coats of Afrikaner and Jersey cattle were short and glossy, very much more sunlight was reflected than in winter.

Kelly, Bond and Heitman (1954) and Mount (1968) reported that white pigs reflected 51% of solar energy (0,4 - 0,1 cm wavelength), while black pigs reflected only 7%.

The energy expenditure of Australian zebra finches dyed black, averaged 23% less than that of white birds at an ambient temperature of 10°C (Hamilton and Heppner 1967).

The outer portions of the bristles from the dorsal parts of haunches and flanks of the collared peccary (*Tayassu tajacu*) are dark, while the inner portions are lighter. In summer, the outer dark portions of the bristles break off, leaving short, light-coloured bristles. Spectrophotometric tests on felt samples showed that reflectance of

solar radiation for an intact pelt was 21,8%. When the upper dark portions of the bristles were cut away, exposing the lower lighter portions, the reflectance more than doubled to 47% (Zervanos and Hadley 1973).

In a study on the distribution of differently coloured cattle in East Africa, Finch and Western (1977) found that the proportion of light-coloured cattle increased linearly with heat stress along geographical and altitudinal gradients. During droughts significantly more light cattle than dark cattle died at mid-altitude and in upland areas, whereas in a lowland area more dark than light cattle died. At high altitude black cattle tended to lose less weight than white cattle during droughts and also to gain weight faster after the onset of rain. The black cattle presumably could save energy when the sun rose, rapidly absorbing radiation rather than sustaining thermogenesis in order to repay the heat debt (Finch and Western 1977). Thus although environmental heat stress appears to be higher on dark than lighter cattle, within the range of dark to light red beef cattle, the darker tended to grow faster (Schleger 1962 ex Finch and Western 1977).

Finch *et al.* (1980) demonstrated the same phenomenon while investigating the metabolic rate of black and white Bedouin goats in the Negev desert. The metabolic rates of the black goats during winter were 25% lower than that of white goats when standing in full sunlight.

Berry (1980) has shown that wildebeest (*Connochaetes taurinus*) orientate laterally towards the sun to exploit solar radiation under cool, sunny conditions; presumably to reduce their energy requirements for the maintenance of body temperature.

These results suggest that the coat colour of a homeothermal animal is of considerable importance in its energy budget. In cold environments, the warming effect of solar radiation can reduce the amount of metabolic heat needed to maintain a stable body temperature. In warm environments, solar radiation will increase the heat load of the animal, ultimately requiring increased evaporative heat loss for the maintenance of a stable body temperature (cf Hofmeyer 1981). In a study on the pelage properties of selected ungulates, Hofmeyer (1981) confirmed that

the darker pelages had the highest absorbance values, while the white coats had the lowest values. While white coats had a lower heat load at the surface of the skin than similarly insulated dark coats, this difference decreased with increasing wind speed.

Although dark coats may be energetically advantageous under certain conditions, it is important to recognize that food is the ultimate source of energy for metabolic processes and radiant or atmospheric energy present during warm weather can only serve to reduce thermal gradients (Moen 1973). According to Needham (1974), dark colours are also the best radiators of internal heat and he suggests that dark colours are useful only under conditions where there is a consistent need to either dissipate internal or absorb external heat. It appears that melanization is triggered during ontogeny in response to an environmental cue (Fabian 1985).

Subspecific variation in coat colour patterns in the bushpig may be explained as follows. Wherever energy conservation can be significantly facilitated through the absorption of solar radiation, dark pelages predominate. This would be where cool, sunny days occur in regions with pronounced winter cold, or at high altitudes. The black, sparse but long-haired coats of adult bushpigs in such areas would absorb solar radiation and the warm air trapped in the coat would result in a reduced body to air temperature gradient. A dark coat colour would thus allow the optimal use of the limited amount of solar radiation penetrating the vegetation canopy of typical bushpig habitats in minimizing heat loss to the environment. The observed winter day activity (6.4.1; 7.3.1.2) of bushpigs in the study area fits in well with this explanation. Where solar radiation is associated with relatively high temperatures, as in the tropics and lowland savanna, lighter coat colours favour the reflectance of radiant heat. Bushpigs in tropical regions experience low temperature only at night, i.e. in the absence of solar radiation, and the energy-conserving function as outlined for dark coats, does thus not apply. Rather, radiant heat loads can be minimized by lighter and denser pelages. The observed coat colour patterns of bushbuck and buffalo can be similarly explained. However, the greater thermal inertia of the buffalo makes it somewhat less prone to accumulating heat from solar radiation.

7.4.3 Aspects of water metabolism

7.4.3.1 Water consumption

The free water consumption estimates of bushpigs on dry pellet rations were 25,0 ml/kg/day in winter and 47,9 ml/kg/day in summer (Table 7/18). This corresponds with a daily water consumption of between 2 and 3 liters per animal, or ca 3,5% of body mass. These water consumption estimates are considerably lower than those for the domestic pig and also somewhat lower than the minimum water requirements of the collared peccary of 38,6 ml/kg/day in winter and 66,5 ml/kg/day in summer (Zervanos 1972). Mean daily water intake in the domestic pig is approximately 100 ml/kg/day (Mount 1968), or of the order of magnitude of 10% of body weight per day at normal temperatures (Mount and Ingram 1971). The range of mean water consumption for the pig was found to extend between 82 and 184 ml/kg/day (Holmes and Mount 1967; Mount *et al.* 1971). Other conditions being equal, young animals have higher water needs per unit of body size than do mature ones. Thus the average water requirement of 30 kg swine was given as ± 200 ml/kg/day (Maynard *et al.* 1979). The water consumption of bushpig tended to be similar to the minimum free water requirements of Hereford cattle, buffalo, eland and wildebeest and higher than that of zebra, cattle, oryx, Thomson's and Grant's gazelle (Table 7/29).

| SPECIES | | ml/kg/day | |
|-------------------|------------------------------|-----------|------------|
| | | 22°C | 22-40°C(b) |
| Hereford | <i>Bos taurus</i> | 41,1 | 60,5 |
| Zebu | <i>Bos indicus</i> | 16,1 | 29,5 |
| Buffalo | <i>Syncerus caffer</i> | 28,0 | 41,5 |
| Eland | <i>Taurotragus oryx</i> | 31,5 | 49,1 |
| Wildebeest | <i>Connochaetes taurinus</i> | 22,3 | 41,2 |
| Oryx | <i>Oryx gazella</i> | 13,0 | 21,1 |
| Thomson's gazelle | <i>Gazella thomsoni</i> | 12,5 | 21,3 |
| Grant's gazelle | <i>Gazella granti</i> | 12,5 | 30,3 |

(a) The amount of water required to maintain the weight of an animal at a level approximately 85% of its initial weight.
 (b) Twelve hours at 22°C and 12 hours at 40°C

The water consumption of bushpig in summer was nearly double of that during winter. Similar magnitudes of increased free water use at high temperatures were found for certain East Africa bovids (Taylor 1969, Table 7/29). Cumming (1975) observed that tame warthogs drank between one and five times a day, with lower frequencies occurring during the cold months. Higher temperatures were also typically associated with higher rates of water intake in the domestic pig (Holmes and Mount 1967, Mount *et al.* 1971). The voluntary water intake in a group of pigs at an environmental temperature of 30°C was increased above that at 20°C by about 40% (Mount 1968). Even higher increases were recorded by Holmes and Mount (1967).

At high temperatures evaporative cooling necessarily becomes important. This is so even in the pig, with its low ability to sweat, since non-evaporative heat loss is progressively reduced towards zero as environmental temperature rises to the level of body temperature (Mount 1968). Evaporative heat loss may take place from skin moistened by perspiration (sweating) or via panting, i.e. evaporative cooling from the respiratory surface, mouth, tongue and nasal mucosa (Vaughan 1972, Moen 1973). High respiratory rates are typical of panting. In the bushpig the respiratory frequency was six times that at ca 30°C compared to the frequency at thermoneutrality (Tables 7/23 and 7/24). The increased water intake by bushpigs during summer is presumably largely associated with some form of evaporative cooling. In the collared peccary, evaporation accounted for 72,4% of the total water loss in summer and 43,0% in winter (Zervanos and Hadley 1973). The main mechanisms of evaporative cooling in the peccary is believed to be panting, rather than sweating (Zervanos and Hadley 1973).

Dependence on free water is commonly reported for wild pigs (Eisenberg and Lockhart 1972, Barrett 1978) and domestic pigs (Mount 1968). However, all feeds supply some water and highly succulent ones, such as silage and green forage, can make a substantial contribution to meet water requirements (Maynard *et al.* 1979). The major moisture source for the collared peccaries maintained in metabolic cages by Zervanos (1972) was preformed water in their vegetable diet. The same appears to be true for wild peccaries whose basic diet is succulent cacti (Eddy 1961, SOWLS 1969 ex Zervanos 1972). Penned peccaries experienced no apparent

ill effects after being on a waterless diet of prickly pear pads only for a period of 2 weeks. Prickly pear plants were found to contain from 78 - 88% water and the fruits from 65 - 75% (Eddy 1961). Free-ranging peccaries, primarily feeding on prickly pear cactus pads, visited water holes only once in 3 to 4 days in summer and there was virtually no drinking of standing water during the winter (Zervanos and Day 1977). Taking 65% as the moisture content of the ingesta, 2,5 liter of water is contained in 3,85 kg of vegetable material consumed. When comparing this with the average bushpig stomach fill mass of 3,2 kg (n = 73; 6.4.1.1) and taking this as the daily turnover of vegetable material, the potential contribution of the ingesta as a source of water becomes apparent. It is thus conceivable that the bushpig, during certain periods, is not strictly dependent on free water intake if preformed water of succulent items is utilized economically, i.e. if evaporative and urinary water losses are limited. The ability to go for long periods without drinking, which bushpigs are most likely to exhibit in winter, could greatly enhance their success in utilising the more arid parts of their range (e.g. Eastern Cape).

7.4.3.2 Control of urinary water loss

Sperber (1944) and Schmidt-Nielsen and O'Dell (1961) have demonstrated a correlation between the ability to concentrate urine maximally and the gross morphology of certain mammalian kidneys. Schmidt-Nielsen and O'Dell (1961) discussed the functional significance of the relative medullary thickness (RMT), which represents the relative length of the countercurrent, multiplier system and as a consequence the concentrating ability of the kidney. Sperber (1944) pointed out the correlation between the RMT and the availability of water in the animal's environment. As a specific example, the Ethiopian and long-eared hedgehogs, which live in the desert, have a greater RMT and produce a more concentrated urine than the European hedgehog, which lives in a mesic environment (Yaakobi and Shkolnik 1974; Table 7/30).

TABLE 7/30: RELATIVE MEDULLARY THICKNESS VALUES FOR SELECTED MAMMAL SPECIES

| SPECIES | RMT | SOURCE |
|---|------|-----------------------------------|
| <i>Hippopotamus amphibius</i> | 1,0 | Sperber (1944) |
| Beaver <i>Castor canadensis</i> | 1,3 | Schmidt-Nielsen and O'Dell (1961) |
| Pig <i>Sus scrofa domestica</i> | 1,6 | Sperber (1944) |
| Bushpig <i>Potamochoerus porcus</i> | 2,7 | This study |
| Man <i>Homo sapiens</i> | 3,0 | Schmidt-Nielsen and O'Dell (1961) |
| Grey rhebok <i>Pelea capreolus</i> | 4,0 | Beukes (1984) |
| Red fox <i>Vulpes vulpes</i> | 4,1 | Noll-Banholzer (1979) |
| Bontebok <i>Damaliscus dorcas</i> | 4,5 | Beukes (1984) |
| Cat <i>Felis domesticus</i> | 4,8 | Schmidt-Nielsen and O'Dell (1961) |
| Wildebeest <i>Connochaetes taurinus</i> | 4,8 | Berry and Louw (1982) |
| European hedgehog <i>Erinaceus europaeus</i> | 4,8 | Yaakobi and Shkolnik (1974) |
| Fennec <i>Fennecus zerda</i> | 5,3 | Noll-Banholzer (1979) |
| Springbok <i>Antidorcas marsupialis</i> | 5,3 | Hofmeyr (1981) |
| Rat <i>Rattus rattus</i> | 5,9 | Gordon (1972) |
| Long-eared hedgehog <i>Hemiechinus auritus</i> | 6,9 | Yaakobi and Shkolnik (1974) |
| Ethiopian hedgehog <i>Paraechinus aethiopicus</i> | 7,5 | Yaakobi and Shkolnik (1974) |
| Gerbil <i>Gerbillus gerbillus</i> | 10,5 | Gordon (1972) |
| Ground squirrel <i>Xerus inauris</i> | 12,4 | Marsh, Louw and Berry (1978) |
| Desert mouse <i>Psammomys obesus</i> | 12,9 | Schmidt-Nielsen and O'Dell (1961) |

Thiessen (1976) reported on the lower medulla to cortex ratio of the domestic pig compared to the European wild boar, suggesting a lowered capacity for urinary concentration of the former. The established RMT value for the domestic pig is 1,6 (Table 7/30), which is similar to the value obtained for Hampshire hogs by Zervanos, McCort and Graves (1983). The significantly higher value found for their feral counterparts (RMT = 2,31) as well as greater urine concentrations, suggests that natural selection for greater RMT may have occurred during the relatively short evolutionary period since their introduction and indicates that selective pressure for increased kidney function can result in relatively rapid morphological and physiological responses (Zervanos, McCort and Graves 1983). Dunson (1974 ex Zervanos, McCort and Graves 1983) similarly found that feral goats in the arid Galapagos Islands had greater RMT values (5,8) than their domestic counterparts (4,4 - 4,9). Although the bushpig RMT value is comparatively low in the general mammalian context (Tables 7/19 and 7/30), it is substantially

higher than that of the domestic pig. The lower water consumption of the bushpig compared to that of the domestic pig is thus possibly related to a higher capacity for urinary concentration.

7.4.4 Physiological response to the thermal environment

7.4.4.1 Body core temperature patterns

The level at which a homeotherm regulates its body core temperature (T_b) depends upon the ratio of the basal rate of metabolism to conductance (M_b/C), and this ratio appears to determine the dependence of T_b on T_a and the precision of thermoregulation (McNab 1969 and 1979). Thus, much of the observed variation in the level of T_b is due to the relative variation in basal metabolic rate and thermal conductance (McNab 1970). The heat flow balance which is determined by the M_b/C ratio results in average mammalian body temperatures being set near 38°C (McNab 1970). It is influenced by a variety of exogenous factors, the most important being exercise and ambient temperature (T_a).

The highest and lowest T_b 's which were determined for unrestrained bushpig were $40,9$ and $36,3^\circ\text{C}$ (Table 7/21). The body temperatures of individual bushpigs under field conditions were regulated within $2-3^\circ\text{C}$, spanning monitoring periods in both seasons (Table 7/21). This represents an intermediate degree of thermostability compared to other large African ungulates (cf Bligh and Harthoorn 1965, Bligh *et al.* 1965).

The general temporal pattern of T_b was that of monophasic nycthemeral variation with the rising phase starting approximately between 02.00 and 03.00 h and reaching maximum values between 14.00 and 15.00h (Table 7/22). The temporal trend of T_b was thus very similar to that of T_a . The mean nycthemeral variation was $0,88^\circ\text{C} \pm 0,24$. Diel oscillations of T_b thus generally remained within a range of $1,2^\circ\text{C}$ (Table 7/22).

Independent of the effect of interdiel T_a fluctuations on variation in T_b , a statistically significant nycthemeral cyclicality was detected (Table 7/22). The average T_b in winter was significantly lower than in

summer (7.3.4), suggesting also a seasonal cycle of T_b (cf Bligh *et al.* 1965).

Activity at normal levels and activity time scheduling had no detectable effect on T_b , with the exception of the alpha boar TD5 during summer (Table 7/22). At that time there were neonates with which TD5 concerned himself. The activity interaction with T_b may be related to a responsive nervousness associated with paternal care. Heightened activity characteristically tends to increase T_b at moderate T_a 's, but might be expected to lower T_b at low T_a 's (cf Hill 1983). Bushpigs schedule their activity to the cooler periods of the day and heat dissipation due to activity is therefore apparently adequate to prevent a rise in T_b as a result of activity.

Experimentally induced forced exercise increased T_b 's to $\pm 42^\circ\text{C}$ (7.3.4), which is relatively close to lethal levels. According to Schmidt-Nielsen (1964 ex Morhardt and Gates 1974) upper lethal T_b 's for mammals are around $42^\circ - 43^\circ\text{C}$. Instances of death from heat collapse when bushpigs are being hunted with dogs are known to occur.

A positive relationship between T_a and T_b is a general phenomenon (e.g. Bligh and Harthoon 1965, Bligh *et al.* 1965, Elder and Rogers 1975, Hofmeyer 1981). The particular thermoregulatory strategy to cope with ambient temperature extremes determines the nature and extent of this inter-relationship and thus also the level of thermostability. At T_a 's below the thermoneutral zone constant T_b 's can only be maintained if heat loss to the environment is compensated for by increasing metabolic heat production. If the animal can tolerate a lowered T_b , the rate of heat loss and metabolic cost for the maintenance of the T_b/T_a gradient will also be lower and metabolic reserves can be conserved.

Above the thermoneutral zone an animal may gain heat from both its own metabolism and from the environment. The rate of heat gain from the environment will be lower if the animal can tolerate an increased T_b , since the higher the T_b the greater is the tendency for heat to flow from the animal to the environment. When $T_b < T_a$, high T_b 's decrease the heat influx, thereby decreasing evaporative requirements (cf Hinds 1973).

In considering the interaction between T_b and T_a , three thermoregulatory conditions may be distinguished:

- (I) minor thermoregulatory adjustments of T_b within the zone of thermoneutrality;
- (II) more substantial adjustments of T_b when thermoregulation must cope with T_a 's outside the thermoneutral zone, and
- (III) run-away T_b during hypo- and hyperthermia, when thermoregulation collapses.

The body core temperature variations of adult-sized bushpigs under condition I (Fig 7/1; 7.4.2.2) were outlined above. Under condition II, juvenile bushpig T_b 's varied between 36,2 and 40,3°C when subjected to T_a 's ranging between ± 10 and 35°C, i.e. from below to above thermoneutrality. The maximum and minimum T_b differences were 2,5; 3,8 and 3,4°C for juveniles TE1, TE2 and TE3 respectively (Tables 7/23 to 7/25). The rectal temperatures of 3 month old domestic pigs were significantly higher at a T_a of 35°C than at 30°C (39,1 - 40,6°C: Ingram 1964a). Under prolonged exposure to a T_a of 33,3°C, individual gilts had T_b 's as high as 41,7°C (Teague, Roller and Grifo 1968). Although pigs hyperventilate under hot conditions, the respiratory evaporation is apparently inadequate for the heat loss required to keep the T_b down when the environmental temperature rises above 30°C (Mount 1979). At ambient temperatures down to ca 16°C bushpig juveniles were found to maintain thermostability, unlike warthogs which quickly responded to these T_a with their T_b 's falling as much as 3,9°C down to ± 35 °C (Sowls and Phelps 1966). According to Cumming (1975) warthogs may allow their T_b 's to fluctuate within a total range of 7°C. Thus thermolability presumably underlies the warthog's ability to permit its T_b to rise during periods of high ambient temperature and to dissipate the excess heat later when ambient temperatures are lower at night (Schmidt-Nielsen, 1966 ex Elder and Rodgers 1975).

Similar interactions between ambient and body temperature appear to be prevalent within the thermoneutral zone (thermoregulatory condition I), underlying the daily and seasonal fluctuations in T_b found in unrestrained bushpig (7.3.4). In addition to the changes of T_b induced

by direct responses to T_a , intrinsic physiological cycles, pre-adapting the organism to an expected change in T_a , appear to be involved in shaping the pattern of T_b rhythms (circadian rhythm component *vide* Table 7/22).

When the ambient temperature is lowered, conductance decreases and eventually reaches a minimum value (C_m) at the lower critical temperature (Aschoff 1981b). A low C_m thus indicates tighter control of heat flux through thermal insulation. For a given organism, different values of C_m can be measured during the day and at night (Aschoff and Pohl 1970); i.e. C_m may depend on circadian phase. Higher minimum conductance values (C_m) are characteristic of activity periods, reflecting a greater physiological readiness to allow heat flow during activity.

The functional significance of this circadian rhythm is believed to be the promotion of heat dissipation during activity when the basal metabolism (M_b) is higher, following its own circadian rhythm. It would also conserve heat during periods of rest when metabolism is low (Aschoff and Pohl 1970, Aschoff 1981b). The daily increase in oxygen consumption often precedes the onset of activity as well as that of food intake (Aschoff and Pohl 1970). Circadian metabolic fluctuations are widely known to persist under constant conditions with regard to activity, feeding and ambient temperature and are considered truly endogenous cycles (Aschoff and Pohl 1970, Schmidt-Nielsen 1979, Aschoff 1981a). With either M_b or C_m , or both, exhibiting circadian cyclicality, it is not surprising that daily cycles of T_b are commonly recorded. In most cases, activity, M_b and T_b have the same circadian period, with day peaks in diurnal species and night peaks in nocturnal species (Schmidt-Nielsen 1979, Aschoff 1981a).

The diurnal domestic pig has a higher metabolic rate, body temperature and activity during the day than during the night (Mount 1979). McCracken and Caldwell (1980), for example found a marked diurnal pattern in heat production; the lowest values were recorded between 14.00 and 08.00h. With pigs confined to temperature rooms, Ingram and Legge (1970a) found little circadian variation in T_b . Any observed variations seemed to relate mainly to feeding and activity. However,

when the pigs had access to a relatively large enclosure, extended day activity occurred. Under these conditions all but one of the 24 hour records obtained from 5 pigs displayed clear nycthemeral variation, the rise of the body temperature during the day being established before feeding (Ingram and Legge 1970a). When a pig was removed from the field to a constant temperature room and confined to a cage, the rhythm was immediately abolished. The possibility thus arose that a nycthemeral rhythm in T_b appears only when there is a variation in the amount of activity over the 24 hour period (Ingram and Legge 1970a). In the rat Heusner (1959, 1963 ex Ingram and Legge 1970a) has shown that when kept at constant temperature and in constant light, the T_b rhythm was in phase with rhythms in activity and metabolism. Further evidence to support the view that temperature rhythms are dependent on variations in activity are derived from the studies of Rawson *et al.* (1965) who found that, although a T_b rhythm can be demonstrated in the dog, no such variation is exhibited by animals which are confined and kept by themselves. In the rat Abrams and Hammel (1965, 1965 ex Ingram and Legge 1970a) found that the temperature rhythm persisted under constant temperature conditions even when the animals were deprived of food, provided they were free to move about. Animals deprived of food and restrained displayed no temperature rhythm.

When rearranging Newton's law of cooling, it may be written as follows: $T_b \approx M/C + T_a$. Thus, T_b increases with an increase in the ratio of M/C , which becomes M_b/C_m when evaluated at the lower limit of thermoneutrality (McNab 1970). This transformation indicates that variations in the level of T_b are due to the relative variation in the basal metabolic rate and thermal conductance. In addition, ambient temperature (T_a) influences T_b when it attains values where changes in conductance (C) cannot maintain heat flow homeostasis. This would occur whenever there is a heat surplus due to increased endogenous heat production or low T_b to T_a gradients, as a result of high T_a levels. As discussed above, circadian rhythm is likely to be involved in the M/C ratio and therefore in T_b . In 5 of the 7 monitoring periods, or in 3 out of the 4 study animals, statistically significant circadian rhythms in T_b were detected and interday T_a variation had an influence on T_b during all summer monitoring periods (Table 7/22). A hypothetical

interpretation of the observed patterns and interactions of Tb and Ta for the bushpig monitored during this study is presented below.

Two types of Tb reaction patterns occur: in group I the diel Tb cycle peaks during the day and in group II at night.

Group I

Changes in Tb during the day are proportional to the diel Ta's, peaking during the day. The interday Tb's vary inversely with the average daily Ta's, i.e. on relatively cool days the Tb's are elevated. This applies to the Tb patterns of TD5 and TD7 in summer and to TD5 and TC2 during winter (Table 7/22). The body core temperatures (Tb) of the animals in this group are relatively high compared to those of group II (Table 7/21).

Group II

Here the intraday changes in Tb are inversely proportional to the diel Ta changes, i.e. the Tb cycle peaks during the night. The interday Tb's vary directly with average daily Ta during summer (TD3, TC2) and inversely during winter (TD3). A clear tendency to relatively lower Tb's within a given season and in comparison to group I animals is observed (Tables 7/21 and 7/22).

For the interpretation of these patterns some fundamental thermoregulatory patterns and postulates need to be recapitulated (cf Aschoff and Pohl 1970):

- (a) Physical temperature regulation depends on the variability of conductance. Diurnal and seasonal rhythms in minimum conductance (C_m) are commonly found in mammals.
- (b) Values of C_m are higher in summer than in winter. An increase in conductance raises the Tb and steepens the slope of the curve describing heat production as a function of Ta.

- (c) At higher C_m values, higher metabolic rates are required to maintain thermal homeostasis. A relatively low C_m allows lower M_b rates.
- (d) High C_m values facilitate heat dissipation, but at the cost of insulating capability (trade-off situation). Accordingly, in the cold, metabolic rates increase less in winter than in summer, which is expected from the lower C_m values in winter.
- (e) Finally, variation in T_b is due to variations in heat production and in heat loss. T_b rises whenever heat dissipation is burdened due to either an increase in metabolic rate relative to conductance or a decreased effective conductance as a result of a low T_b to T_a gradient.

Group I

Conductance can only vary within the maximum physiologically possible range in upward deviation from C_m . The C_m constitutes the setpoint, which implies that, when low, the maximum conductance is lower than when C_m is high (trade-off). A cycling C_m setpoint, tracking the expected diel T_a rhythm thus has the advantage that the effect of the trade-off is partially alleviated. It allows a higher maximum conductance when warm during the day and more effective heat conservation with a lower C_m when cooler at night. Both circadian and circannual rhythmicity in C_m is postulated and the bushpig data may be interpreted in this way (lower T_b 's at night and during winter for group I animals: Tables 7/22 and 7/21).

Elevated T_b 's apparently occur under two sets of circumstances: On relatively cool days in summer (T_a effect inverse) and during the hours around noon (circadian rhythm; Table 7/22). On cool days in summer, the T_a during the day does not rise as on the average day (Fig 7/1), but the cycling C_m is relatively high then. Metabolic heat loss compensation then presumably sets in, leading to a rise in T_b ($T_b \approx M/C$). In a hot environment the advantage of having a skin temperature (T_s) higher than ambient is that conduction and convection can supplement other avenues of heat loss. Panting, as opposed to sweating, allows an animal to maintain a higher T_s . A high T_s , thus,

although it causes some heat flow from the skin towards to body core (heat retroflux), is an advantage in the heat balance of the animal (Schmidt-Nielsen 1964 ex Zervanos 1975). High T_a 's during the day reduce the T_b/T_a gradient, thereby making heat dissipation more difficult. This is counteracted by vasodilation and increased T_s in proportion to T_a , so that a maximally possible T_b/T_a gradient may be maintained. Whilst establishing a higher T_s/T_a gradient, the body core to skin thermal gradient is decreased, lowering the direct rate of heat flux from the core to periphery and thereby resulting, on balance, in higher T_b 's.

The suggested circannual (seasonal) and circadian thermoregulatory adjustment through the corresponding cyclicity in C_m has obvious advantages in the attainment of an optimal balance between energy conservation in relatively cool periods and flexibility in minimizing thermal stress during relatively warm periods. Such adaptability is expected to reduce the effect of thermal constraints on both intensity and temporal extent of activity, which is of particular advantage when much activity input is required per unit of food available.

Group II

It is well established that in many organisms circadian rhythms are involved in the control of circannual rhythms by participating in the mechanism of photoperiodic time measurement (Gwinner 1981b). The T_a to T_b reaction patterns in the Group II cases are amenable to interpretation in such a way that the interconnectedness of circannual and circadian C_m rhythmicity is borne out.

(a) TD3

In this animal T_b was found to be essentially non-rhythmic over the diel period in both seasons (Table 7/22). During summer body core temperatures were elevated on relatively warm days. This may be interpreted as the result of heat dissipation problems on warm days as a result of inadequate diel and seasonal C_m adjustment. If in accordance with this, a seasonally intermediate and non-adjusted C_m setting is postulated, the inverse T_a/T_b interrelationship, found during the winter

monitoring period, follows logically. On cool winter days C_m is not low enough to prevent the need for metabolic compensation for heat loss. Associated with this, we then have elevated T_b 's on such days. From this interpretation it appears that a lack of diel C_m adjustment (rhythm) is associated with non-adjustment also in the seasonal context. The correctness of this reasoning, as well as the interconnectedness between circadian and circannual C_m rhythmicity is further supported by the inverse diel T_b rhythmicity in case b (TC2) below. The lack of endogenous thermoregulatory rhythmicity of TD3 may have been associated with an undiagnosed illness which manifested itself in sporadic spasmodic convulsions (Table 1/2).

(b) TC2 in summer

With this animal the body core temperature patterns were inverse to those exhibited in the group I cases. T_b peaked at night and during summer T_b was lower than the winter T_b (Tables 7/22 and 7/21). These patterns may be related to those recorded for *Peromyscus maniculatus*, where continuous exposure to dominant mice led to phase shifting of T_b cycles in subordinates (Andrews 1978 ex Hill 1983). In addition, and especially among subordinates, high population densities were found to result in phase shifts in metabolic cycles which were desynchronized from activity cycles (Farr and Andrews 1978 ex Hill 1983). TC2, a foreigner, introduced to the group was presumably just tolerated, occupying a very low status. In addition, TD3 had farrowed, possibly intensifying the dominant-subordinate gradient.

With a diel C_m cycle reaching its minimum value during the warm parts of the day, a compensating tendency would be expected to attain the relatively high average C_m needed to cope with high summer T_a 's. The associated low M/C_m ratio would favour the relatively low average seasonal T_b which was found (Table 7/21). The night peak in T_b would result from metabolic heat loss compensation, which is expected with a high C_m during periods with relatively low T_a 's. Following this reasoning the conductance was adequate to prevent a rise in T_b on cool days but elevated T_b 's would be encountered on warm days. This was indeed found to be the case (proportional T_a effect: Table 7/22).

The Tb rhythm of domestic pigs, dogs and rats is apparently abolished in the absence of opportunity for extended activity (Rawson *et al.* 1965, Ingram and Legge 1970a). Unlike the bushpig, the Tb peak of these species at normal levels and rhythms of activity coincides with their activity peaks. This is presumably as a result of heat production from activity, combined with relatively high Ta for diurnal species (domestic pig and dog) and Mb peaks with heat production from activity for small-sized nocturnal species (rat). In these species conductance is geared to cope with heat dissipation under these circumstances. Thus, in the absence of heat production from activity, the rate of heat dissipation is sufficient to prevent a heat build-up resulting in increased Tb's. No Tb rhythm is therefore detectable any more. Diurnal activity in captive European wild boar, as opposed to their greater degree of nocturnal activity under free-ranging conditions, may be similarly explained (6.4.2.4.). In the latter case Ta extremes, combined with heat production induced by extended activity, are avoided. As previously noted there is a trade-off between greater efficiency in heat dissipation and lower efficiency in heat conservation. By avoiding having to cope with the burden of heat accumulation, heat conservation efficiency is enhanced. This should be energetically advantageous, particularly under conditions of food scarcity.

In regions of the world with strongly seasonal continental climates there is very little, if any, overlap in the daily Ta ranges between summer and winter. Under such conditions mammals generally exhibit seasonal changes in morphological thermal insulation, mainly relating to pelage characteristics.

Broad diel Ta ranges and day-to-day variability are characteristic of continental climates. Morphological insulation cannot be adjusted in the short-term to adapt to these changes. Hence we find a more pronounced seasonal switching from winter day to summer night activity. This appears to be the pattern of activity in European wild boar in continental Russia (Sludskii 1956), of peccaries in Arizona (Zervanos 1972) and feral pig in hot arid subtropical areas. In areas with less seasonal and diel Ta variation, seasonal day to night activity switching is less pronounced or absent.

7.4.4.2 Thermoneutrality

The concept of thermoneutrality is based on ambient temperature and the principal determining factors are body size, thermal insulation, condition (via plane of nutrition) and acclimatization (cf Mount 1979). The effective critical temperatures at any given time will vary with prevailing weather factors (air movement; rain), time lapse since feeding, group association and whether active or resting (cf Verstegen 1971, Mount and Ingram 1971, Mount 1979). The most stressful weather combination is that of low temperatures, high rates of air movement and rain (Bianca 1976). Higher wind speeds are beneficial for an animal in a hot environment, if $T_a < T_b$, reducing the environment heat load on the animal. In a cold environment, however, high wind speeds result in elevated lower critical temperatures, thus increasing the demands on metabolic heat production (Hofmeyer 1981). In terms of its thermal effect a 0,05 m/s increase in air movement is equivalent to a 1°C decrease in environmental temperature (Close 1981). Acclimatization to the cold usually entails increased pelage insulation or increased basal metabolic rate, or both. For example, the collared peccary exhibited a narrow thermoneutral zone with a lower critical temperature of 25°C in winter and 28°C in summer and upper critical temperatures of 30 or 35°C respectively. To compensate for poor insulation, winter animals exhibited an increased BMR (Zervanos 1975).

Lower critical temperature estimates for the domestic pig by Verstegen (1971) range between 12 and 20°C for the body weight range of 80 to 10 kg. From birth to maturity the lower critical temperatures range from 34°C down to 10°C (Mount 1979). At a body weight of 10 kg the minimum critical temperature is about 19°C (Bianca and Blaxter 1961 ex Curtis 1970). The optimum temperatures for the fattening of domestic pigs determined by various authors ranged between 10 and 25°C (Sainsbury 1972). These values are relatively high when compared to that of 0°C for cold-adapted boars (Irving, Peyton and Monson 1956). The variable results found in the literature are presumably attributable to the host of influencing factors mentioned above. In addition, pigs kept out of doors were reported to seek shelter on dry days only when the air temperature fell towards 5°C, which was considerably below the critical temperature (Ingram and Legge 1970b). It was concluded that the pig

tolerates some degree of thermal discomfort before modifying its behaviour, especially when foraging is at stake.

Thermal conductance is a function of the surface-to-volume ratio (size) and the surface-specific insulation (McNab 1974). Increasing body size decreases the percentage of that part of the heat loss in the cold which results from increased heat conduction. Consequently, larger animals can generally stand a cold environment with less difficulty than small animals, because the basal metabolic rate of homeotherms increases with the 0,75 power of body weight, whereas conductance rises only with the square root of body weight (Kleiber 1972). Lower critical temperatures are approximately linearly related to body weight at the same feeding level and decrease with ca 1°C for every 10 kg increase in body mass in the case of the domestic pig (Verstegen 1971). The lower critical temperature of the bushpig with a 10 kg mass may be taken as 13°C (7.3.5; Fig. 7/2). From the relationship of Verstegen (1971), the lower critical temperature at 10 kg body mass may be extrapolated to 11°C at 30 kg, 8°C at 60 kg and 6°C at 80 kg.

Unlike the domestic pig, the juvenile bushpig appears to be comparatively well insulated relative to the adult (juvenile hair coat density 2 x that of the adult: Table 7/14). The critical temperature to body size gradient is presumably less steep than the 1°C/10 kg in the domestic pig. Also the range of optimal temperatures for productivity extend to colder levels as the plane of nutrition is increased (Mount 1979). The experimental animals could feed to satiation (7.3.5), which is unlikely to be continuously so for free-ranging bushpigs. Their lower critical temperatures may therefore be expected to be relatively higher than those established experimentally.

The lower critical temperature of an adult bushpig should accordingly be taken to be closer to 8°C than 6°C. This contention is supported by sheltering and nest-building behaviour around this temperature. When not accompanied by juveniles less than one month old, nest-building was undertaken at ambient temperatures of 10°C and lower during rain (Table 7/13) and the average temperature of 4-hour winter night rest periods was 8°C (Table 7/10). The extent and seasonal nature of potential cold stress periods may now be derived from the Table 7/31 below.

| TABLE 7/31: MONTHLY PERCENTAGES OF DAYS WITH MINIMUM AMBIENT TEMPERATURES \leq POTENTIAL LOWER CRITICAL TEMPERATURES X (DIEPWALLE 1982) | | | | | | | | | | | | | | |
|---|----|----|----|----|----|----|---------------------------|----|----|----|----|----|--------|--------|
| X°C | J | F | M | A | M | J | J | A | S | O | N | D | SUMMER | WINTER |
| 12 | 23 | 21 | 29 | 63 | 71 | 80 | 90 | 90 | 70 | 71 | 66 | 61 | 45 | 77 |
| 11 | 19 | 11 | 16 | 50 | 45 | 70 | 90 | 87 | 65 | 61 | 53 | 32 | 32 | 68 |
| 10 | 6 | 4 | | 40 | 39 | 67 | 84 | 77 | 33 | 39 | 27 | 6 | 14 | 57 |
| 9 | 3 | | | 30 | 32 | 60 | 68 | 74 | 20 | 26 | 17 | 3 | 8 | 47 |
| 8 | | | | 23 | 19 | 57 | 55 | 45 | 10 | 23 | 13 | | 6 | 35 |
| 7 | | | | 20 | 6 | 40 | 32 | 23 | 7 | 10 | 7 | | 3 | 21 |
| 6 | | | | 13 | 6 | 33 | 13 | 13 | 3 | 6 | | | 1 | 13 |
| SUMMER: OCTOBER - MARCH | | | | | | | WINTER: APRIL - SEPTEMBER | | | | | | | |

April to October are the main months with ambient temperatures which would require the use of energy for thermogenesis in the adult bushpig. Activity scheduling (7.3.1.2) is in accordance with this. Cold stress may however, also be experienced in other months, depending on body size, and when relatively low temperatures are associated with rain (7.3.1.3).

Based on the onset of panting of resting juveniles, the upper critical limit of thermoneutrality may be taken as ca 30°C (7.3.5). Heat relief behaviour, such as wallowing or seeking cool, moist resting sites, would be expected at such ambient temperatures, although the larger-sized adult, due to a greater thermal inertia, may experience less discomfort when at rest at 30°C (7.3.5). However, the upper critical temperature for activity would be lower than 30°C, particularly for the adult (*vide* Table 7/10).

7.4.5 Temperature regulation in the juvenile

The range of thermal conditions in which infant mammals have control over their body temperature is very much narrower than that of adults of the same species (Alexander 1975). The small size of the newborn animal means that its surface area to body weight ratio is large compared to that of the adult and it will therefore tend to lose heat more rapidly in a cool environment (Whittow 1971). In addition, the newborn pig has a very low fat content and the lack of subcutaneous fat and an effective coat, results in very low thermal insulation (Mount 1963). After one

week the body fat content may approach 10% and the cold resistance has then increased considerably (Mount 1979). Lower critical temperatures of the domestic piglet are given as 35°C at birth, 29°C up to 4,1 kg weight and 24°C at 10 kg at low rates of air movement (less than 0,15 m/s) (Sainsbury, 1972).

The mammalian young not only has a higher value of the lower critical temperature, but it also has the ability to increase its heat production very rapidly and to attain a high maximum metabolic rate (Bianca 1976). This enables newborn animals to control their body temperatures in spite of their unfavourable surface to mass ratios. Therefore, size at birth is only a crude guide to thermal stability and homeothermy can usually be maintained, but at the price of a very high food intake (Alexander 1975). Newborn piglets quickly use up their small energy reserves under cold stress and if the temperature is too low, high mortalities may result (English *et al.* 1977).

The great majority of mammalian species appear to have brown fat at birth but in some it only develops post-natally (Alexander 1975). Brown fat has a high metabolic capacity and is a major site of non-shivering thermogenesis (Smith and Horwitz 1969). Brown fat may be distinguished from white fat by its colour, which ranges from pale buff to dark reddish brown, and its multi-locular cell structure. The colours derive largely from blood haemoglobin and to some extent from heme porphyrins and flavin compounds (Smith and Horwitz 1969). The deposition of brown fat may be induced by short periods of daily cold exposure (Wunder 1981). Non-shivering thermogenesis greatly widens the climatic limits in which homeothermy can be maintained and it considerably lowers the minimum temperature tolerated (Alexander 1975). The newborn domestic piglet apparently has no brown fat (Le Blanc and Mount 1969 *ex* Alexander 1975) and does not produce heat by non-shivering thermogenesis (Whittow 1971). The absence of brown fat seems paradoxical, as the neonates are amongst the smallest relative to adults amongst ungulates and are particularly prone to mortality from hypothermia (Alexander 1975). However, it is possible that brown fat only develops some time post-partum, as in the hamster (Smith and Horwitz 1969). No information is available for European wild boar neonates. Yellowish-brown subcutaneous fat was observed in pre-weaning

bushpig juveniles, but whether this constituted BAT was unfortunately not verified microscopically.

Domestic animals have been selected and bred for productive traits and were often shielded from certain selective pressures operative in the wild. They may thus be poorly adapted to their meteorological environment (Bianca 1976). In contrast to domestic piglets, which have a meager pelage, pelage removal significantly impaired cold resistance of neonatal wild piglets (Foley *et al.* 1971 ex Hansen *et al.* 1972). Neonatal wild piglets had a greater pelage weight density (mg/cm^2) and hair density (hairs/cm^2) than domestic piglets (Hansen *et al.* 1972) and were markedly more thermostable in the cold (cf Curtis 1970). Lower critical temperatures are therefore presumably not as high in wild boar or bushpig neonates as in the domestic piglets. For wild neonates the factors directly influencing external thermal insulation, such as air movement and wetness, are likely to be relatively more important than low ambient temperature *per se*. Access to energy needed for thermogenesis, through sucking, is also required.

Suid rearing behaviour is very much geared to minimizing heat loss from the young and to providing a regular source of energy through nursing. Heat loss is minimized through huddling, nest-building and appropriate spatiotemporal activity scheduling. Wild boar juveniles in Russia, up to the age of one month feed only during the day and have to return to the nest at night (Sludskii 1956). The same phenomenon, albeit not as pronounced, was observed in the bushpig (5.3.2.1). The relative cold-sensitivity of suid neonates is also reflected by the consistent use of nests for protection against cold, wetness and wind for the first 1 - 2 weeks post-partum (Sludskii 1956, Gundlach 1968). A rain shower may kill the entire litter (Buss 1972). The timing and duration of activity of European wild boar neonates outside the farrowing nest depends largely on the prevailing air temperature (Gundlach 1968). The energy-saving effect of huddling also appears to be important. The European wild boar sow is reported hardly to leave the nest during the first two weeks if the young are born early in the season (Sludskii 1956). Nest-building and huddling appears to be similarly important in bushpig juvenile survival (5.3.2.4). Four out of twelve young born in the study

enclosure died before weaning. Three of these deaths were associated with relatively cold and wet periods.

Both huddling and nest-sheltering reduce the effect of air movement through their wind-breaking action and reduction of exposed body surfaces. In domestic piglets an increase in air movement from 0,08 m/s, i.e. approximating still air condition, to 0,35 m/s brings about a reduction of nearly 50% in the skin-air thermal insulation (Mount and Ingram 1965). Doubling of air velocities was found to result in a rise of the lower critical temperature of 5,6°C in young domestic piglets (Sainsbury 1972). At an environmental temperature of 20°C the huddled group had a metabolic rate much closer to that of the larger pig than to that of the single newborn pig (Mount 1979). The majority of losses in newborn domestic pigs occur in the first few days of life and are primarily due to chilling. Mortality rates are high, generally 20 - 25% of those born alive (Sainsbury 1972).

The post-neonatal phase is marked by a rapid increase in size (9.3.1) which, by itself, diminishes the animals' cold sensitivity progressively (cf Mount 1979). Animals with greater masses are more efficient in the conservation of heat energy and it is therefore energetically advantageous if the animal enters its first winter as large as possible (Moen 1973). For example, the temperature and precipitation over an 18-month period was important to the recruitment of young in wapiti (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) (Picton 1984). The birth peak of the bushpig in spring makes adaptational sense in minimising neonatal mortality and ensuring that maximum size is attained at the onset of the first winter.

7.4.6 Energy requirements

Many factors influence the rate of energy expenditure in mammals, the most important of which is body size (McNab 1983). Basal metabolic rates also correlate with food habits, behaviour types (e.g. arboreal versus terrestrial) and climate (McNab 1986). Grazing and meat-eating are correlated with high basal rates relative to the Kleiber relation, compared with low rates in folivory and frugivory.

Terrestrial species like the bushpig, feeding opportunistically on a mixture of fruit, herbs, vertebrates and invertebrates, may be expected to have intermediate basal rates (cf McNab 1986).

The heat input required per unit of body weight for the maintenance of body temperature falls due to an increase in body size alone, as a result of the diminishing surface to mass ratio. This underlies the Kleiber relation, with $70 \text{ kcal/kg}^{0.75}/\text{day}$ as a mean value for standard metabolism in different species (Moen 1973). The basal metabolic rates so calculated hold reasonably well in older animals if standard conditions, i.e. inactivity, thermoneutrality and post-absorptive state, are met (Mount 1968). Young pigs have a higher metabolic rate (ca $130 \text{ W}^{0.75}$; Close and Mount 1975) than that predicted from the mean calculated interspecies value. This "overshooting" of basal rates is believed to permit the young to grow faster than they would with lower basal rates (McNab 1983, cf Derting 1989). To achieve the post-absorptive condition, up to 7 days of fasting may be required (cf Hofmeyer 1981), which is often not applicable to BMR estimates.

The fasting metabolic rates for the domestic pig of 73 and 64 $\text{kcal/kg}^{0.75}/\text{d}$, for 50 and 100 - 120 kg animals respectively, are close to $70 \text{ kcal/kg}^{0.75}/\text{d}$ (Verstegen 1971). The RMR estimates for bushpigs and European wild boar (Table 7/26 and 7/27) originated from young, growing animals. Scaling these values according to metabolic mass for adult size classes (7.3.5) must therefore be taken to constitute overestimates.

The metabolic rate of a mammal under any particular set of circumstances may be compartmentalized to take the following form:

$$\text{MR} = c\text{Mr} + \text{Mt} + \text{Ma} + \text{Mp}$$

$$\text{MR} = \text{total metabolic rate}$$

$$c = \text{a coefficient to modify metabolism for the posture associated with activity (Schmidt-Nielsen 1972 ex Wunder 1975)}$$

$$\text{Mr} = \text{resting metabolic rate (maintenance)}$$

- Mt = metabolism associated with temperature regulation outside the thermoneutral zone
- Ma = metabolism due to activity
- Mp = productive energy retention = growth, energy storage and reproduction.

When the ambient temperature is lowered below the TNZ, energy consumption tends to increase by about the same amount at a high level of activity as at rest, i.e. thermogenesis due to exercise is added to thermogenesis due to cold down to a certain temperature (cf Searcy 1980). This is most likely related to the coefficient "c". Extra heat loss below the lower critical temperature is nearly linear (Versteegen 1971). Animals either avoid (reduced activity) or compensate (increased activity) for any increased thermogenic energy requirements. Moen (1973) provided some guidelines on the energy requirements associated with activity and reproduction of ruminants. For the European wild boar, Jezierski and Myrcha (1975) state that the metabolic rate of the pregnant sow is about 10% higher than that of the non-gravid individual.

Estimates of the metabolic requirements of free-ranging mammals in natural habitats roughly parallel basal requirements, but at a higher level. The estimates usually vary between 1,5 and 3 times basal values (cf Damuth 1981). For example, field metabolic rates in howler monkeys (*Alouatta palliata*) averaged 2 x BMR (Nagy and Milton 1979). The total metabolic requirements are usually taken as 2 - 3 times maintenance requirements (Müller and Kirchgessner 1979). From the data of Jezierski and Myrcha (1975) for European wild boar, Briedermann (1986) derived a factor of 2,5 times RMR as an indication of the total metabolic energy requirement. Due to the factors discussed, this may be an overestimate and a factor of 2,5 x BMR be more realistic. The available data on the bushpig is incomplete and does not have the necessary resolution to quantify the energy budget reliably. The bushpig and the European wild boar appear to be physio-ecologically broadly similar. A factor of 2,5 x BMR is thus taken to serve as a crude guide for the expected total average energy requirement of free-living bushpigs.

7.5 Synopsis

- (I) Activity scheduling in the bushpig was geared to avoid ambient temperature extremes. Activity occurred preferentially between 18 - 22 h in both seasons. Resting in summer occurred mainly between 10 and 18 h and in winter between the 10 - 14 h and 2 - 6 h.
- (II) Behavioural thermoregulation included wallowing, lying in extended posture and exposure to air movement at high temperatures and resting after midnight in winter, sheltering, huddling and nest-building at low temperatures.
- (III) Bushpig pelage characteristics apparently constitute a compromise between effective heat dissipation and some thermal insulation. The black colour of the pelage is possibly involved in the use of solar radiation in order to reduce body to ambient temperature gradients on cool sunny days.
- (IV) The water use of the bushpig, amounting to 2 - 3,5 l/day/animal, is higher in summer, presumably due to increased requirements for evaporative heat loss. Water requirements are much lower than those of domestic pigs.
- (V) Individual within-season average body core temperatures were found to lie between 37,4 and 39,9°C. Nycthemeral body core temperature rhythms peaking around 14 - 15 h, were recorded. The rhythms had diel amplitudes of 0,6°C and body core temperatures were regulated within a total range of 2 - 3°C per individual.
- (VI) The thermoneutral zone for 10 kg bushpig juveniles was estimated to lie between 13 and 30°C and that for adults between 8 and 25°C. Chilling and the resulting associated negative energy balance appears to be an important factor in neonatal mortality and various features of rearing are seemingly directed to counteract this (farrowing season, nest-building, activity scheduling).
- (VII) The resting metabolic rate of bushpigs weighing about 10 kg was estimated as ca 130 kcal/kg^{0,75}/day. This is similar to corresponding estimates in the domestic pig and European wild boar.

8. FEEDING ECOLOGY

8.1 Diet

8.1.1 Introduction and methods

Information on diet is of basic importance in understanding the ecology of an animal. Bushpig diet was investigated with the aim of evaluating food availability and determining foraging constraints. It was also hoped to assess the ecological impacts of foraging by bushpigs.

Basic data were gathered by stomach content analysis. Material consisted of 204 stomach samples from the Southern Cape and 56 from the Eastern Cape. Stomach contents dominated by agricultural food items were recorded, but excluded from detailed analysis. After collection, stomach contents (1.3.2) were mixed, washed and screened through two superimposed sieves, of mesh size 4,75 mm and 2,36 mm. The fragments remaining on the sieves were placed on a laboratory tray and sampled systematically according to the point frame method (Chamrad and Box 1964). This involved placing a rod with pins, spaced one centimeter apart, over the fragments spread out on the tray. A fragment hit by the point of a pin was identified or numbered and placed in a container for later identification. A minimum of 200 hits were taken per sample and tallied on an appropriate form by plant part and species (or specimen number in the case of unidentified fragments). Forage classes employed are listed in Table 8/1.

The aim with the point frame method analysis is to quantify the relative volumes of the various food items in any particular stomach. Bias results from the fact that items with a relatively high surface area to volume ratio are recorded out of proportion to their contribution in terms of volume. A certain amount of bias in the relative volumes is therefore unavoidable. However, visual comparison confirmed that the relative contribution of items in terms of volume was approximated reasonably well.

8.1.2 Results

8.1.2.1 Forage classes

The forage fraction data was analyzed using multivariate analysis of variance on the log-transformed forage percentages (Table 8/1). The class "subterranean" includes roots, tubers and corms, whereas "fruit" also includes seeds.

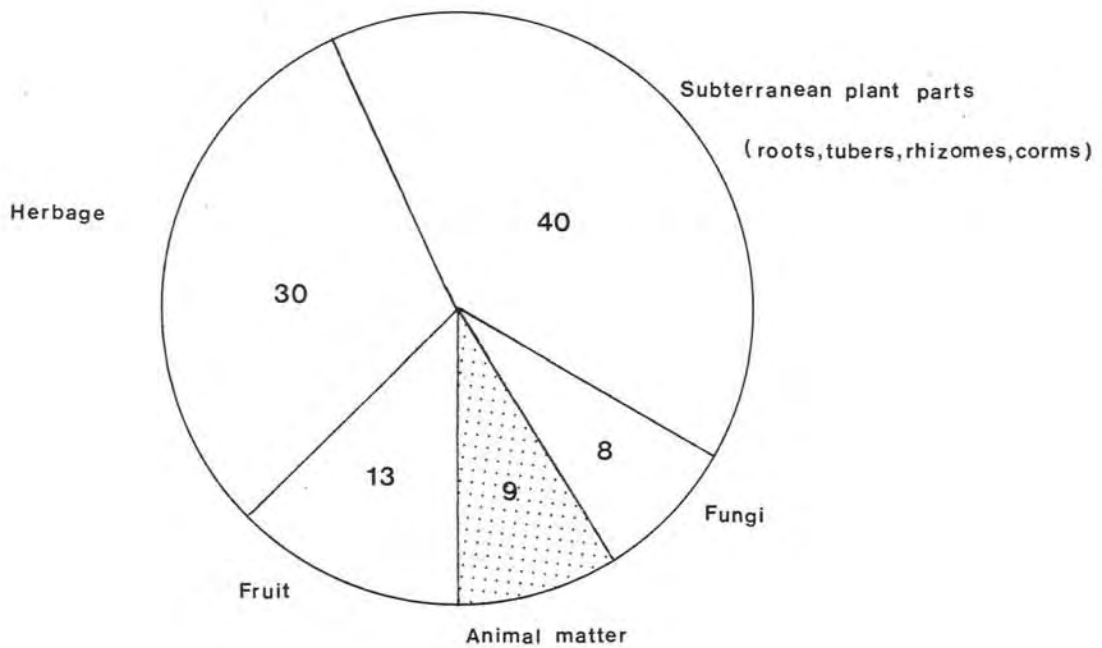
| FORAGE CLASS | REGION * | FORAGE FRACTIONS (%) ** | | | | | P< |
|-------------------------|----------|-------------------------|--------------|--------------|--------------|--------------|--------|
| | | Summer | Autumn | Winter | Spring | Total | |
| OF PLANT ORIGIN | S E | 94,7 87,1 | 95,4 95,2 | 91,0 86,9 | 94,5 88,8 | 93,6 88,4 | 0,05 |
| Fruit | S E | 19,3 23,8 | 19,2 11,9 | 16,8 9,1 | 9,1 5,9 | 15,1 10,5 | 0,05 |
| Herbage | S E | 30,7 26,3 | 37,6 10,6 | 24,7 31,9 | 40,4 28,9 | 33,3 27,8 | 0,001 |
| Subterranean | S E | 18,4 37,0 | 15,0 72,7 | 40,4 45,4 | 31,3 54,0 | 29,1 49,9 | 0,005 |
| Fungi | S E | 26,4 0 | 23,5 0 | 9,1 0 | 13,4 0 | 16,0 0 | 0,0001 |
| OF ANIMAL ORIGIN | S E | 5,3 12,9 | 4,6 4,8 | 9,0 13,1 | 5,5 11,2 | 6,4 11,6 | 0,05 |
| Invertebrate | S E | 0,5 5,9 | 2,0 0 | 5,2 3,2 | 1,8 0,4 | 2,6 2,3 | 0,01 |
| Vertebrate | S E | 4,8 7,0 | 2,6 4,8 | 3,8 9,9 | 3,7 10,8 | 3,8 9,3 | 0,001 |
| * S : Southern Cape | | E: Eastern Cape | | | | | |
| ** Summer: Dec/Jan/Feb. | | Autumn: March/April/May | | | | | |
| Winter: June/July/Aug. | | Spring: Sept/Oct/Nov. | | | | | |

All forage fraction totals differ regionally. The "fruit" and "herbage" classes were lower in Eastern Cape bushpigs, but flesh and subterranean plant organs feature more prominently than in the Southern Cape. Significant seasonal effects became apparent for the herbage ($P < 0,01$),

subterranean ($P < 0,001$), fungi ($P < 0,01$) and invertebrate ($P < 0,01$) fractions in the Southern Cape and for the subterranean fraction ($P < 0,05$) in the Eastern Cape.

A general description of the diet in terms of forage fractions was obtained by pooling data from the two regions with equal weighting (Figure 8/1).

FIG.8/1: BUSHPIG FORAGE CLASS PERCENTAGES (CAPE PROVINCE)



8.1.2.2 Diet composition by item

In this section diet composition is described in terms of items present, using one or more of the following four parameters:

- (I) Percentage presence (PP): the number of stomach contents in which the item was present, irrespective of its quantity, expressed as a

percentage of the total number of stomach contents sampled, per region. This index may be taken to reflect the spatiotemporal ubiquity of the food item.

- (II) Mean bulk percentage (MBP): the mean of the contents fractions of the item for the stomach contents in which the particular item occurred. This parameter reflects both availability of the item in the environment and its selection by the foraging animal.
- (III) Percentage of forage class (PFC): the percentage of the forage class (ex Table 8/1) which is contributed by the specific item.
- (IV) Percentage of total diet (PTD): the percentage contribution of the item to the total diet.

The quantitative relationships between these parameters are expressed below:

$$PP = \frac{n_i}{n} \times 100$$

where n_i = number of stomach contents with item and n = total number of stomach contents sampled, i.e. 204 and 56 for the Southern and Eastern Cape, respectively.

$$MBP = \frac{\sum_{i=1}^{n_i} (\text{percentage occurrence of item in stomach vide 8.1.1})}{n_i}$$

$$PTD = \frac{n_i \times MBP}{n} \quad \text{and}$$

$$PFC = \frac{PTD}{MCP} \times \frac{100}{1}$$

where MCP = the mean forage class percentage ex Table 8/1.

(a) Fruit

In the Southern Cape, fruit from the seven most important plant species makes up 86% of the fruit fraction.

| | <u>PP</u> | <u>MBP</u> | <u>PFC</u> | <u>PTD</u> |
|---|-----------|------------|------------|------------|
| <i>Podocarpus falcatus</i> | 16 | 25,9 | 27,7 | 4,2 |
| <i>Olea capensis</i> ssp. <i>macrocarpa</i> | 10 | 28,4 | 18,4 | 2,3 |
| <i>Rhoicissus tomentosa</i> | 10 | 15,0 | 10,3 | 1,6 |
| <i>Podocarpus latifolius</i> | 4 | 34,8 | 9,0 | 1,4 |
| <i>Quercus robur</i> | 8 | 15,3 | 8,4 | 1,3 |
| <i>Diospyros dichrophylla/whyteana</i> | 5 | 21,9 | 7,8 | 1,2 |
| <i>Ocotea bullata</i> | 5 | 13,7 | 4,4 | 0,7 |

The remaining 14% comprises the sporadic occurrence of fruit or seed material of *Kedrostis nana*, *Rapanea melanophloeos*, *Rothmannia capensis*, *Calodendron capense*, *Restio* spp. and material of uncertain identity.

The relatively high mean bulk percentages for *Podocarpus latifolius*, *Olea capensis* ssp *macrocarpa*, *Podocarpus falcatus* and *Diospyros* spp fruit reflect their concentrated availability at the time of foraging. In 6 of the 7 years sampled (1978 - 1984), fruit of *Podocarpus falcatus*, *Rhoicissus tomentosa* and *Diospyros* spp fruit was taken , suggesting that it is available in most years. In contrast, *Podocarpus latifolius* and *Olea capensis* ssp *macrocarpa* fruit were only present in the diet in 4 and 3 of these 7 years respectively, coinciding with the fruiting events of these species, which occur only every 2 to 4 years (cf Phillips 1931). *Podocarpus falcatus* trees are comparatively rare in the forest (2,9 stems/ha) compared to *Olea capensis* ssp *macrocarpa* (53 stems/ha) and *Podocarpus latifolius* (34 stems/ha; regional means of trees 30 cm DBH and larger, Departmental records). Yet, the fruit of this species forms the most important item of the fruit fraction in the Southern Cape. This is taken to be partly the result of annual availability and preferential foraging.

Fruit is of lesser importance in the diet of bushpigs sampled in the Eastern Cape (n = 56). Fruit, or seed only, of the following species were identified (PP in parentheses): *Opuntia* spp (14), *Podocarpus*

falcatus (5), pineapple (4) and *Rhoicissus tomentosa*, *Diospyros dichrophylla* and *Euclea natalensis* in one stomach each.

(b) Herbage

The Southern Cape herbage fraction (ex Table 8/1) consists of 38,7% fern fronds, 46% monocotyledon foliage and 12,3% dicotyledon foliage.

| | <u>PP</u> | <u>MBP</u> | <u>PFC</u> | <u>PTD</u> |
|-----------------------------|-----------|------------|------------|------------|
| <i>Blechnum punctulatum</i> | 41 | 24,3 | 29,7 | 9,9 |
| Cyperaceae | 39 | 16,7 | 19,4 | 6,5 |
| <i>Chlorophytum comosum</i> | 27 | 19,5 | 15,8 | 5,3 |
| <i>Asplenium rutifolium</i> | 18 | 16,4 | 8,7 | 2,9 |

The fern fronds fraction consists virtually entirely of *Blechnum punctulatum/capense* and *Asplenium rutifolium*. Foliage of *Carex clavata* and *Schoenoxiphium* spp are the dominant items under Cyperaceae, *Chlorophytum comosum* foliage forms about three-quarter of the monocotyledonous foliage fraction. Other monocotyledonous species contributing to the herbage fraction are rather less important and include *Zantedeschia aethiopica*, *Aponogeton distachyos*, *Hypoxis angustifolia*, *Habenaria arenaria*, *Impatiens* sp and graminoids. Of the dicotyledonous foliage fraction forbs of Asteraceae are the most important.

The contribution of the herbage fraction to the diet of Southern Cape bushpigs is significantly higher in autumn and spring (Table 8/1), coinciding with the rainfall peaks (2.3.1.1). These peaks are particularly marked in the case of fern fronds and dicotyledonous foliage.

The important diet items of the herbage fraction from bushpigs sampled in the Eastern Cape were as follows:

| | <u>PP</u> | <u>MBP</u> | <u>PFC</u> | <u>PTD</u> |
|-----------------------------------|-----------|------------|------------|------------|
| <i>Aloe cf ciliaris</i> | 36 | 25,6 | 32,9 | 9,1 |
| Aizoaceae (cf <i>Mestoklema</i>) | 16 | 32,2 | 18,6 | 5,2 |
| Agricultural legumes | 7 | 67,6 | 17,4 | 4,8 |
| Graminoids (winter oats) | 20 | 23,6 | 16,7 | 4,6 |
| <i>Cyphostemma</i> spp | 5 | 34,0 | 6,6 | 1,8 |

(c) Subterranean plant parts

In the Southern Cape the subterranean plant part fraction is composed of 54,3% fern rhizomes, 38,9% tubers, 5,7% roots and 1,1% corms.

| | <u>PP</u> | <u>MBP</u> | <u>PFC</u> | <u>PTD</u> |
|---------------------------------------|-----------|------------|------------|------------|
| <i>Pteridium aquilinum</i> rhizomes | 52 | 27,0 | 48,3 | 14,1 |
| <i>Zantedeschia aethiopica</i> tubers | 17 | 19,6 | 11,6 | 3,4 |
| <i>Rhoicissus</i> spp tubers | 9 | 27,7 | 8,4 | 2,4 |
| <i>Hypoxis angustifolia</i> tubers | 7 | 15,7 | 3,7 | 1,1 |

Items of lesser importance include tubers of Orchidaceae (e.g. *Habenaria arenaria*), *Ipomea batatas* and corms of *Hexaglottis virgata*, *Watsonia* spp and *Oxalis* spp.

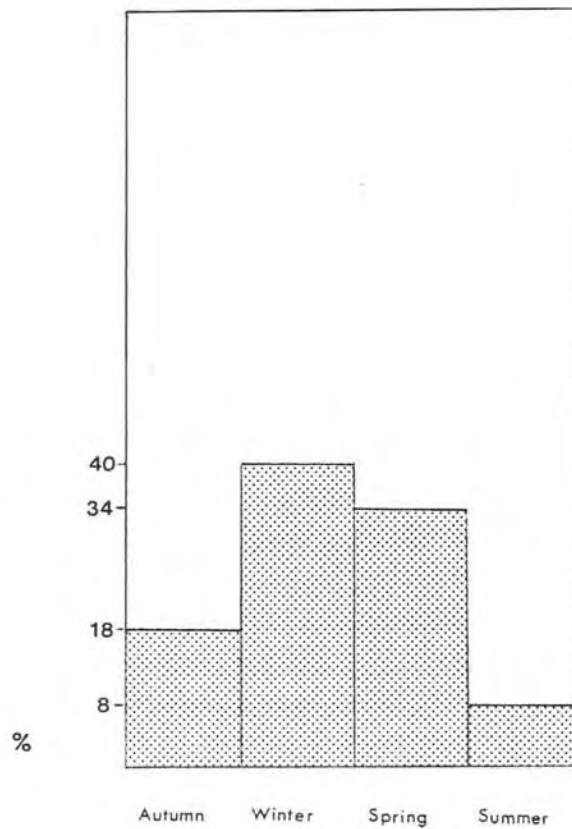
The subterranean fraction contributed disproportionately to the diet during winter and spring (8.1.2.1). The rhizomes of *Pteridium aquilinum* are palatable for bushpigs only when the nutrients are concentrated in them during winter and spring (Fig. 8/2).

About 50% of the total Eastern Cape bushpig diet consisted of subterranean plant parts (8.1.2.1, Table 8/1), notably of the tubers of Vitacea (*Rhoicissus digitata/tridentata* and *Cyphostemma cirrhosum/quinata*).

| | <u>PP</u> | <u>MBP</u> | <u>PFC</u> | <u>PTD</u> |
|-------------------------------|-----------|------------|------------|------------|
| Vitaceae tubers: | 68 | 55,8 | 75,9 | 37,9 |
| <i>Rhoicissus</i> spp tubers | 50 | 53,2 | 53,3 | 26,6 |
| <i>Cyphostemma</i> spp tubers | 18 | 63,2 | 22,6 | 11,3 |
| <i>Watsonia</i> spp corms | 9 | 23,3 | 4,2 | 2,1 |

Other items include corms of *Oxalis* spp., *Hexaglottis* sp., *Ferraria crispa*, tubers of Orchidaceae and of unknown identity, as well as Hyacinthaceae bulbs.

FIG.8/2: SEASONAL WEIGHTING OF BRACKEN RHIZOME USE
IN SOUTHERN CAPE BUSHPIGS



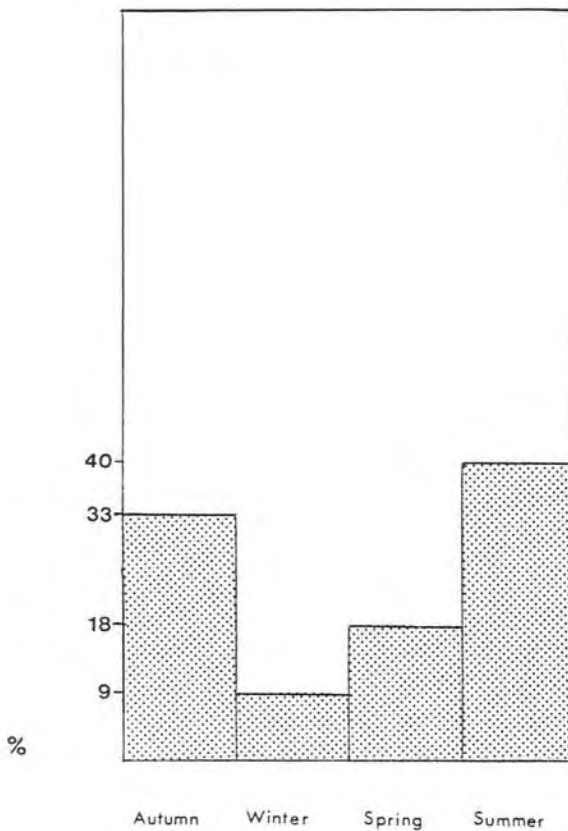
(d) Fungi

Fungi are absent from the diet of bushpigs in the Eastern Cape, presumably as a result of the aridity of the region. The role of fungi in the diet of Southern Cape bushpigs is quantified below:

| | <u>PP</u> | <u>MBP</u> | <u>PFC</u> | <u>PTD</u> |
|----------------------------------|-----------|------------|------------|------------|
| <i>Rhizopogon</i> sp (hypogeous) | 58 | 24,6 | 89,6 | 14,3 |
| Agaricales (above-ground) | 18 | 6,3 | 7,2 | 1,2 |
| Lycoperdales (earth-stars) | 3 | 5,4 | 1,3 | 0,2 |

Seasonal peaks in availability of or selection for *Rhizopogon* are evident in summer and autumn (Fig. 8/3).

FIG.8/3 : SEASONAL WEIGHTING OF RHIZOPOGON USE
IN SOUTHERN CAPE BUSHPIGS



(e) Food of animal origin

Food of animal origin, particularly that obtained by scavenging on vertebrates, plays a greater part in the diet of Eastern Cape bushpigs (cf Table 8/1).

| | <u>PP</u> | <u>MBP</u> | <u>PFC (Animal)</u> | <u>PTD</u> |
|-----------------------|-----------|------------|---------------------|------------|
| <u>Southern Cape:</u> | | | | |
| Vertebrata | 62 | 6,1 | 59,4 | 3,8 |
| Invertebrata | 51 | 5,1 | 40,6 | 2,6 |
| <u>Eastern Cape:</u> | | | | |
| Vertebrata | 68 | 13,7 | 80,2 | 9,3 |
| Invertebrata | 21 | 6,1 | 19,8 | 2,3 |

In the Southern Cape, the rainfrog (*Breviceps fuscus*) was the most important single item in the animal fraction. It occurred in 43% of all 204 stomach contents sampled and contributed 28% in bulk to the animal fraction. Small stock (i.e. goats and sheep) were recorded in 10 of the 56 stomach contents sampled in the Eastern Cape, contributing nearly 50% to the Eastern Cape vertebrate fraction and forming nearly 4,6% of the total diet. Bird and reptile fragments were occasionally recorded in the stomach contents from both regions.

Larvae of Coleoptera dominated the invertebrate fraction. A full list of all positively identified invertebrate taxa is given below (the frequencies represent the number of stomach contents in which each was found).

Larvae

| | |
|---------------|----|
| Coleoptera | 49 |
| Scarabaeidae | 25 |
| Tenebrionidae | 3 |
| Alleculidae | 3 |
| Diptera | 10 |
| Trichoptera | 2 |
| Lepidoptera | 1 |

Adult forms

| | |
|------------------------------|---|
| Coleoptera | 7 |
| Myriapoda | 6 |
| Dictyoptera (Blattaria) | 3 |
| Annelida (earthworms) | 3 |
| Diplura (Japygidae) | 2 |
| Orthoptera (Stenopelmatidae) | 2 |
| Scorpionidae | 2 |
| Isopoda | 1 |

Overall, diet items of animal origin were found in 83% and 88% of the stomach contents from the Southern and Eastern Cape respectively. In both regions, the animal fraction was higher for females compared to that of males:

| | <u>MCP: M</u> | <u>MCP: F</u> | <u>df</u> | <u>F</u> | <u>P<</u> |
|---------------|---------------|---------------|-----------|----------|--------------|
| Southern Cape | 5,66 | 7,17 | 1 | 4,04 | 0,05 |
| Eastern Cape | 6,04 | 15,69 | 1 | 7,48 | 0,01 |

Regional dietary characteristics

By listing all items contributing at least 3% in bulk to the total diet, the diet of bushpigs may be characterized for the two regions, as follows:

Southern Cape

PTD

| | |
|---|-------------|
| Hypogeous fungal bodies of <i>Rhizopogon</i> | 14,3 |
| Bracken rhizomes (<i>Pteridium aquilinum</i>) | 14,1 |
| <i>Blechnum punctulatum</i> fronds | 9,9 |
| Cyperaceae foliage | 6,5 |
| Vertebrate and invertebrate animal matter | 6,4 |
| <i>Chlorophytum comosum</i> foliage | 5,3 |
| <i>Podocarpus falcatus</i> fruit | 4,2 |
| Arum lily tubers (<i>Zantedeschia aethiopica</i>) | <u>3,4</u> |
| | <u>64,1</u> |

Eastern Cape

PTD

| | |
|--|-------------|
| <i>Rhoicissus</i> tubers | 26,6 |
| <i>Cyphostemma</i> tubers | 11,3 |
| Vertebrate animal matter | 9,3 |
| <i>Aloe ciliaris</i> foliage | 9,1 |
| <i>Opuntia</i> fruit | 5,2 |
| Mesem foliage (Aizoaceae) | 5,2 |
| Foliage of agricultural legumes | 4,8 |
| Graminoid foliage (mainly winter oats) | <u>4,6</u> |
| | <u>76,1</u> |

8.1.2.3 Man-introduced food items

These include those food items associated with agriculture or exotic species introduced for non-agricultural purposes. In some cases they are problem plants due to their invasive capacity. The data available is not regionally comparable and does not give an unbiased picture of the real importance, or lack thereof, of these anthropogenic food items. It was not always known whether bushpig which were culled had access to agricultural food sources. Interpretation was further complicated by the fact that a variable, but not precisely determinable, proportion of hunts were undertaken in response to depredation problems on agricultural crops or alleged predation on small stock. Stomach samples from such animals are unlikely to give a representative picture of the overall regional diet.

Stomach content analyses presented above (8.1.2.1; 8.1.2.2) excluded samples which on inspection were clearly dominated by agricultural food. However, these food items were recorded. In the Southern Cape, 60 bushpigs were shot in potentially depredation-induced hunts, 49 in the plateau zone and 11 in the Langkloof. The ingesta of 18 of these animals (30%) were dominated by agricultural foods, including maize (*Zea mays*), wheat (*Triticum aestivum*), lucerne (*Medicago sativa*), fresh growth of corn (*Zea mays*) and apple (*Malus pumila*). Acorns (*Quercus robur*) were also taken where and when available.

In the 56 stomach samples from the Eastern Cape which were analysed (8.1.2.1, 8.1.2.2), *Opuntia* fruit, pineapple, agricultural legumes and graminoids and carrion from small stock amounted to 19,6% of the diet (8.1.2.2). The ingesta of another 15 animals were dominated by maize (n = 4), lucerne (n = 3), pineapple (n = 3), small stock carrion (n = 3), wheat (n = 1) and sweet potato (n = 1). Thus in the total of 71 samples from the Eastern Cape, non-natural food items contributed approximately 38%, by volume. This estimate should however, only be taken as representative of those bushpig populations hunted. There was a bias towards hunting in areas where problems of bushpig damage to agricultural crops were probably particularly pronounced.

8.1.3 Discussion

8.1.3.1 Interspecific comparisons

The only local study on bushpig feeding is that of Phillips (1926a). Most of the food items listed by Phillips (1926a) were however not verified by this study. Other records of bushpig diets include those of Thomas and Kolbe (1942), Maberly (1967), Breytenbach and Skinner (1982), Jones (1984) and Melton, Cooper and Whittington (1989). The main conclusions on the nature of bushpig diets were confirmed during the present study. Bushpigs are omnivorous generalists, feeding opportunistically but primarily on subterranean plant organs and above-ground herbaceous plant material. Forage selection appears to be a function of availability and phenology of the vegetation. The only other well-studied omnivorous suid species, the European wild boar (Briedermann 1986) also shows great spatiotemporal plasticity in its diet. The main forage classes correspond to those of the bushpig. The diets of these two omnivorous suids are compared below.

In the diets of European wild boars the mean animal fraction varied between about 1% and 10% by volume (Haber 1966 ex Briedermann 1986: 6,2%; Briedermann 1968, 1976: 4 - 5%; Henry and Conley 1972: 6,4%; Kozlo 1975 ex Briedermann 1986: 1,5% in spring - 8% in winter; Groot-Bruinderink 1977: 7%, Schnorrenberg 1979: 9%; Genov 1981: 9%; Howe *et al.* 1981: 2%). Although volumes are small, animal matter is considered to be of great nutritional significance as a source of high quality

protein (Schnorrenberg 1979, Genov 1981). The animal fraction in the bushpig diet is of similar magnitude to that reported for the European wild boar. It appears to be an opportunistic dietary item, its intake being limited by availability, and consisting of a wide variety of invertebrate and vertebrate species. The high intake of animal matter by bushpig females suggests it to be of importance in terms of sufficient quantities of high quality protein for reproduction. More high quality animal protein is apparently available to the bushpigs of the Eastern Cape compared with the Southern Cape (Table 8/1). Small stock farming in the Valley Bushveld of the Eastern Cape is partly involved but wild mammalian vertebrates are also considered more abundant in the Eastern Cape (2.5). Flesh is generally obtained by bushpigs through scavenging, but allegations of small stock predation under certain circumstances are made locally in the Eastern Cape.

A consistent seasonal pattern is evident in the diet of the European wild boar and feral pigs. Herbage, i.e. growing green above-ground plant material, is primarily taken during spring and early summer, or during the wet season depending on the climatic regime. Subterranean food items are typically utilized during autumn and winter (Sludskii 1956, Briedermann 1968, Eisenberg and Lockhart 1972, Kozlo 1975 ex Briedermann 1986, Scott and Pelton 1975, Genov 1981, Baber and Coblentz 1987). Acorns (*Quercus* spp) and beech nuts (*Fagus* spp.) are preferred and important food items over much of the area inhabited by European wild boars (Schnorrenberg 1979, Briedermann 1986). After good fruiting years this source of food is available almost throughout the year (Groot-Bruiderink 1977, Wood and Roark 1980, Briedermann 1986).

In areas where these tree species form 10 - 20% of the forest, a European wild boar population with a pre-farrowing density of 1/100 hectare can be sustained nutritionally from autumn to spring during a mast year (Briedermann 1986). During these years ca 50% of the total volume of food consumed may consist of such fruits (Briedermann 1986). The long-term means of the fruit fraction in bushpig diets were 10,5% in the Eastern Cape and 15,1% in the Southern Cape. Prickly pear (*Opuntia* sp) fruit was taken in the Eastern Cape, as it is by other suids (cf Baber and Coblentz 1987) and peccaries (*Tayassu tajacu*) in arid parts of the world (Low 1970).

Herbage consumption by bushpigs is also related to periods of increased plant growth. In the Southern Cape the spring and autumn peaks coincide with rainfall peaks and sufficiently high ambient temperatures for growth. This is clearly shown by *Blechnum punctulatum* fronds, in accordance with their growth cycle (cf Milton 1987). No seasonal trend in herbage consumption was evident for Eastern Cape bushpigs. This may be related to opportunistic plant growth in the region, where winter temperatures are high enough for growth whenever sufficient moisture is available (2.4.2.5). Quantitatively, the herbage fraction appears to be of greater importance in the bushpig and other suids in subtropical and tropical areas (cf Eisenberg and Lockhart 1972, Giffin 1974) than for suids in temperate regions with access to mast fruiting or agricultural crops (cf Genov 1981, Briedermann 1986). For example in the mountain pasture habitat of Mauna Kea (Hawaii), grasses made up the major portion of the food in the diet of the feral pig (*Sus scrofa*). These grasses did not however appear to be sufficient as a maintenance diet when eaten exclusively (Giffin 1974). In the rain forest habitat of Hawaii, tree fern (*Cibotium* sp) was the most important food species throughout the year. Pigs broke open the trunks of this fern to obtain the starchy interior (Giffin 1974). Similar foraging behaviour was observed on only one occasion in the present study when bushpigs attempted to feed on tree fern heart (*Alsophila capensis*) in the Southern Cape forests. In the rain forests of Hawaii, the pigs appear to subsist entirely on tree fern heart, earthworms, sedges or grass and fern fronds (Giffin 1974).

Subterranean plant material is of greatest importance in the diet of bushpigs during winter, but also in autumn and spring (Thomas and Kolbe 1942, Breytenbach and Skinner 1982, this study). In the Southern Cape, the subterranean fraction predominates in winter and spring, mainly because of the consumption of bracken (*Pteridium aquilinum*). The seasonal pattern of bracken rhizome consumption is believed to be due to its high food value during the dormant season and because of the limited availability of alternative food items. Bracken is one of the most widely distributed vascular plants (Page 1976) and its rhizomes are consumed by suids all over the world (e.g. Thomas and Kolbe 1942, Briedermann 1968, 1976, 1986, Giffin 1974, Groot-Bruiderink 1977). For the European wild boar in Europe, subterranean plant items such as tubers, rhizomes and roots in general and bracken rhizomes in

particular, are considered to constitute winter subsistence food only, gaining increased importance when mast fruits or agricultural foods, like potatoes, are not available (Briedermann 1986). Subterranean plant food items are generally of greater importance in natural environments (cf Kozlo 1975 ex Briedermann 1986). For the bushpigs of the Eastern Cape, their importance is highest in autumn and lowest during the summer, presumably reflecting the availability of superior alternative foods.

European wild boar in Sri Lanka are reported to feed extensively on subterranean fungi (Eisenberg and Lockhart 1972). Hypogeous fungi (*Rhizopogon* sp.), forming 14,3% of the Southern Cape bushpig diet, was quantitatively the most important dietary item. Epigeous fungi (mushrooms), in contrast, were only a minor component in the diet of bushpigs and other suids (Briedermann 1976, 1986, Wood and Roark 1980). Hypogeous fungi are generally preferred to epigeous fungi by mammals; differential palatability or nutritional value may be involved in determining this preference (Maser, Trappe and Nussbaum 1978).

Fruits of mast fruiting tree species and cultivated plants form the basic food of European wild boar all over Europe (cf Genov 1981, Briedermann 1986). In addition to a strong seasonal element, the food resource is characterized by longer term irregular interannual periods of superabundance. The diet of bushpigs most closely resembles that of omnivorous suids in subtropical and tropical regions (cf Eisenberg and Lockhart 1972, Giffin 1974). Seasonal changes of diet, the importance of fruits and the contribution of agricultural crops, are less pronounced than in the European wild boar of temperate regions. The variability in the diet of omnivorous suids is indicative of a marked dietary plasticity and adaptability to the food resources available and underlies their widespread distribution (cf Briedermann 1986).

8.1.3.2 Diet selection

A diet must provide the essential nutrient fractions (e.g. proteins, carbohydrates and minerals). The economic availability of nutrients depends on the concentration of the food items in space and time and on their nutrient content. The nutrients must be sufficiently concentrated

and available, i.e. palatable and digestible. The nature of food resources are fully discussed in section 8.2, while nutrient content and digestibility are dealt with in section 8.3.

(a) Subterranean foods

Subterranean plant organs form the largest forage class (Fig. 8/1) and the staple source of carbohydrates (8.3.3.2: Table 8/7, 8.3.3.6) in the diets of bushpigs. Bracken rhizomes were the main components of this class in the Southern Cape and tubers of Vitaceae (*Rhoicissus tridentata/digitata*; *Cyphostemma* spp.) in the Eastern Cape. These items were available in superabundance, but their digestibilities are apparently reduced by high tannin contents (8.3.3.5c). High tannin stomach digesta were invariably dominated by tubers and fruit of the Vitaceae, *Oxalis* corms, bracken rhizomes or fronds of *Blechnum capense*.

Tubers, and often also rhizomes, represent large stores of high quality food, which are defended by deep underground location or secondary compounds (Janzen 1978). The underground plant parts of many Eastern Cape species listed as edible by Fox and Young (1982) or Palmer and Pitman (1972), were not found in the diet of bushpigs. These include the underground storage organs or roots of species such as *Cussonia* spp, *Fockea edulis*, *Vigna vexillata*, *Pelargonium rapaceum* *Moraea tripetala* and *Crassula ovata*. Many others not listed as edible, but with "starchy" underground structures occurred: tubers of Cucurbitaceae (*Kedrostis*, *Zehneria* and others), *Pachypodium succulentum* *Sansevieria*, *Mestoklema tuberosum*, *Strelitzia juncea* and *Dioscorea* spp. None of these species were taken by bushpigs to any appreciable degree. The tubers of *Fockea edulis* are dug out and consumed by Africans, but are inaccessible for bushpigs due to their deep underground position (Plate 11c). *Mestoklema tuberosum* tubers contain an alkaloid, *Kedrostis nana* hydrocyanic acid and the tubers of the wild forms of *Dioscorea* are poisonous due to the alkaloid dioscorine or dihydrodioscorine (Watt and Breyer-Brandwijk 1962). The tubers of *Rhoicissus*, although consumed extensively by bushpigs according to this study and also in Zululand (Kingdon 1979) are considered poisonous (Watt and Breyer-Brandwijk 1962). They are however reported as edible by Palmer and Pitman (1972). Their classification as "poisonous" probably originated from their high

tannin content mentioned by Watt and Breyer-Brandwijk (1962) and found in this study. The tannin levels therefore presumably result in an otherwise superabundant source of carbohydrates serving only as an item in a subsistence diet.

In the Southern Cape the diversity and prevalence of plant species with underground storage organs is much lower than in the Eastern Cape. Bracken (*Pteridium aquilinum*) rhizome material is the bulk carbohydrate subsistence diet. Its starch reserves are replenished by photosynthesis and later by mobilization of carbohydrates when fronds senesce (Fletcher and Kirkwood 1979). Rhizome carbohydrate content decreases from spring to early summer, followed by an increase which continues until the fronds die in winter. The lowest carbohydrate levels are thus found in early summer (Williams and Foley 1976). This also explains the seasonal pattern in bracken rhizome consumption by bushpigs (Fig. 8/2: 8.1.2.2). Apart from starch, bracken rhizomes contain large amounts of tannin and indigestible fibre (Ewart 1909 *op. cit.* Watt and Breyer-Brandwijk 1962) which reduces their value as food items. High tannin levels were also found in this study. The chemical defence of such abundant and easily accessible food concentrates is in accordance with antiherbivore defence theory (8.2.3).

The rhizomes of other ferns, notably those of *Rumohra adianthiformis* were not taken by bushpig; presumably due to effective toxic deterrents. In contrast, agricultural tubers (e.g. potatoes) are largely devoid of digestibility-reducing or toxic secondary compounds, accounting for the attraction of such food items for the bushpig.

(b) Herbage

Herbage in the diets of bushpigs consisted largely of *Blechnum punctulatum* fronds, Cyperaceae and *Chlorophytum comosum* foliage in the Southern Cape and *Aloe ciliaris*, Aizoaceae and agricultural legumes and graminoids in the Eastern Cape. Stomach contents dominated by herbage are characterized by relatively low tannin levels (data inspection of analyses in section 8.3.3.5c). This fits the general pattern that tannins are much more prevalent in woody dicot leaves than grass leaves (Cates and Rhoades 1977). Monocotyledons have no hydrolyzable tannins

and relatively few have condensed tannins (Swain 1979). It appears that plant secondary compound levels largely limit the selection of herbage items to certain ferns, monocotyledons, agricultural greenery and annual forbs (8.1.2.2).

Herbage food items serve, *inter alia*, as a source of protein (8.3.3.2: Table 8/7), especially during periods of active plant growth (8.1.2.2; 8.1.3.1).

(c) Fruit and seeds

Fruit and seed material plays a relatively small role in the total bushpig diet (8.1.2). This may be ascribed to its erratic availability in space and time and structural or chemical antiherbivore defences (cf Janzen 1978b). Seeds are nutrient-rich (Janzen 1978b), some have high carbohydrate contents, others fats or proteins.

Podocarpus falcatus endosperms are particularly rich in fat (8.3.3.2; Table 8/7). The seed of *Olea capensis* ssp. *macrocarpa* is reported to contain oils and proteins (Phillips 1928). When available during fruiting years, the fleshy pericarps of the drupes of *Olea capensis* ssp. *macrocarpa* and the fleshy swollen receptacles of *Podocarpus latifolius* seed provide an abundant source of carbohydrates. *Podocarpus falcatus* trees are comparatively rare (± 3 stems/ha in the Knysna forests) and good fruiting years of all three species may occur only every second to fourth years (Phillips 1928, 1931). During fruiting years, fruit material of *Olea capensis* ssp. *macrocarpa* (53 stems/ha) and of *Podocarpus latifolius* (34 stems/ha) is available in superabundance. Whilst still juicy, it is swallowed, rather than chewed, resulting in high ingestion rates (cf Rogers 1987). The seeds then remain uncrushed.

Podocarpus latifolius seed samples were analysed and 29 dichloromethane-extractable compounds identified (Prof V. Pretorius, Institute for Chromatography, University of Pretoria). The main constituents included caryophyllene, pinene, muurolene, humilene, linonene, copaene and cadinene. Such terpenoid substances are found in the seed oils of many plant species (Seigler 1979) and terpenes are commonly involved as deterrents to seed-eating (Janzen 1978). Swallowing *Podocarpus*

PLATE 10

- a. Ironwood, *Olea capensis* subsp. *macrocarpa*, seedlings from bushpig droppings.
- b. Yellowwood, *Podocarpus latifolius*, fleshy, swollen receptacle (2) and seed (1) (Photograph by C.J. Geldenhuys).
- c. Kalander, *Podocarpus falcatus*: sclerotesta (1), endosperm (2) and epimatium (3) (Photograph by C.J. Geldenhuys).
- d. Yellowwood seeds, *Podocarpus latifolius*, in bushpig droppings (two germinated seeds marked with arrows).

a



b



c



d



latifolius fruit instead of chewing it also minimizes the exposure of the digestive tract to seed terpenes (Plate 10b). The outer fleshy layer of the seed shell, the epimatium, of *Podocarpus falcatus* seeds is also very resinous and presumably contains terpenes similar to those in *Podocarpus latifolius* (Plate 10c, page 406). Only *Podocarpus falcatus* seeds devoid of the epimatium were ingested by bushpigs. Whereas vervet monkeys (*Cercopithecus pygerythrus*) and baboons (*Papio ursinus*) apparently peel off the epimatium (Geldenhuys 1975), the bushpig has to rely on it being removed by other animals or by decay, before fruits are ingested.

When the outer fleshy part of *Olea capensis* ssp. *macrocarpa* fruit has dried or decayed away, the seeds are chewed and crushed, giving access to the nutrient rich endosperm. During the initial phase, when the outer fleshy part of the fruit is still attached, the fruit is swallowed. The seeds may then pass through the digestive tract intact and germinate from faecal pellet groups (Plate 10a, page 406).

(d) Animal matter and fungi

Animal material provides sources of highly digestible protein, animal fat and certain vitamins (Briedermann 1986). Invertebrates often have high fat contents (8.3.3.2: Table 8/7). Considerably more vertebrate animal matter appears to be available to bushpigs in the Eastern than in the Southern Cape (8.1.2.1). This is presumably related to the higher soil nutrient status in the Eastern Cape, resulting in higher vertebrate population densities and turnover (2.2.3.2; 2.5).

Hypogeous fungi often contain high concentrations of nitrogenous compounds, vitamins and minerals (Cork and Kenagy 1989). The hypogeous fungus *Rhizopogon* is a major dietary item of bushpigs in the Southern Cape. It has a relatively high crude protein content (8.3.3.2: Table 8/7). However, the actual level of available protein is uncertain. Although the sporocarps have high concentrations of nitrogen, a large proportion of this nitrogen may be in the indigestible spores and the relatively indigestible cell walls of the peridium (cf Cork and Kenagy 1989).

It may be concluded that bushpig food items are either relatively abundant and of lower nutritional value or of higher nutritional value, but scarce. Very seldom are high quality foods abundant.

8.2 Foraging and the nature of food resources

8.2.1 Foraging style and patterns

Bushpigs obtain the largest proportion of their food requirements from the ground surface and upper subsurface layer, i.e. the litter layer to about 5 cm into the soil or humus layer. The associated foraging behaviour is called superficial rooting and also termed "ploughing". The subterranean food items are unearthed by lifting the snout forward and upward through the earth or litter layer. The protruding nose is placed over the morsel which can only then be ingested into the inferiorly situated mouth. Food items are then picked up with the aid of the lower incisors, lips and tongue. Olfaction plays a prominent role in locating of food.

In moist or loose earth the snout may be worked well into the soil in pursuit of deeper subterranean food items (deep rooting). To do this, the nose may be used in a spade-like fashion, whilst the body is held stiff and moved back and forth to create the necessary digging forces. If the soil is tractable, food items are frequently excavated from as deep as 30-40 cm below ground surface. Unlike the warthog, the major digging forces in the bushpig act not on the point of the snout, through the rhinarium, but chiefly on and through the bridge of the snout, proximal to the rhinarium (cf Cumming 1975). As Ewer (1958a) pointed out, this region of the bushpig snout shows evidence of strengthening by the horizontal nasals and vertically placed maxillae, which abut onto a strengthened palatal maxillary region. When digging deep and encountering resistance, European wild boar may kneel down onto their carpal joints (Briedermann 1986). Such behaviour was not observed during digging in the bushpig, but the presence of carpal callosities, or at least carpal pads devoid of hair, suggests that it may occur. Kneeling during stationary feeding was observed in the enclosure (Plate 11b).

In addition to superficial and deep rooting, a third foraging technique employed by the bushpig may be termed "grazing". While grazing, bushpigs typically hold their heads low and nip at the vegetation with short lateral movements of the head. Grass tufts are sometimes "nosed" out of their positions and ingested entirely. Reminiscent of similar behaviour in the dog, larger food items from which bits are bitten off, may be held down with the fore-foot. As a true omnivore, the foraging style of the bushpig is generally very similar to that of *Sus* (Hennig, 1981, Krosniunas 1985, Briedermann 1986). In accordance with their omnivorous habits and dispersed food resources, bushpigs and European wild boars tend to move continuously while foraging, stopping only when a clump of food is discovered.

When foraging in a group, bushpigs tend to be spaced out in a variably extended formation. Potential costs of group foraging may result from competition and may be related to status. Benefits may be an increased probability of finding food patches. Stomach fill masses of males were higher than those of females ($t = 2,367$ $df = 112$ $P < 0,05$: 8.3.3.6), perhaps as a result of male dominance (5.2.2.1). Under normal circumstances, subordinate individuals were not excluded from feeding sites, but under certain competitive situations, subordinates had restricted access to food. Krosniunas (1985) in her study on feral pigs observed that in extreme cases, provisioned food or other rich food sites were dominated by adult males who prevented other group members from approaching. Her results indicated that differences in relative individual foraging success within a pig group were related to rank, but the extent of competitive inequalities among individuals was related to patch characteristics, such as the amount and distribution of food.

Local enhancement is a process by which an animal's attention is directed to a particular object or particular part of the environment (Thorpe 1963 ex Krosniunas 1985). As observed in the study by Krosniunas (1985), the discovery of a buried food site by a pig resulted in the rapid attraction of one or more pigs through fine-grained local enhancement. Facilitation of food-finding may be an important benefit of group foraging in pigs, by reducing the search time associated with obtaining patchy foods. Field studies of two species of peccaries *Tayassu tajacu* (Byers and Bekoff 1981) and *Tayassu pecari* (Kiltie and

PLATE 11

- a. Bushpig rootings for bracken rhizomes (*Pteridium aquilinum*).
- b. Kneeling during feeding (Enclosure A: Goudveld).
- c. *Fockea edulis* tuber, showing its inaccessible underground position; Eastern Cape (Photograph: E. van Jaarsveld).

a



b



c



Terborgh 1983) suggest that local enhancement may also occur in these social species (cf Krosniunas 1985). In her experiments, one of the potential cues leading to local enhancement was believed to have been changes in movement that accompanied the discovery of a buried food site. Reduction or cessation of movement could signal other pigs that a rich food site had been located. Due to the typically dispersed and patchy distribution of bushpig food items (8.2.5), searching is an important element of feeding. When food is encountered it usually means the presence of more in the immediate vicinity. Under such conditions it is plausible that group foraging in extended formation enhances food finding by increasing the probability of food patch detection.

Krosniunas (1985) indicated that food patch characteristics may be important in determining both the extent of competitive differences among group members and pig group sizes. An increase in food abundance resulted in an increase in observed group size. Similar factors may underly the trend of peccary herd size to fragment more readily in tropical forest (greater degree of food dispersion) than temperate latitudes (Robinson and Eisenberg 1985), as well as pair or group splitting in response to changing food abundance and distribution in the bushpig (4.3.1.3; cf Ghiglieri *et al.* 1982).

8.2.2 The bushpig niche

With its bunodont dentition and monogastric digestive system, the bushpig is adapted to an omnivorous diet of food items with high caloric content and nutrient density. This consists primarily of reproductive tissues (seed, fruit) and energy storage organs (tubers, rhizomes) and, to a lesser extent, actively growing soft herbaceous plant tissues. Animal matter is ingested opportunistically. The digging capabilities of the bushpig extend the area from which food may be procured up to 0,5 m below ground level. Its feeding stratum may therefore be taken as $\pm 0,5$ m above and below the ground surface.

In bushpig habitat suitable dietary items must be available uninterruptedly within the feeding stratum. The major plant growth form assemblages (biomes) within its geographic range are shrublands (fynbos, steppe vegetation), savanna/grasslands and forest (including forest

formations from rainforest to xeric scrub forest). Only in forests are suitable food items more or less continuously available. In mature fynbos, whatever suitable food items which may occur, are inaccessible due to the dense and sclerophyllous nature of the vegetation. Arid shrublands provide only inadequate food resources for most of the time. Not being adapted to grazing, grass-dominated vegetation types, such as woodland, savanna and grasslands, cannot provide sufficient food resources throughout the year. In these vegetation types grasses also tend to competitively exclude other plant growth forms which might have contributed to forage in the feeding stratum. Thus, from a food resource perspective, suitable bushpig habitat may be taken to coincide with forest plant formations.

Tinley (1982) has outlined the edaphoclimatic basis of the distribution of forest versus savanna/grasslands. The overwhelmingly important factor was soil moisture balance, which is a function of factors such as soil texture and consistency, presence or absence of a pan horizon, distance of this horizon from the surface, macro- and microrelief and salinity. In montane situations, with high orographic rainfall, grasslands occur on soils with an impervious or poor subsoil drainage, while forest occurs on free draining or relatively porous soils, but of sufficient depth for a favourable soil moisture balance. The soil under grassland is waterlogged when rains occur and dries out excessively during dry periods. Savannas are typically on soils with seasonally extreme moisture conditions (Tinley 1982). In summary, the edaphic control of the distribution of these ecosystems is through soil moisture balance with forest occurring on high water-retaining, but relatively well-drained sites, and grassland and savanna on both gley soils or deep horizonless sands which result in similar seasonal extremes of moisture availability (Tinley 1982).

The controlling interrelationships described above relate to the summer rainfall regions. The graminoid growth form, especially C_4 -grasses, appears to be competitive only under conditions of sufficient soil nutrients in the growing season, i.e. summer rainfall (cf Bond 1981, Cowling 1983). In nutrient-poor environments with a winter or non-seasonal rainfall regime, forest is replaced by fynbos on sites with seasonal moisture stress, although the actual boundary between the two

biomes may also have been shaped by fire history (cf Geldenhuys 1989). The absence of a seasonally pronounced or predictable period of moisture stress favours forest, from tropical rainforest to xeric scrub forest (Valley Bushveld), depending on the degree of moisture availability.

The distinguishing edaphoclimatic feature of bushpig habitat, be it forest, riverine or xeric scrub forest, is the lack of pronounced seasonality in terms of moisture stress. Bushpig habitat is thus essentially non-seasonal in terms of overall food resource availability; i.e. relatively stable compared to the food availability for savanna grazing herbivores.

8.2.3 Plant survival and herbivore food resources

The main thesis presented in this section is how the nature of herbivore food resources in terms of quality, dispersion and predictability is determined by plant survival strategies. Central to plant survival is the reduction of plant tissue availability to herbivores through the defensive effect of a variety of secondary compounds. These include the terpenoids (Mabry and Gill 1979), alkaloids (Robinson 1979), saponins (Applebaum and Birk 1979), proteinase inhibitors (Ryan 1979) and phenolic compounds, such as tannin and lignin (Swain 1979).

The ruminant digestive system appears to be more effective in the detoxification of plant toxins than others (Freeland and Janzen 1974). For non-ruminant herbivores any plant defensive substances may thus have even greater implications. Herbivores specializing in particular plant tissues may be equally affected, since plant defensive substances may occur in any type of plant tissue. For example, underground plant organs often contain the same secondary compounds as are found in the above-ground portions of the plant, sometimes even in higher concentrations (McKey 1979).

Rhoades (1979) formulated two fundamental postulates of optimal defense theory:

- (I) Organisms evolve and allocate defenses in the way that maximizes individual inclusive fitness.

- (II) Defenses are costly to organisms in terms of fitness. The less well defended individuals therefore have higher fitness than more highly defended individuals when enemies are absent.

Postulate I is more an axiom than an hypothesis, which can only be tested indirectly. Rhoades (1979) provides and discusses evidence for hypotheses stemming from postulate II. The main determinant of the fitness cost of plant defense is believed to be the metabolic cost of synthesis and storage of defensive compounds. Energy (in ATP) thus diverted must be subtracted from that available to the plant for *i.a.* the production of new nutrient-capturing tissues and reproduction (Rhoades 1979).

Loss of plant tissue to herbivores results in loss of fitness. The defence costs of preventing such loss similarly results in loss of fitness due to reduced resource availability for growth (here taken to include both somatic growth and propagule production) and thus interplant competitive ability. Environmental factors (e.g. soil nutrients, climate) determine the optimal allocation of resources in this trade-off between defence and growth. Environmental factors modify the nature of and the degree to which the selective pressures (plant predatory biotic agencies) act on the vegetation in two ways:

- (I) By influencing the degree of susceptibility of the vegetation to herbivory.
- (II) By influencing the conditions for the biotic agencies responsible for the selective pressure, and thus the level of predatory pressure acting on the plants.

In a habitat that has extremely low primary productivity, yet a climate favourable to herbivores year round, there should be very strong selection for plants that invest heavily in chemical defenses (Janzen 1974).

According to the model of Coley (1983) habitat quality is a major selective force behind the evolution of different defensive systems. High quality habitats are defined as environments in which rapid growth is possible, in low quality ones growth is limited by some abiotic

factors (light, nutrients). Following from the apparent trade-off between growth and defense, poorly defended species should be favoured when habitat quality and growth potential are high relative to herbivory (Bryant *et al.* 1983, Coley *et al.* 1985). Under such conditions it would be possible for undefended species to tolerate herbivory if the reduction in growth (productivity) due to losses was less than the alternative costs of defense. For example, in the absence of herbivory, the palatable morph of *Asarum caudatum* that lacked the chemical deterrent had higher growth rates and produced more seeds than did the unpalatable morph (Cates 1975 *ex* McKey 1979). Low defense levels are only possible if herbivore populations do not increase indefinitely in response to food availability, but are partially limited by other factors. In habitats with low growth potential or high herbivory, the relative losses to herbivory are potentially greater and well-defended species would be at a competitive advantage (Coley 1983, Coley *et al.* 1985). In summary, where and when rapid tissue accumulation (somatic growth or propagule production) is possible, it is competitively superior to invest in it rather than in defense. The "where" and "when" is a function of resource availability in space (habitat quality) and time (seasonality).

In order to survive, plants or plant parts must either evade predation through "escape" in time or space, or invest sufficiently in defence. Escape in time involves being susceptible to herbivory for relatively limited periods only, thus preventing population buildups of herbivores through bottle-necks in food availability. While the plants are available to herbivores, predator satiation applies. Examples of this strategy are fast growing tissues during restricted growing periods, annuals, deciduousity or mast fruiting. The plant tissues involved are typically poorly defended chemically and otherwise (Rhoades 1979). This strategy is particularly prevalent in strongly seasonal environments (e.g. growth flushes in spring of temperate regions or grasses in the savanna). The outcome, in terms of herbivore food availability, is a spatially concentrated superabundance of food over a limited time span or at infrequent intervals (mast fruiting).

Escape in space for plants means being "rare" or occupying protected sites (e.g. bulbs in rock crevices). For herbivores harvest

profitability is low either because of the difficulty of finding the plants or because of obstructions to harvesting. Plant structures to which this strategy applies are similarly poorly defended chemically and therefore comparatively palatable when "found" by herbivores. Escape in space only works against generalist herbivores; i.e. those that would lose their generalist versatility when specializing in host-finding adaptations. Effective host-finding specialisation could then nullify the advantage of being "rare". Specialisation by herbivore predators may however overcome any form of defense, resulting in dynamic adaption and counteradaptation. Plant structures which are not "rare" in space or time must of necessity reduce their palatability (nutrient availability) through structural (thorns, sclerophylly) or chemical defences. All three major strategies, i.e. escape in time, space or defence essentially function by reducing harvesting profitability for predators, resulting in reduced predation pressure per unit of plant tissue.

Plant defense substances may be grouped into two major categories based on their general mode of action against herbivores:

- (a) Extremely toxic substances which act on the metabolic processes of the herbivore, thereby reducing its fitness (Rhoades and Cates 1976). These substances form "qualitative" barriers to herbivores (Feeny 1976). These include most of the alkaloids, the cyanogenic glycosides, glucosinolates and some terpenoids.
- (b) Digestibility-reducing substances act by reducing the availability of plant nutrients to herbivores by complex-binding. These substances, acting as "quantitative" (dosage-dependent) barriers to herbivores, include many phenolics (mainly tannins) and some terpenoids (Feeny 1976). There are two types of plant protein digestibility-reducing substances. The first type, which include the hydrolyzable and condensed tannins, are generalized protein complex agents. They disrupt digestion by reducing the availability of substrate peptide groups to the digestive enzymes and possibly by complexing with the enzyme itself. The second class of digestibility-reducing substances are specific inhibitors of proteolytic enzymes (Rhoades and Cates 1976). Not only the availability of plant protein, but also of starch (plant

polysaccharides) may be reduced by enzyme and substrate complex formation (cf Feeny 1970).

Under conditions where high levels of past or present predation pressure are possible, chemical defense may be expected to be particularly common. This expectation is borne out by observations. In the tropics the absence of winters which could control herbivore numbers, suggests that they should have a higher predation potential. Janzen (1975) regards this as the reason for the higher levels of chemical plant defense encountered in the tropics. Also, under conditions where the loss of tissue represents a severe energy loss, such as for vegetation on low productivity sites, adequate chemical protection is adaptive. This is borne out by the prevalence of high levels of chemical defense on low productivity sites, such as tropical white sand soils and swamp or montane forests (Janzen 1974 and 1975). The vegetation of dystrophic environments in Africa exhibits a higher level of chemical defense in both forest and savanna (Tinley 1977, McKey et al. 1978, Owen-Smith and Cooper 1987). A summary of the relationships discussed above is presented in Table 8/2.

| TABLE 8/2: RELATIVE PREDOMINANCE OR LEVEL OF CHEMICAL DEFENSE | | |
|---|------------------|-----------------|
| ATTRIBUTE | LOW | HIGH |
| Tissue maturity | Immature | Mature |
| Tissue Permanence | Deciduous | Evergreen |
| Life span | Annuals | Perennials |
| Seral stage | Early succession | Late succession |
| Plant abundance | Rare | Common |
| Seasonality | Pronounced | Weak |
| Productivity | High | Low |

Food items acceptable to the bushpig have a relatively high caloric and nutrient density. From the foregoing discussion it is clear that such items must of necessity be rare in time and space in a non-seasonal environment. In the absence of pronounced seasonality which would lead to regular pulses of food availability, food shortages or surpluses are largely unpredictable. Bushpig food resources are therefore typically dispersed and unpredictable, but relatively stable (8.2.5).

8.2.4 Regional differences in habitat quality

Suitable habitat for bushpig in the Cape Province extends over two particularly divergent environments. In the Southern Cape most of it occurs in relatively mesic Afromontane forest growing on acid, nutrient-poor soils. In the Eastern Cape bushpig are found primarily in relatively xeric thicket (2.4: Valley Bushveld), growing on base-rich soils.

Southern Cape forest soils are derived from Table Mountain Sandstone (2.2.2). These "white sand soils" are nutrient-poor due to the geological base material as well as to nutrient leaching (cf Janzen 1974 and 1975). Nitrogen, phosphorus and potassium levels are on the whole lower than those of other tropical forests (Van Daalen 1984). The soils also have a low cation exchange capacity (6,8 me%) and especially high carbon/phosphorus ratios, implying poor nutritional status (Van Daalen 1984). Foliar nutrient analyses of several tree species reflect the low soil nutrient status, especially that of phosphorus (Koen 1984). Evergreenness and sclerophylly predominate under such conditions. Loveless (1961 and 1962 ex Van Daalen 1984) regarded the sclerophyllous leaf as the expression of a metabolism found in plants that can tolerate low levels of phosphate. Due to the limitations on the rate of nutrient assimilation in such areas, a loss of even small amounts of plant tissue results in nutrient losses that are greater than the cost of chemical defence substances. This may explain not only why evergreen trees and sclerophylly predominate under such conditions, but also why the vegetation contains high levels of secondary compounds, primarily phenolics (tannins). According to a pilot study conducted on Knysna forest tree and shrub foliage, an average total phenol content of 44,3 mg/g leaf material (dry weight) was determined (n = 18, range: 6,3 - 95,4; data from Seydack and Glyphis 1980 and Koen, pers. comm.). The high tannin concentration of the white sand soil vegetation is reflected by so-called "black-water rivers", also found in the Southern Cape.

With respect to the Eastern Cape, the soil variables S (cation exchange capacity), available calcium and phosphorus and total nitrogen were significantly positively correlated with the incidence of taxa of Tongaland-Pondoland origin (prevalent in the Valley Bushveld). The pH

values of soils from Valley Bushveld sampling sites were consistently and significantly higher than those from Afromontane forest sites, indicating higher nutrient availability (Cowling 1982). The average cation exchange capacity of sites sampled in the Valley Bushveld amounted to 5 - 17,5 me% as opposed to only 6,3 me% for Afromontane forest sites (cf Cowling 1982), clearly indicating a higher soil nutrient status in the first case (refer also to 2.2.3.2). The Valley Bushveld is characterized by a great diversity of growth forms, including leaf and stem succulent shrubs, trees and vines, arborescent rosette succulents, succulent herbs, large and small-leaved sclerophyllous and orthophyllous shrubs, grasses, forbs, annuals and geophytes (Cowling 1982). This is presumably partly associated with the relatively high soil fertility and aridity. The greater development of underground storage organs is presumably an adaptation to water stress (Medina 1983). As discussed for the Southern Cape, there is a general inverse correlation between soil fertility and leaf longevity, i.e. between poor soils and evergreenness (Cowling 1982). This suggests a low potential for renewal of plant tissue on such sites. As a result of lower photosynthetic rates and larger amounts of structural carbon per leaf (Grime and Hunt 1975) and a higher investment in chemical defense, evergreen plants tend to have a lower maximum growth rate and therefore a lower competitive ability than deciduous plants on fertile soils (Goldberg 1982). Valley Bushveld lacks pronounced seasonality (seasonally unpredictable rains), and Cowling (1982) explained the evergreenness of subtropical thicket in terms of the plants' capacity for opportunistic growth whenever conditions are suitable.

The habitat differences outlined are believed to underly differences in nutrient content and nutrient availability of plant matter obtainable from these environments by herbivores.

Nutrient content and density

On nutrient-poor soils, slower rates of forest regrowth and lower rates of propagule production have been observed (Janzen 1974). In such forests, plants depending on fast growth, like deciduous plants, vines and annuals, are poorly represented (Janzen 1974). These observations

suggest a lower protein productivity of plants on nutrient-poor soils. Also, plants growing on nutrient-poor soils commonly contain less minerals than those on nutrient-rich substrates (cf Janzen 1974). For example, *Crudia amazonica*, a tree common on river-flooded sites in South America, has leaves containing less phosphorus and potassium when flooded by "black water" than when flooded by "white water" rivers (Williams *et al.* 1972 ex Janzen 1974).

These findings agree with the postulates and hypotheses of Bell (1982) regarding the relationships between the quality of plant tissue as food for herbivores and environmental factors. Total plant production is unrelated to herbivore food quality, which is expressed by the ratio of metabolic constituents (M) to structural constituents (C); the M/C ratio (Bell 1982).

Protein production and thus also soluble carbohydrate production appears to be strongly influenced by soil nutrient availability (Bell 1982), as indicated by cation exchange capacity, the pH and the concentration of available phosphorus. Data from Grimsdell and Bell (1974), from the Bangeulu floodplain in Zambia, show a significant relationship between protein production and cation exchange capacity at a series of floodplain sites (Fig. 8/4). There is a strong correlation between protein and phosphorus content of plant matter (Joubert, Stindt and Perold 1969, Waterman *et al.* 1980).

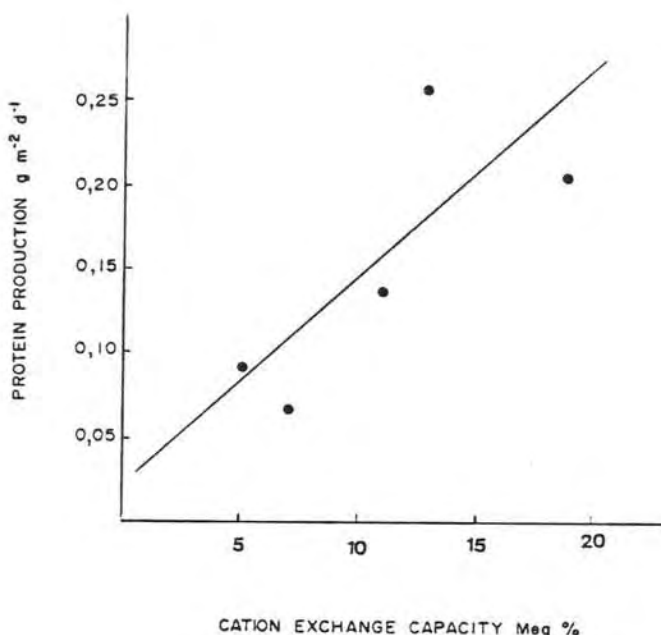
Bell (1982) explains the relationship by pointing out the essential role played in protein construction by several ions that occur in the soil solution, but not in the atmosphere, for example, phosphorus, sulphur and potassium.

Structural carbohydrate production is much less closely dependent on soil nutrient availability, since carbohydrates are largely composed of the airborne nutrients, carbon dioxide and water. As a result of this difference between metabolite and structural production, the food quality of plant material, the M/C ratio, is a function of soil nutrient availability. Furthermore, Bell (1982) suggests that high rainfall and long growing seasons tend to result in a reduction of the M/C ratio. This is in line with data from a number of crop yield tests quoted by

Russell (1962) which indicate that both the relative and total nitrogen production of certain crops may be reduced in relation to increasing water availability.

FIG.8/4: RELATIONSHIP OF PROTEIN PRODUCTION TO SOIL CATION EXCHANGE CAPACITY

(Grimsdell and Bell 1974)



In summary, the total volume and the quality of plant production are dependent upon the balance between the availability of water and that of soil nutrients. Whereas total production is positively related to water availability, quality (M/C ratio) is positively related to soil nutrient availability and may be negatively related to water availability (Bell 1982).

Nutrient availability

According to the hypothesis originally proposed by Janzen (1974), plant communities growing under poor soil nutrient conditions are less able to afford the loss of metabolic tissues to herbivores than those growing

under better conditions. As a result, they make a higher investment in secondary defensive chemicals in order to protect themselves against offtake by herbivores. Davies *et al.* (1964) found that for all 8 tree species examined, leaves of individuals growing on base-poor sites contained higher levels of condensed tannins than did those of individuals from base-rich sites. Subsequent growth experiments showed that nitrogen and phosphorus deficient plants consistently contained higher levels of polyphenols than did the controls. Similarly, Del Moral (1972) and Lehman and Rice (1972 *ex Chew and Rodman* 1979) observed that plants deficient in nitrogen, potassium or phosphorus may produce 10- to 20-fold increases in various phenolic compounds compared to control plants.

For African savanna environments, Owen-Smith and Cooper (1987) report that plants known to have chemical defenses against vertebrate herbivory are prominent on nutrient-deficient soils, while those with structural defenses (thorns) are prominent on fertile soils. Probably the best studied comparison of rainforests is that between the sites at Kibale, Uganda (nutrient rich) and Douala-Edea, Cameroon (nutrient poor) (McKey *et al.* 1978, Waterman *et al.* 1980). The Douala-Edea soils are predominantly sandy with an average pH of 3,92 while the Kibale soils are sandy loams or sandy clays with a pH of 5,92. Ash, percent nitrogen and % phosphorus were significantly higher in foliage of trees from Kibale compared to those of Douala-Edea (12,1 vs 3,7; 2,8 vs 1,7; 0,171 vs 0,086 respectively: McKey *et al.* 1978). Total phenolic content from Douala-Edea was approximately twice that of Kibale (75,7 vs 35,2 mg/g dry plant material: McKey *et al.* 1978). The content of condensed tannins, and to a lesser extent of total phenolics, was found to be negatively correlated with digestibility. The negative correlation was stronger in material from the Cameroon site, where the vegetation contained considerably higher concentrations of tannins and generally was less digestible, than that from the Uganda site (Waterman *et al.* 1980). The lower population density of *Colobus* monkeys at Douala-Edea was attributed to lower food availability due to digestive inhibition by high phenolic levels (McKey *et al.* 1978). Similarly, population densities of capuchin or *Cebus* monkeys, which are frugivore-omnivores inhabiting a wide variety of South American forest types, are significantly lower in "black water" than in "white water" drainages

(Robinson and Redford 1986). These interactions may be summarized by concluding that the metabolic constituents of plant communities growing on nutrient-poor soils are apparently less available to herbivores than those on fertile soils.

On nutrient-rich sites, plant material apparently has a higher nutrient content, which is also less defended, i.e. is more readily available to herbivores. The resource quality is high. High rates of replacement of either vegetative or reproductive tissues are dependent on a sufficiency of resources and are therefore more often maintained in nutrient-rich environments (high resource renewability). Reproductive tissues are particularly affected. The poorer the site, the greater the share of the resource budget which must go into vegetative parts of the plant, and the less is available for propagule production (Janzen 1983). In nutrient-poor environments less, but chemically better protected fruit is produced, or fruiting intervals are longer (cf Janzen 1983). Both herbivore food resource quality and renewability is accordingly expected to be higher in the Eastern than in the Southern Cape.

8.2.5 The nature of food resources

A food item is defined as a discrete "packet" of food ingested as a unit; e.g. a tuber or a mouthful of ironwood fruit. A food patch is a population of suitable food items between which there is an absence of searching and minimal movement (a population of arum lily tubers in a vlei, a patch of ferns, a potato field or yellowwood fruit beneath their mother tree). Food patch size relates directly to the areal extent of the population of food items. If food resources are considered dispersed, it implies relatively low patch size and density. Clumping of food patches implies that they are not distributed randomly in space, but concentrated, irrespective of their density.

Availability of food resources tend to fluctuate over time. Substantial regular (seasonal) or irregular (unpredictable) fluctuations are typical of *i.a.* savanna and deserts. In contrast, tropical rainforests are taken as stable environments with relatively stable overall food resource levels. However, food availability may nevertheless be unpredictable in terms of short-term shortages or surpluses on a

relatively small spatiotemporal scale. Thus, in tropical regions, although food levels may be adequate for maintenance most of the time, they are not necessarily always sufficient for successful reproduction. The term predictability is thus taken to relate more to surplus food resource levels needed for reproduction.

The hunter-grazer distinction (cf Stenseth 1981) is relevant. Food items constitute a large part of the environment of the herbivore. Herbivores may adopt a grazing or a pursuing feeding strategy and the quality of available items is the critical foraging element. The hunter(predator or omnivore) has to adopt a food searching strategy and the quantity of suitable items is critical. Both the quality and quantity of available food items is largely dependent on renewability. For plant material, renewability may be defined as the rate of replacement of organs with assimilative, storage or reproductive functions. It depends on growth and reproductive frequency. As has been explained in the previous section (8.2.4), plant tissue renewability is governed by soil fertility and climate.

Species richness and the associated site dominance by few species is inversely related to soil nutrient availability (Tilman 1982). This implies that food resource concentration (patch size) is potentially lower in nutrient-poor environments.

The nature of food resources may thus be characterised by their dispersion, stability, predictability and renewability (cf 8.2.2, 8.2.3, 8.2.4). From what is known about the diets of the four selected suid species (this chapter, Cumming 1975, Mason 1982, D'Huart 1978, Briedermann 1986), the nature of their food resources may be tentatively characterized as shown in Table 8/3.

Crucial features of the food resource base (Table 8/3) refer to those spatiotemporal characteristics of availability which are presumed to exert a predominant influence on the sociobiology of a particular species. These influences were discussed in relation to social organization in Chapter 4 and will be further dealt with in the synthesis of suid life history strategies in Chapter 12.

TABLE 8/3: FOOD RESOURCE CHARACTERIZATION FOR FOUR SELECTED SUID SPECIES

| SPECIES | DISPERSION | STABILITY | PREDICTABILITY | RENEWABILITY |
|------------------------------------|---|-----------|----------------|-----------------|
| Bushpig | Dispersed | Stable | Unpredictable | Variable |
| Warthog | Concentrated | Unstable | Predictable | Seasonally high |
| Giant forest hog | Concentrated | Stable | Predictable | Relatively high |
| Wild boar | Concentrated | Unstable | Unpredictable | Seasonally high |
| CRUCIAL FEATURES OF FOOD RESOURCES | | | | |
| Bushpig | Dispersion | | | |
| Warthog | Intra-annual instability | | | |
| Giant forest hog | Renewability | | | |
| Wild boar | Intra-annual instability/interannual unpredictability | | | |

Efficient foraging is believed to be particularly important where suitable food items are spatially dispersed, as in the case of the bushpig. This aspect deserves further detailed study. Preliminary comments are presented in the next section (8.2.6).

8.2.6 Optimal foraging

Foraging strategy is commonly taken to include the following components: diet selection, food patch choice, food patch residence time and food search path (Pyke, Pulliam and Charnov 1977). Natural selection will favour those individuals in a population which contribute the most to subsequent generations. Optimal foraging theory hence assumes that natural selection will result in a change over time of the average foraging behaviour in the population towards that which gives maximum fitness (Pyke, Pulliam and Charnov 1977). Although optimal foraging was not studied directly, some observations are discussed in terms of optimal foraging theory as a basis for further study.

Herbivores are typically faced with the problem of selecting food of adequate quality from an apparent surplus of potential food items (cf Owen-Smith and Novellie 1982). Although all elements of efficient foraging may come into play, diet and patch selection are clearly of paramount importance for true herbivores. Carnivorous predators on the other hand must find prey items in sufficient quantity but may be limited by constraints placed on searching success. Omnivores are

believed to occupy an intermediate position. The dispersed, high nutrient density food items may be viewed as "stationary prey" and consequently the "search" rather than the "selection" element is likely to predominate in bushpig foraging. Food patch residence time and search paths are accordingly considered to be most important.

(a) Optimal diet selection

The basic predictions of the optimal diet model are as follows (Emlen 1966, Schoener 1971, Townsend and Hughes 1981, Pyke, Pulliam and Charnov 1977, Sinclair, Krebs and Smith 1982):

- (I) Whether a food type is eaten depends on the abundance of higher ranking (higher quality) foods.
- (II) The number of lower ranking foods in the diet decreases as the abundance of a high ranking item increases, i.e. diet diversity is greatest under conditions of low overall food abundance.
- (III) Food types are added or dropped from the diet in rank order, i.e. there are no partial preferences.

Some empirical support for these predictions exists (e.g. Clark 1982, MacCracken and Hansen 1987).

The central prediction that a more productive environment should lead to a more restricted diet in terms of numbers of different species eaten, could not be tested in the bushpig. Clearcut criteria for determining food abundance were difficult to define. Comparisons between Southern and Eastern Cape were invalidated by major differences in the composition of stomach contents collected in the two regions. Also, in a patchy environment, the diet diversity prediction is unlikely to apply in the case where the search element predominates in foraging (MacArthur and Pianka 1966). The body of optimal diet theory cited also largely ignores sampling and nutrient constraints as factors affecting the optimization of diets (Westoby 1978). Its predictions are only legitimate where food types do not vary in nutritional properties, as for carnivores. Where nutrient constraints apply, an optimal predator may show partial preferences (Westoby 1978). Reduced food

specialisation with increased food availability may then be just as likely as the converse (Rapport 1980).

Nevertheless, the perceived availability of high quality food would appear to decrease the inclination to ingest lower quality items and to sample items of unknown quality (e.g. novel capture bait). Krosniunas (1985) observed that feral pigs often showed an initial reluctance to eat a novel food and usually only did so after repeated contact with the item over several days. This was common even for foods which were eventually preferred. Similar behaviour has been reported in the bushpig by local naturalists. It is suggested that novel foods do not fall within the search image existing when they are first encountered and are only incorporated after repeated sampling. A novel food item may only be sampled after repeated contact. Bushpigs may also be more inclined toward sampling when actively searching rather than during directional movement to known food patches or areas. The difficulty of capturing bushpigs adjacent to agricultural fields or when agricultural foods are generally abundant in an area may be explained in this way.

(b) Optimal patch choice

Bushpigs are able to memorize particularly profitable food patches or areas, as shown by their regular visits to feeding places established for hunting purposes or to agricultural fields. Apart from these known sites, the spatiotemporal distribution of food patches is such that bushpig foraging is mainly a matter of optimising search and patch residence times.

(c) Optimal patch residence

In order to maximize foraging reward, animals may employ a variety of strategies in terms of the optimal foraging effort to be invested per food patch (cf McNair 1983):

Residence time strategy (RT): The forager remains in a food patch until its residence time reaches a fixed value and then leaves.

Giving-up time strategy (GUT): The forager keeps track of the time since the last food encounter within the patch and leaves if this exceeds a certain value. Krebs, Ryan and Charnov (1974) found that giving up times were constant for all patch types within an environment and were inversely related to the average capture rate for the environment (also Charnov 1976).

Yield strategy (Y): The forager keeps track of its cumulative energy intake since encountering a patch and leaves when a certain yield has been achieved. The "hunting by expectation" hypothesis states that an animal learns to expect a certain amount of food from each patch and leaves it when it has obtained that amount of food (Gibb 1962 ex McNair 1982).

Which strategies are superior under the various possible circumstances varies according to a variety of factors (Pyke 1984) and cannot be discussed here fully. One of the principal findings of McNair (1982) was that the same GUT should not be applied to patches of different quality in the same habitat. Instead, larger GUT's should be used in better patches. He also showed that neither an optimal GUT strategy nor an optimal RT strategy is always superior to the other. Further, hunting by expectation may be superior to both (McNair 1982). Stevens and Charnov (1982) have pointed out that in a stochastic environment, foragers are and should be sensitive to both mean and variance of the distribution of food reward. They accordingly stated that, as a general rule, if the food requirement is low compared to expectations, then the forager should stay longer than expected by mean-maximization; if the requirement is high, the forager should stay for a shorter period than expected by mean-maximization.

All three strategies involve thresholds of departure which should be influenced by specific patch quality (intra-patch factors) and overall habitat quality. This depends on average patch quality in the habitat and the required interpatch search input (inter-patch factors). Lloyd (1987) aptly pointed out that the primary adaptive trade-off is not between one patch and another, but between increasing the amount of time spent in each patch and decreasing the number of patches visited. Bushpigs were repeatedly observed to leave rich food patches long before

all the readily available food items had been eaten (e.g. artificially established feeding places; acorns below a group of *Quercus robur* trees). This type of foraging behaviour is hypothetically interpreted as "hunting by expectation."

(d) Optimal search path

If food patch distribution is clumped, an animal may profit by altering its search path after a successful encounter with a food patch (Alcock 1979). Many studies have shown that animals become less directional in their movements or tend to engage in area-restricted searching after encountering large amounts of food or food odour (authors cited by Pyke 1974, Pyke, Pulliam and Charnov 1977, Pyke 1984). Bushpigs were observed to revisit feeding places repeatedly at short intervals (ca 10 - 30 minutes). This may have been the outcome of area-restricted searching behaviour.

8.3 Nutrition

8.3.1 Introduction

The nutritional contents of the diet (8.1) and the retrieval of its components by the animal are explored in this section. Particular emphasis is placed on regional differences because they provide the key to the understanding of salient interactions between the edaphoclimatic environment and vegetation as a source of food for bushpigs.

Some of the general principles involved were introduced in section 8.2. The specific elements linking environment, food resources and bushpig population responses, are presented. Finally, the basis is laid for the thesis that the nutritional constraints experienced by herbivores and resulting from plant life history tactics underly congruent life history strategies in the herbivore populations (Chapter 12).

8.3.2 Methods

Limited information was obtained on food consumption of captive bushpigs (1.3.4), but this section is based primarily on information from analyses performed on post-mortem biological samples (1.3.2). The sampling techniques were described in section 1.3.2.3. The programme was designed to gain greater insight into the nutritional adequacy and digestibility of bushpig diets, microbial fermentation and dietary factors interfering with efficient nutrient digestion and absorption.

Intestines were dissected out and their lengths measured. Gastric and caecal capacities were determined by measuring the volume of sand and water filling these organs respectively. Sand was used as filler for stomachs since water tended to extend them unrealistically.

(a) Nutritional adequacy

(I) Weende or Proximate analysis

Frozen stomach ingesta and rectal faeces samples were dried and ground for further analyses carried out at Elsenburg and the Faculty of Agriculture, University of Stellenbosch. Standard AOAC (1965) methods were used for proximate analyses.

Nitrogen was determined by the Kjeldahl method and the nitrogen content multiplied by a factor of 6,25 to obtain percentage crude protein. Percentage ether extract (primarily lipids) was determined by ether-hexane extraction. Crude fibre percentage was determined by boiling in acid and alkali and subsequent ashing. The percentage of nitrogen-free extract was determined by calculating the difference between the summed percentages of crude protein, lipid, crude fibre, ash and 100%.

(II) Total soluble carbohydrates

Total soluble carbohydrate levels were determined for 71 stomach samples according to the method of Dubois *et al.* (1956) and the results expressed as percentage dry matter.

(III) Phosphorus, calcium and potassium

Samples prepared for the Weende analysis were used.

Total phosphorus was determined colorimetrically by the Technicon Auto Analyser (molybdate) method and calcium by atomic absorption spectroscopy. Potassium was determined by flame photometry (Saasveld Forestry Research Centre). The results are expressed as percentage dry matter.

(IV) Liver trace element status

Preserved portions of the ventral lobe of the liver were dried to constant weight and ground to a fine powder. Duplicate aliquots (1,0g) were digested in an equivolume concentrated nitric and perchloric acid solution, heated on a sandbath until digestion was complete and solutions were clear. The trace elements Cu, Fe, Zn and Mn were measured by atomic absorption spectroscopy (Regional Veterinary Laboratory, Stellenbosch).

(b) Determination of digestibility

(I) Acid-insoluble ash

For the indicator method of determining apparent digestibility coefficients, acid-insoluble ash (AIA) content in both stomach ingesta and rectal faeces was determined as indicator substance. The 2N HCL analytical procedure was used (Van Keulen and Young 1977) (Elsenburg: Department of Agriculture)

(II) Nylon bag technique

Samples from 10 bushpig stomachs were dried, ground and placed in polyester nylon bags (25 x 40 mm) with a 53 mm mesh. Twenty bags were used per sample, each containing one gram of dried material. Three experimental domestic pigs were involved in the experiment. The nylon bags were inserted through a duodenal cannula into the gastrointestinal tract of a pig while it was eating and recovered in the faeces. The bags were retrieved immediately after

defaecation, washed in cold water to remove contaminating faecal material, frozen and freeze-dried. The residues left in the bags were analysed for dry matter and nitrogen and the disappearance of organic matter and crude protein ($N \times 6,25$) thus determined (Animal and Dairy Science Research Institute, Irene). For further details of the method refer to Petry and Handlos (1978), Sauer *et al.* (1983) and Graham *et al.* (1985).

(III) Partial *in vitro* protein digestibility: pepsin digestion

One gram of dried, ground and homogenized stomach contents was digested with 100 ml of pepsin/HCL mixture at 37°C for 24 hours (0,2% pepsin in 0,075 N HCL). The residue was filtered through Whatman's No. 2 filter paper, washed with warm, distilled water and oven-dried. A 500 ml sample was used for Kjeldahl nitrogen determinations (modified procedure based on Ramachandra *et al.* 1977). Partial *in vitro* protein digestibility was calculated from the difference between the amount of nitrogen before and after pepsin digestion (Saasveld Forestry Research Centre).

(c) Digestibility-reducing factors

(I) Polyphenols

The polyphenol content of stomach samples was determined by the modified Jerumanis (1972) procedure, as described by Daiber (1975) (Animal and Dairy Science Research Institute, Irene) The assay measures total phenolics through reaction with a ferric agent (Jerumanis 1972) and provides a comparable measure to the Folin-Denis method (Mole and Waterman 1987).

Condensed tannin levels were determined at the Saasveld Forestry Research Centre according to the method of Porter *et al.* (1986).

(II) Acid-detergent lignin and fibre

Acid-detergent lignin and acid-detergent fibre contents were determined at the Animal and Dairy Science Research Institute, Irene, using the procedure of Goering and Van Soest (1970).

(III) Tannin/protein precipitation

The degree of protein precipitation of tannins in the stomach ingesta was estimated by the radial diffusion method (Hagermann 1987). An aliquot of an aqueous/acetone extract of sample is placed in a well in a protein containing gel. The tannins in the extract then diffuse through the gel, precipitating the protein and forming a visible ring. The square of the diameter of this ring was then taken as a measure of protein precipitated. The tests were carried out at the Saasveld Forestry Research Centre.

(d) Microbial fermentation

(I) The concentrations of volatile fatty acids in gastric and caecal fluids of bushpigs were determined by gas liquid chromatography according to the procedure reported by Erwin *et al.* (1961). The work was done at the Animal and Dairy Science Research Institute, Irene. The VFA concentrations were used as indicators of the incidence and degree of microbial fermentation.

(II) Diaminopimelic acid (DAPA) contents were determined for 6 faecal samples in order to determine the proportion of nitrogen of bacterial origin. The determinations were carried out by the Animal and Dairy Science Research Institute, Irene, according to the method laid down by the AOAC (1984).

8.3.3 Results

8.3.3.1 Features of the digestive system

(a) Dimensions of the tract

The dimensions of the alimentary tract of three adults bushpigs were determined (8.3.2):

| | SH48 (F) | SH45 (F) | CT7 (M) |
|----------------------------|----------|----------|---------|
| Stomach (cm ³) | 6 500 | 6 600 | 4 300 |
| Duodenum (m) | 12,9 | 13,0 | 14,8 |
| Caecum (cm ³) | 1 030 | 1 100 | 1 100 |
| Colon (m) | 5,5 | 3,6 | 4,0 |
| Rectum (m) | 1,6 | 1,9 | 1,9 |

A precise value for the capacity or length of any part of the alimentary tract is difficult to obtain (Kidder and Manners 1978). This is particularly so for the stomach and the given values presumably do not represent maximum possible extension for food storage. Caecum capacities are more accurate, since caecum walls are less distendable.

The bushpig has a glandular, unilocular (simple) stomach, like the European wild boar (Briedermann 1986). Analyses of the mass of stomach contents are presented in section 8.3.3.6. The ratio of small to large intestine length amounts to 3,1/1 in the bushpig, which is similar to that of the domestic pig and European wild boar (cf Briedermann 1986). Calculated on the basis of dimensions given by Comberg *et al.* (1978), the corresponding ratio rather is 5/1 for the domestic pig. The large intestine is relatively well developed whenever retention of fibrous herbage for microbial degradation is important (Rérat 1978, Schieck and Millar 1985). This fits in with the better digestion of fibrous food by European wild boar compared to the domestic pig (Schnorrenberg 1979).

(b) Gastric pH-values

Estimates of pH taken with litmus paper strips during evisceration ranged between 2 and 6 (n = 21). More accurate instrumental pH determinations were performed on 6 bushpig stomachs. Values from the pyloric and caudal sections of the stomach did not differ greatly nor consistently and those for the mixed stomach contents were within the range reported above (2,61; 2,09; 5,31; 4,18; 4,07; 3,55).

Gastric pH values in the domestic pig are reported to lie between 2,0 and 5,5 (Argenzio and Southworth 1974). The upper part of this range is suitable for supporting protozoa and bacteria (Langer 1979). Relatively high volatile fatty acid concentrations were measured in bushpig stomachs (part (d) below) which is indicative of microbial fermentation. Fermentation of carbohydrate, with the formation of lactic and volatile fatty acids, occurs in the stomachs of domestic pigs (Kidder and Manners 1972). It appears that if the stomach contents are dominated by sugars and starches, relatively high pH values occur and allow the microbial fermentation of carbohydrate, whereas pepsin activity in protein digestion requires low pH conditions (pH 2-4: Kidder and Manners 1972). Low gastric pH values would thus be measured when protein was being digested.

(c) Digestive symbionts

Gut microbes consist of two main groups, the bacteria and protozoa (Van Hoven and Boomker 1985). Protozoa were not found in gastric fluid samples (n = 4), but were present in those samples taken from the caecum and colon (n = 9; Prof Van Hoven, University of Pretoria). The following species were identified:

| | <u>Caecum</u> | <u>Colon</u> |
|--------------------------------------|---------------|--------------|
| <i>Holophryoides ovalis</i> | X | X |
| <i>Paraisotricha colpoidea</i> | | X |
| <i>Blepharosphaera intestinalis</i> | X | X |
| <i>Blepharosphaera ellipsoidalis</i> | X | X |
| <i>Didesmis ovalis</i> | X | X |
| <i>Didesmis quadrata</i> | X | |
| <i>Blepharoprosthium pireum</i> | X | X |

Some of these protozoa are also found in the gut of horses, cattle, sheep (Hsiung 1930; Grain 1966) and black and white rhinoceros (Van Hoven pers. comm.)

Certain bacteria are less sensitive to low pH found in the stomach than the protozoa (Van Hoven and Boomker 1985) and only bacteria thus appear responsible for microbial fermentation in bushpig stomachs.

(d) Volatile fatty acid concentrations

Volatile fatty acid (VFA) determinations were carried out on digestive fluids from the stomach (n = 27) and caecum (n = 25). The results are summarized below (Table 8/4).

| TABLE 8/4: VOLATILE FATTY ACID CONCENTRATIONS IN BUSHPIGS | | | | | |
|---|--|-----------|-----------|------------|------------|
| | Volatile acid fractions (mmole/100 ml) | | | | |
| | Acetic | Propionic | Butyric | Isovaleric | TOTAL |
| <u>STOMACH</u> | | | | | |
| \bar{x} | 6,37 | 3,22 | 0,85 | 0,01 | 10,45 |
| s | 4,86 | 2,10 | 0,86 | - | 7,50 |
| Range | 0,43-18,84 | 0,41-8,54 | 0,17-3,09 | 0-0,07 | 0,89-26,70 |
| % | 61 | 31 | 8 | | |
| <u>CAECUM</u> | | | | | |
| \bar{x} | 9,53 | 2,49 | 0,59 | 0,01 | 12,61 |
| s | 5,01 | 1,83 | 0,49 | - | 7,07 |
| Range | 0,45-17,82 | 0,08-7,56 | 0,01-1,79 | 0-0,06 | 0,56-25,04 |
| % | 73 | 22 | 5 | | |

In the domestic pig, organic acids are found in all regions of the alimentary tract, the amount and type of acid being related to the region of the tract, the diet and the age of the animal (Cranwell 1968). Other factors which may influence the concentration of organic acids include frequency of feeding, the interval between feeding and sampling and the rate of passage of the digesta. These factors should be controlled through standardization if comparisons are to be made between animals, diets and ages (Cranwell 1968). Standardization was obviously not possible during this study. This may explain why no apparent relationships were found between diet composition and total VFA concentrations or relative proportions of the various acids. Similarly,

Barrett (1978) did not find any significant correlation of total VFA content with food items in the stomach or with estimated time since feeding in feral hogs studied in California, USA. In the domestic pig, diet (especially cellulose content) has been found to influence the total VFA concentrations or their relative proportions, or both (Friend *et al.* 1963, Farrell and Johnson 1970, Argenzio and Southworth 1974, Langer 1978, Kass *et al.* 1980, Holechek *et al.* 1985, Stanogias and Pierce 1985b).

The chief sites for the production and absorption of VFA in the pig were shown by Elsdon *et al.* (1946) to be the caecum and colon. Appreciable amounts of VFA are however also found in the stomach and small intestine, indicating that microbial fermentation was taking place in these parts (Friend *et al.* 1963, Argenzio and Southworth 1974, Maynard *et al.* 1979). Data on proportions of caecal VFA of domestic pigs taken from the literature is contrasted with that on the bushpig below (percentages):

| <u>Acetate</u> | <u>Propionate</u> | <u>Butyrate</u> | <u>Authors</u> |
|----------------|-------------------|-----------------|-------------------------------|
| 67 | 19 | 14 | Elsden <i>et al.</i> (1946) |
| 60 | 30 | 7,5 | Friend <i>et al.</i> (1963) |
| 60 | 21 | 17 | Farrell and Johnson (1970) |
| 65 | 27 | 8 | Kennelly <i>et al.</i> (1981) |
| 73 | 22 | 5 | This study |

The total VFA concentrations determined for bushpig stomach and caecum digesta have the same order of magnitude as those found in the domestic pig. Total VFA concentrations in the caeca of pigs was about 8,5 meq/100ml in animals fed a low protein/high fibre diet and 20,0 meq/100ml for conventionally fed animals (Argenzio and Southworth 1974). Stomach and caecal VFA concentrations were 14,7 and 21,5 meq/100ml respectively (Friend *et al.* 1963). Kennelly *et al.* (1981) give a value of 12,1 meq/100ml for domestic pig caecal contents.

Total concentrations, as well as molar proportions, of VFA in both stomachs and caeca of bushpigs are similar to those found in other non-ruminants and ruminants (cf Van Hoven and Boomker 1985).

8.3.3.2 Nutrient content of diet

The nutrient fractions identified by the Weende or Proximate analysis contain a variety of substances, as shown below, but do allow a crude assessment of nutrient content of the diets analyzed (McDonald *et al.* 1973).

| | |
|----------------------------|---|
| Crude protein: | proteins, amino acids, amines, nitrates, nitrogenous glycosides, glycolipids, B-vitamins. |
| Crude fibre: | cellulose, hemicelluloses, lignin. |
| Ether extract: | fats, oils, waxes, organic acids, pigments, sterols, certain vitamins. |
| Ash: | major essential elements (Ca, K, Mg, Na, S, P, Cl), essential trace elements (Fe, Mn, Cu, Co, I, Zn, Mo, Se,) and other non-essential elements. |
| Nitrogen-free extractives: | cellulose, hemicelluloses, lignin, sugars, fructosans, starch, pectins, organic acids, rennins, tannins, pigments, water-soluble vitamins. |

The results of Weende analyses performed on bushpig stomach contents samples are presented in Table 8/5.

| | | PCP | PCF | PEE | PA | NFE |
|--|-----------|------|------|------|-------|-------|
| TOTAL (Both regions) | \bar{x} | 14,1 | 20,2 | 6,0 | 12,4 | 47,2 |
| | n | 147 | 144 | 129 | 132 | 123 |
| | s | 4,70 | 9,12 | 4,74 | 9,87 | 14,73 |
| | Minimum | 6,4 | 5,7 | 1,0 | 0,9 | 7,9 |
| | Maximum | 34,9 | 52,3 | 27,9 | 43,0 | 79,8 |
| EASTERN CAPE | \bar{x} | 14,7 | 19,9 | 5,9 | 15,8 | 43,0 |
| | n | 58 | 57 | 55 | 51 | 50 |
| | s | 5,81 | 7,96 | 5,35 | 11,18 | 16,65 |
| SOUTHERN CAPE | \bar{x} | 13,7 | 20,4 | 6,0 | 10,3 | 50,0 |
| | n | 89 | 87 | 74 | 81 | 73 |
| | s | 3,79 | 9,87 | 4,27 | 8,35 | 12,60 |
| PCP: Percentage crude protein PCF: Percentage crude fibre PEE: Percentage ether extract PA : Percentage ash NFE: Nitrogen-free extract (percentage by subtraction) | | | | | | |

The same data is summarized on a seasonal basis in Table 8/6.

| (n in parentheses) | | PCP | PCF | PEE | PA | NFE |
|---|--------|----------|----------|---------|----------|----------|
| EASTERN CAPE | Summer | 15,2 (5) | 22,1 (5) | 8,2 (5) | 17,8 (5) | 36,7 (5) |
| | Autumn | 13,5 (6) | 18,9 (6) | 5,5 (6) | 20,3 (6) | 40,2 (6) |
| | Winter | 15,0(24) | 20,1(23) | 5,2(23) | 15,4(20) | 43,2(19) |
| | Spring | 14,7(23) | 19,5(23) | 6,3(21) | 14,3(20) | 45,3(20) |
| SOUTHERN CAPE | Summer | 13,0(19) | 20,7(19) | 5,8(18) | 11,9(19) | 49,8(18) |
| | Autumn | 11,6 (8) | 14,9 (8) | 4,7 (8) | 14,9 (8) | 59,3 (8) |
| | Winter | 14,0(24) | 19,9(23) | 5,8(19) | 11,5(21) | 49,2(18) |
| | Spring | 14,4(38) | 21,8(37) | 6,7(29) | 9,1(33) | 48,1(29) |
| Summer: December - February Autumn: March - May Winter: June - August Spring: September - November | | | | | | |

Analysis of variance of the log-transformed percentages to investigate the effects of region, age, sex, season and reproductive state in females, produced only the following significant differences (Table 8/5):

- (I) PA of Eastern Cape > PA of Southern Cape ($P < 0,005$).
- (II) NFE of Southern Cape > NFE of Eastern Cape ($P < 0,01$).
- (III) PEE of the juvenile age class (8,87%) > PEE of the yearling (5,30%), subadult (5,94%) and adult (5,41%) age classes ($P < 0,05$).
- (IV) PCF of pregnant females (24,5%) > PCF of lactating (16,4%) or non-reproductive (17,5%) females ($P < 0,01$).
- (V) PA of lactating females (25%) > PA of pregnant (9,7%) and non-reproductive (13,7%) females ($P < 0,05$).

Although not statistically significant, crude protein percentages tend to differ between males and females, particularly during spring:

| | <u>PCP</u> | |
|---------|---------------|----------------------|
| | <u>SPRING</u> | <u>OTHER SEASONS</u> |
| MALES | 13,0 (n = 16) | 13,8 (n = 70) |
| FEMALES | 15,4 (n = 22) | 14,4 (n = 77) |

The nutrient fractions from stomachs dominated by specific dietary items are summarized in Table 8/7. Patterns which are to be expected emerged: fruit and subterranean plant organs are rich in carbohydrates and have relatively low protein contents. The reverse applies to herbage and flesh. The high fat content (PEE) of *Podocarpus falcatus* seed is noteworthy since this is favoured by bushpigs. Further analysis revealed a consistent contribution of *Podocarpus falcatus* seed to high PEE's. The mean PEE of 12 stomach contents with *Podocarpus falcatus* seed constituting more than 10% composition by volume was 12,0% ($s = 5,66$), as against 5,01% in those stomach contents where the seed contributed less than 10% ($s = 2,90$; $n = 54$). These means differ significantly ($t = 6,202$ $df = 64$ $P < 0,001$). The values obtained for separate analyses of hypogeous *Rhizopogon* fruiting bodies were 18,2 and

16,3 crude protein, which compare well with the value for stomach contents dominated by this item (Table 8/7).

| TABLE 8/7: CRUDE NUTRIENT CONTENTS OF BUSHPIG STOMACHS WITH RELATIVELY HOMOGENEOUS INGESTA (SOUTHERN AND EASTERN CAPE) | | | | | | |
|---|------------------|------------------|------|------|------|------|
| Dominant dietary fraction of stomach contents | % of contents | Weende fractions | | | | |
| | | PCP | PCF | PEE | PA | NFE |
| Fruit: <i>Olea capensis</i> ssp <i>macrocarpa</i> | 73,3 | 12,2 | 13,6 | 3,1 | 1,2 | 69,9 |
| <i>Podocarpus falcatus</i> | 74,2 | 9,3 | 49,5 | 13,0 | 4,8 | 23,4 |
| <i>Zea mais</i> (maize) | 80,0 | 9,0 | 5,7 | 1,8 | 3,7 | 79,8 |
| <i>Rhoicissus tomentosa</i> | 94,0 | 9,6 | 44,8 | 4,5 | 1,9 | 39,2 |
| Herbage: <i>Medicago sativa</i> (lucerne) | 58,6 | 26,2 | 14,1 | 4,0 | 10,6 | 45,1 |
| <i>Blechnum punctulatum</i> | 94,0 | 16,9 | 19,8 | 7,7 | 11,3 | 44,3 |
| <i>Schoenoxiphium</i> sp | 85,0 | 13,0 | 15,2 | 5,4 | 26,1 | 40,3 |
| <i>Aloe ciliaris</i> | 94,5 | 8,4 | 17,7 | 2,1 | 15,6 | 56,2 |
| Lucerne/Aloe sp | 86,7 | 23,5 | 22,9 | 3,5 | 3,6 | 46,5 |
| Aizoaceae | 82,8 | 14,8 | 20,8 | 5,1 | 16,5 | 42,8 |
| Tubers: <i>Solanum tuberosum</i> (potatoes) | 88,0 | 10,4 | 10,0 | 4,0 | 18,8 | 56,8 |
| <i>Cyphostemma</i> sp | 84,6 | 8,6 | 16,6 | 2,1 | 13,0 | 59,7 |
| <i>Rhoicissus</i> spp | 97,5 | 11,7 | 25,2 | 1,6 | 16,8 | 44,7 |
| <i>Rhoicissus</i> spp | 97,0 | 9,6 | 10,5 | 3,5 | 2,9 | 73,5 |
| Rhizomes: <i>Pteridium aquilinum</i> | 79,6 | 10,8 | 16,6 | 2,7 | 22,6 | 47,3 |
| Corms: <i>Oxalis</i> sp | 76,9 | 7,8 | 14,3 | 1,4 | 1,5 | 75,0 |
| Hypogeous fungi: <i>Rhizopogon</i> sp | 94,5 | 16,4 | 14,4 | 4,0 | 15,1 | 50,1 |
| Flesh: Small stock | 75,0 | 20,1 | 8,2 | ? | 36,4 | ? |
| Invertebrata | 54,4 | 10,8 | 14,7 | 15,5 | 3,8 | 55,2 |
| FOOD TYPE MEANS: | | | | | | |
| Fruit | | 10,0 | 28,4 | 5,6 | 2,9 | 53,1 |
| Herbage | | 17,1 | 18,4 | 4,6 | 13,9 | 45,9 |
| Subterranean organs | | 9,8 | 15,5 | 2,6 | 12,6 | 59,5 |
| Flesh | | 15,4 | 11,4 | ? | 20,1 | ? |

Weende analyses were also performed on some samples of rectal faeces. These cannot automatically be assumed to represent the digestive waste products of forage similar in composition to that currently found in the stomach. Digestibilities also differ between forage types. Nevertheless, a certain degree of correlation does appear to exist between Weende fraction percentages of stomach contents and rectal faeces:

PCP

$Y = a + b X$

where y = fraction percentage in rectal faeces

X = fraction percentage in stomach

$Y = 10,01 + 0,313 X$ $X = 14,2$ $Y = 14,5$

$r = 0,314$ ($t = 2,626$ $df = 63$ $P < 0,01$)

PCF

$r = 0,783$ ($t = 9,830$ $df = 61$ $P < 0,001$)

PEE

$r = 0,224$ ($t = 1,576$ $df = 47$ NS)

PA

$r = 0,797$ ($t = 8,751$ $df = 44$ $P < 0,001$)

The crude fibre fraction is largely equivalent to cellulose (Schneider and Kirchgessner 1978). Acid-detergent fibre (ADF) and acid-detergent lignin (ADL) were also determined (Table 8/8) because these values bear a closer relation to forage digestibility than the crude fibre fraction (Van Soest 1982).

| TABLE 8/8: ACID-DETERGENT FIBRE AND ACID-DETERGENT LIGNIN LEVELS OF BUSHPIG STOMACH INGESTA (PERCENTAGE DRY MATTER) | | | |
|---|---------------------|----------------------|-----------------------|
| Percentage Acid-detergent Fibre | | | |
| Southern Cape | \bar{x} s n | 40,02 13,58 30 | t = 1,21 NS |
| Eastern Cape | \bar{x} s n | 36,26 10,26 30 | |
| Agriculture (Pooled over regions) | \bar{x} s n | 20,10 6,70 7 | t = 3,95 P < 0,001 |
| Percentage Acid-detergent Lignin | | | |
| Southern Cape | \bar{x} s n | 22,29 12,27 30 | t = 2,07 P < 0,05 |
| Eastern Cape | \bar{x} s n | 16,99 6,75 30 | |
| Agriculture (Pooled over regions) | \bar{x} s n | 9,99 4,51 6 | t = 2,42 P < 0,05 |

The nitrogen free extract (NFE) of the Weende analysis is not a reliable indicator of available dietary carbohydrates. NFE values are inflated with lignin and hemicellulose contents (Schneider and Kirchgessner 1978). Total soluble carbohydrates were therefore determined on 71 bushpig stomach samples. The Southern Cape mean value of 14,16% of the dry matter ($s = 7,29$; $n = 35$) was significantly higher ($t = 2,70$; $P < 0,01$) than the Eastern Cape mean of 10,27% ($s = 4,60$; $n = 36$).

8.3.3.3 Mineral nutrition

Phosphorus and calcium levels of stomach ingesta were determined. The resultant overall means on a dry matter basis were 0,284 and 1,090% respectively ($n = 84$ $s = 0,271$ for phosphorus; $n = 83$ $s = 0,942$ for calcium). Regional means are given below (% DM of ingesta):

| | <u>Phosphorus</u> | <u>Calcium</u> | <u>Ca/P-ratio</u> |
|----------------------------|-------------------|----------------|-------------------|
| Southern Cape ($n = 42$) | 0,203 | 0,58 | 2,86 |
| Eastern Cape ($n = 42$) | 0,365 | 1,59 | 4,36 |

The data exhibited strong skewness and further values were obtained from an analysis carried out on ln-transformed data. The main effects on P- and Ca-levels in the analysis of variance were region (R), reproductive condition (RC: L lactating; P pregnant, N non-reproductive; M males) and month of the year:

| <u>Main Effects</u> | <u>df</u> | <u>F-ratio</u> | <u>Significance level</u> |
|------------------------|-----------|----------------|---------------------------|
| <u>LOGPHOS</u> | | | |
| Region | 1 | 5,695 | $P < 0,05$ |
| Reproductive condition | 3 | 4,586 | $P < 0,01$ |
| Months | 11 | 1,066 | NS |
| <u>LOGCALC</u> | | | |
| Region | 1 | 49,070 | $P < 0,0001$ |
| Reproductive condition | 3 | 2,529 | NS |
| Months | 11 | 1,271 | NS |

The dietary P-levels of lactating bushpig females ($\bar{x} = 0,62$) were higher than those of non-reproductive females ($\bar{x} = 0,23$), pregnant females ($\bar{x} = 0,19$) and males ($\bar{x} = 0,19$). Dietary Ca-levels of Eastern Cape bushpigs ($\bar{x} = 1,27$) were higher than those of the Southern Cape ($\bar{x} = 0,49$).

Mean potassium levels in stomach ingesta also differed significantly between the regions ($t = 2,17$ $P < 0,05$; Southern Cape $\bar{x} = 0,67\%$ $s = 0,352$ $n = 34$; Eastern Cape $\bar{x} = 0,89\%$ $s = 0,481$ $n = 36$; means expressed as percentages of dry mass of stomach ingesta).

8.3.3.4 Trace element status

Trace element levels of bushpig livers are contrasted with those of the domestic pig and European wild boar in Table 8/9.

| TABLE 8/9: TRACE ELEMENT LEVELS IN SUID LIVERS (in parts per million DRY MATTER) | | | | | |
|---|---|--|---------------------------------------|---------------|------------|
| Trace Element | | BUSHPIG | | Domestic Pig* | Wild Boar* |
| | | Southern Cape | Eastern Cape | | |
| <u>Copper</u> | \bar{x} n s Minimum Maximum | 13,74 206 3,61 3 25 | 15,47 86 5,66 5 30 | 21 | 16 |
| <u>Iron</u> | \bar{x} n s Minimum Maximum | 620,41 206 246,64 130 1872 | 691,76 86 280,81 167 1964 | 466 | 217 |
| <u>Zinc</u> | \bar{x} n s Minimum Maximum | 124,14 206 24,46 50 254 | 123,14 86 24,68 66 240 | 182 | 148 |
| <u>Manganese</u> | \bar{x} n s Minimum Maximum | 7,41 206 2,37 2 16 | 8,50 86 3,62 1 19 | 7,4 | 9,1 |
| <u>Molybdenum</u> | \bar{x} n s Minimum Maximum | 1,53 41 0,58 0,7 2,9 | 1,25 86 0,77 0,1 4,8 | 2,42 | 0,99 |
| * op. cit. Briedermann (1986) | | | | | |

Analysis of variance regarding the effects of sex, region and season were performed on the data. Mean Cu and Mn-levels were higher in the Eastern Cape bushpig livers than those of the Southern Cape (both $P < 0,005$). Mo-levels were higher in the Southern Cape ($P < 0,01$). Whether these statistical differences have biological meaning is unclear and rather doubtful. There were no significant differences in trace element level related to sex.

Iron, zinc and molybdenum levels exhibit statistically significant seasonal cycles (Fe: $P < 0,0001$; Zn: $P < 0,005$; Mo: $P < 0,0005$). The levels of these trace elements peak in July, February and November respectively (cosine trend analysis *vide* Cryer 1986). The biological meaning of these seasonal cycles, if any, is unclear.

8.3.3.5 Nutrient digestibilities

(a) Digestibility assessment with the indicator method

An inert reference substance in the feed, the concentration of which can be determined in the faeces, can serve as an indicator of the volume of faeces resulting from a particular volume of feed. By determining the ratio of the concentration of the reference substance to that of a given nutrient in the feed, the digestibility of the nutrient can be obtained without measuring either the food intake or faeces output (McDonald *et al.* 1973, Maynard *et al.* 1979). The reference indicator should be totally indigestible and unabsorbable. Substances such as lignin (McDonald *et al.* 1973) or acid-insoluble ash (AIA; Van Keulen and Young 1977) have been used as reference indicators with success. The digestibility percentages of nutrients are then calculated as follows:

$$\text{DIGESTIBILITY} = 100 - 100 \left[\frac{\% \text{ Indicator in feed}}{\% \text{ Indicator in faeces}} \times \frac{\% \text{ Nutrient in faeces}}{\% \text{ Nutrient in feed}} \right]$$

Acid-insoluble ash determinations were available for 26 stomach ingesta/rectal faeces sample pairs for which also nutrient contents were known from Weende analysis. Mean AIA marker concentrations were 0,786 and 2,100% in feed and faeces respectively. The following mean nutrient digestibilities were calculated:

| | |
|-----------------------|-------|
| Crude protein | 61,8% |
| Crude fibre | 58,1% |
| Ether extract | 81,0% |
| Nitrogen-free extract | 70,4% |
| Ash | 28,1% |

Although the faeces samples were not directly derived from the associated stomach ingesta, the above values are nevertheless considered meaningful approximations of nutrient digestibilities in the bushpig.

(b) Digestibility according to the nylon bag technique

Selected bushpig stomach ingesta from the Southern and Eastern Cape (n = 10) were subjected to *in vivo* domestic pig digestion (8.3.2). Dry matter and protein digestibilities were determined (Table 8/10).

Digestibilities according to the nylon bag technique (Table 8/10) were substantially lower than those determined with the indicator method. This is presumably attributable to the faster rate of passage of the experimental ration than would have been the case if the food intake consisted predominantly of the bushpig type of food contained in the nylon bags. Digestibility tends to be inversely related to the rate of passage (Robbins 1983). Additionally, the intestinal symbiont fauna (cf 8.3.3.1c) and gut dimensions (8.3.3.1) in the domestic pig may have been suboptimal for the digestion of the type of diet consumed by bushpigs.

| Region | | PERCENTAGE DIGESTIBILITY | |
|----------------|-----------|--------------------------|---------|
| | | Dry matter | Protein |
| Southern Cape | \bar{x} | 32,2 | 43,1 |
| | s | 19,6 | 18,7 |
| | n | 5 | 5 |
| Eastern Cape | \bar{x} | 29,2 | 29,6 |
| | s | 16,3 | 8,5 |
| | n | 5 | 5 |
| Regions pooled | \bar{x} | 30,7 | 36,3 |
| | s | 17,0 | 15,4 |
| | n | 10 | 10 |

(c) Nutrient retrieval comparisons

For most feed/faeces sample pairs, AIA determinations were not available due to lack of sufficient rectal faecal material for all the assays. Of the Weende fractions, ash is considered the most inert. Using ash as reference indicator thus should allow a crude evaluation of relative nutrient retrieval. Following the same rationale as that of the formula in section "a" above, a relative nutrient retrieval (RNRI) index is defined:

$$\text{RNRI} = \frac{\% \text{ Weende fraction in feed}}{\% \text{ Weende fraction in faeces}} \times \frac{\% \text{ Ash in faeces}}{\% \text{ Ash in feed}}$$

Bushpigs classed as 'lean' according to the visual subcutaneous fat index or which had marrow fat percentages of ≤ 70 (9.3.3.2) were classed as in 'poor' condition. All others were considered to be in 'average' to 'good' condition. The index defined above was then used to test whether animals in poor condition consumed food of lower digestibility.

| <u>Condition class</u> | <u>RNRI</u> | | |
|------------------------|--------------------------------------|----|------|
| | <u>Crude Protein</u> | | |
| | \bar{x} | n | s |
| Poor | 1,63 | 9 | 0,56 |
| Average/Good | 2,93 | 32 | 2,42 |
| | <u>Ether + Nitrogen-free Extract</u> | | |
| | \bar{x} | n | s |
| Poor | 2,19 | 8 | 0,79 |
| Average/Good | 3,68 | 25 | 1,08 |

The difference in the RNRI for crude protein between animals of poor or average/good condition, approached significance ($t = 1,935$ $df = 39$ NS) For the combined 'fat' and 'carbohydrate' fractions, the difference was statistically significant ($t = 3,590$ $df = 31$ $P < 0,01$).

The explanation for this finding may either be that animals in poor condition have a lower digestive efficiency or only had access to poorer quality food. The latter explanation is favoured.

Differences in nutrient retrieval of crude protein between Eastern and the Southern Cape bushpigs were investigated in the same way, with negative results. This was contrary to expectation in view of a significantly higher protein feed to faeces ratio in the Eastern Cape, suggesting higher protein digestibility.

| <u>Region</u> | <u>PCP (Feed) / PCP (Faeces)</u> | | |
|---------------|----------------------------------|----|------|
| | \bar{x} | n | s |
| Eastern Cape | 1,39 | 7 | 0,49 |
| Southern Cape | 1,00 | 58 | 0,31 |

These means differ significantly ($t = 2,921$ $df = 63$ $P < 0,01$), indicating a higher apparent protein recovery for the bushpigs in the Eastern Cape.

The validity of the RNRI depends on the equal absorbability of ash for the categories under comparison (poor versus average/good condition animals, Eastern versus Southern Cape animals). It could be that a greater proportion of the dietary ash is absorbed by the bushpigs in the Eastern Cape (the nutrient-rich region) than by those in the Southern Cape. Any higher protein digestibility in the Eastern Cape would then not be revealed by this approach.

In contrast to the percentage dietary ash, the percentage crude fibre was similar in the diets of bushpig in the two regions (Table 8/5). Applying the RNRI to crude protein, but using crude fibre as reference substance, produced the following results:

| <u>Region</u> | <u>RNRI</u> | | |
|---------------|----------------------|----|------|
| | <u>Crude Protein</u> | | |
| | \bar{x} | n | s |
| Southern Cape | 1,15 | 52 | 0,49 |
| Eastern Cape | 1,50 | 6 | 0,48 |

The relative nutrient retrieval index for crude protein in the Eastern Cape is not significantly higher statistically ($t = 1,66$ $df = 56$ NS).

This is presumably merely the result of the low sample size for the Eastern Cape values.

(d) Digestibility reduction by plant secondary compounds

It was suspected that the apparently lower protein digestibility of crude protein in the diet of Southern Cape bushpigs could be the result of digestibility-reducing substances, such as tannins (8.2.3; 8.2.4). However, mean percentage polyphenol levels in their stomach ingesta ($\bar{x} = 0,388$ $n = 37$ $s = 0,515$) were not different from those in the Eastern Cape ($\bar{x} = 0,372$ $n = 37$ $s = 0,283$). Neither did condensed tannin levels differ between the two regions (Southern Cape: $\bar{x} = 1,41\%$ $s = 0,87$ $n = 44$; Eastern Cape: $\bar{x} = 1,40\%$ $s = 0,60$ $n = 45$).

Ramachandra *et al.* (1977) established a negative relationship between tannin levels and *in vitro* protein digestibility in finger millet, *Eleusine coracana* (cf also Chibber *et al.* 1980). They estimated protein digestibility with pepsin hydrolysis. Although this method is of limited value for the establishment of digestibility coefficients, since it involves the action of only one enzyme, it may be useful for comparative purposes (McDonald *et al.* 1979). The same procedure was followed for bushpig ingesta, but no correlation was found between polyphenols or condensed tannin contents and protein digestibility. Mean protein digestibilities determined in this way were equal for both regions (Southern Cape: $\bar{x} = 24,5\%$ $n = 40$ $s = 13,08$; Eastern Cape: $\bar{x} = 24,5\%$ $n = 38$ $s = 15,41$). These results are probably not really surprising. Whereas Ramachandra *et al.* (1977) worked with a single type of food substance and a single type of tannin, the above investigation involved a great variety of different ingesta compositions, with varying digestibilities, and numerous types of tannins of diverse taxonomic origin and presumably variable protein precipitating potentials (cf Martin and Martin 1982, Wisdom *et al.* 1987). It should also be borne in mind that the stomach ingesta were subject to variable periods of *in vivo* predigestion before the sample animals were shot.

In 10 cases both polyphenol and VFA concentrations were known for the same stomach ingesta. These were inversely correlated ($r = -0,68$ $t = 2,62$ $df = 8$ $P < 0,05$). This negative correlation improved to

$r = -0,83$ ($t = 3,94$ $df = 7$ $P < 0,01$) after removal of an outlier value. VFA concentrations in the caecum were also negatively correlated with polyphenol levels of stomach ingesta ($r = -0,70$ $t = 2,59$ $df = 7$ $P < 0,05$). These findings suggest that high polyphenol levels have a depressive effect on microbial fermentation.

The efficiency of protein precipitation by tannins from different species is highly variable and tannin concentration therefore does not automatically indicate relative protein complex binding potential across species (Wisdom *et al.* 1987). The protein precipitation efficiency of extracts from 78 bushpig stomach ingesta were determined according to the diffusion method (8.3.2.c: Hagermann 1987). Detectable levels of protein precipitation were only found in 18 of the samples. There was no regional effect, nor was there any relationship between tannin content and protein precipitation (Table 8/11).

| TABLE 8/11: CONTINGENCY BETWEEN PERCENTAGE TANNIN CONTENT (DM) AND THE INCIDENCE OF PROTEIN PRECIPITATION | | |
|---|---------------------------|-------------|
| PROTEIN PRECIPITATION | PERCENTAGE TANNIN CONTENT | |
| | $\leq \bar{x}$ | $> \bar{x}$ |
| PRESENT | 7 | 7 |
| ABSENT | 26 | 18 |
| | 33 | 35 |
| G = 0,356 (NS) | | |

The analytical situation and interpretation is presumably confounded by the variable and diverse mixes of dietary items, especially in terms of protein content and its degree of hydrolysis. In view of the inverse relationship between microbial activity and tannin content of ingesta, the absence of any relationship between tannin content and protein precipitation may possibly imply that the toxic effect of the tannin, rather than complex binding, causes reduced microbial fermentation.

(e) ADF-bound nitrogen

Comparison of nitrogen contents of ingesta samples and ADF-residues revealed that 61% of the N content was bound up in the ADF residue (n = 68). It contained on average 1,13% N (based on dry mass). The mean ADF-bound N was 57% for the Eastern Cape samples (n = 36) and 65% for the Southern Cape samples (n = 32). This difference was not statistically significant (arcsine transformed data: $t = 1,51$ NS).

The high percentage of N bound to ADF should be interpreted with caution in terms of its relevance to digestibility. It is suspected that it is an effect of heat-damage to protein during drying. Such damaged protein formed through the Maillard reaction is quantitatively recoverable in acid detergent fibre (Van Soest 1982).

(f) Faecal nitrogen composition

In order to evaluate any digestibility constraints, it is of value to know what proportion of the faecal nitrogen is of direct dietary origin, i.e. undigestible dietary substance, and what is of metabolic origin, i.e. primarily representing symbiotic bacteria. Diaminopimelic acid (DAPA) is specific to bacteria and its level in the faeces allows the estimation of bacterial nitrogen content of the faeces (cf Orskov 1982). The mean DAPA levels, in g/100g faecal dry matter, were determined as follows: Southern Cape (n = 3): 0,013%; Eastern Cape (n = 3): 0,017%; pooled (n = 6): 0,015%. Taking 0,8g DAPA as equivalent to 100g bacterial protein (Orskov 1982) and 16% of this protein as nitrogen, the percentage bacterial nitrogen of the total faecal nitrogen was calculated as follows (mean faecal nitrogen content of corresponding samples in parentheses): Southern Cape: 12% (2,14% N); Eastern Cape: 20% (1,71% N); pooled: 16% (1,93% N). The regional differences in bacterial nitrogen percentage cannot be accepted with confidence due to low sample sizes.

8.3.3.6 Long-term diet characterization with stable isotopes

Stable carbon isotope ratios have been used to assess animal diets and to reconstruct prehistoric diets of animals and humans (De Niro and

Epstein 1978a, Van der Merwe and Vogel 1978, Vogel 1978, Tieszen *et al.* 1979, Tieszen and Imbamba 1980, De Niro and Epstein 1981, Ambrose and De Niro 1986, Sealy *et al.* 1987, Van der Merwe *et al.* 1988, Tieszen *et al.* 1989). Studies of animals fed diets of known isotopic composition have demonstrated that the stable carbon and nitrogen isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of an animal's tissues are a function of those of its diet (e.g. Tieszen *et al.* 1983). When the isotopic compositions of important food resources are different, isotopic ratios of animal tissue can serve as indicators of food consumption and habitat use. Carbon isotopes may be used to discriminate between grazers and browsers in savanna grasslands, forest floor and savanna grassland herbivores and forest floor and forest canopy species (Ambrose and De Niro 1986). Nitrogen isotopes were used in the assessment of the proportions of legumes in the diet, distinguishing marine from terrestrial dietary contributions and the reconstruction of the proportions of animal food eaten (Sealy *et al.* 1987).

Carbon and nitrogen isotope data available for bushpigs from this study and other sources are given in Table 8/12.

| TABLE 8/12: STABLE ISOTOPE VALUES OF BUSHPIG COLLAGEN | | | | | | | |
|--|-----------------------|---|-------------|-----------------------|---|------------|----------------------------|
| LOCALITY | $\delta^{13}\text{C}$ | | | $\delta^{15}\text{N}$ | | | SOURCE |
| | \bar{x} | n | Range | \bar{x} | n | Range | |
| <u>Southern Africa</u> | | | | | | | This study* |
| Southern Cape | -21,0 | 5 | -20,3/-21,5 | + 7,9 | 5 | +5,3/+10,4 | |
| Eastern Cape | | | | | | | |
| Bathurst | -19,6 | 3 | -18,6/-20,4 | + 7,0 | 3 | +5,7/+7,9 | |
| Adelaide | -16,3 | 2 | -15,4/-17,3 | + 8,1 | 2 | +7,8/+8,4 | |
| Albany | -12,0 | 1 | | +11,2 | 1 | | Vogel (1978) |
| <u>Eastern Africa</u> | | | | | | | Ambrose and De Niro (1986) |
| Forest | -18,0 | 8 | -14,0/-23,4 | + 7,1 | 8 | +4,1/+9,5 | |
| Bush/Savanna | -21,1 | 4 | -19,9/-23,4 | | | | |
| | -14,7 | 3 | -14,0/-15,9 | | | | |
| Analyses were carried out at the Division of Earth, Marine and Atmospheric Science and Technology, CSIR (Dr J C Vogel) | | | | | | | |

The N isotope data (Table 8/12) does not appear to convey any particular information. No regional differences are evident, with the exception of the elevated value for the most arid locality (Albany). This is in

agreement with N isotope patterning over the moisture availability gradient (Sealy et al. 1987).

The carbon isotope values from both the study area and from Eastern Africa (Table 8/12) exhibit a congruent dichotomy over environments characterized by divergent nutrient and moisture status. The nutrient-poor, moister environments (Southern Cape, East African forest) are characterized by more negative carbon isotope values than those from the nutrient-rich, more arid parts (Eastern Cape, East African bush/savanna). The aridity gradient is also evident over localities within the Eastern Cape (localities of increasing aridity: Bathurst, Adelaide, Albany).

Plants making use of the C₄ and CAM (crassulacean acid metabolism) photosynthetic pathways have relatively high carbon isotope ratios and occupy habitats with tropical (warm, moist, exposed to solar radiations) and arid conditions respectively (Szarek and Ting 1977, Vogel et al. 1978, Tieszen et al. 1979, Winter 1985). Important dietary items of Eastern Cape bushpigs, such as *Aloe spp.* and *Rhoicissus digitata* (8.1.2.2), are reported to be CAM plants (Black and Williams 1976). The Albany carbon isotope value is apparently associated with a diet consisting of approximately 60% C₄ or CAM plants (Vogel 1978). According to its isotope values, the Southern Cape bushpig diet consists virtually exclusively of C₃-plant items. This is in agreement with the findings from stomach contents analysis (8.1.2.2)

8.3.3.7 Food requirements

(a) Stomach fill mass analysis

In Table 8/13, the stomach fill mass data from bushpigs with live mass > 50 kg, are summarized. Except where indicated otherwise, masses were derived from animals shot during the morning. Those of bushpigs shot in the evening were, on average, lower ($t = 2,403$ $df = 92$ $P < 0,05$).

| TABLE 8/13: BUSHPIG STOMACH FILL MASS DATA (kg) | | | |
|---|----------------|----|------|
| | \bar{x} (kg) | n | s |
| <u>Eastern Cape</u> | | | |
| Total | 3,67 | 64 | 1,67 |
| Males | 4,12 | 27 | 2,02 |
| Females: Non-reproductive | 3,28 | 17 | 1,26 |
| Pregnant | 3,13 | 12 | 1,00 |
| Lactating | 3,75 | 8 | 1,72 |
| <u>Southern Cape</u> | | | |
| Total | | | |
| Shot in evening | 2,75 | 44 | 1,35 |
| Shot in morning | 3,41 | 50 | 1,31 |
| Males | 3,70 | 21 | 1,56 |
| Females: Non-reproductive | 3,11 | 18 | 1,02 |
| Pregnant | 3,32 | 9 | 1,30 |
| Lactating | 3,35 | 2 | 0,78 |
| <u>Southern and Eastern Cape pooled</u> | | | |
| Males | 3,94 | 48 | 1,83 |
| Females | 3,27 | 66 | 1,19 |
| Natural food contents | 3,38 | 95 | 1,31 |
| Agriculturally dominated contents | 4,43 | 19 | 2,12 |

Stomach fill mass did not differ between the two regions ($t = 0,904$ $df = 112$ NS), nor between pregnant and non-reproductive females ($t = 0,065$ $df = 54$ NS). The slightly higher values of lactating females did not differ significantly from those of pregnant and non-reproductive females ($t = 1,158$ $df = 64$ NS). The mean male value was higher than that of females ($t = 2,367$ $df = 112$ $P < 0,05$) and the contents of stomachs dominated by agricultural food items were heavier than those where natural food items predominated ($t = 2,841$ $df = 112$ $P < 0,01$).

The stomach fill mass difference between the sexes is not necessarily biologically meaningful. Agricultural food items are normally more concentrated than natural food items and tend to be consumed *ad libitum*, which would explain the heavier stomach contents.

(b) Food consumption in captivity

The food consumption of a singly housed male bushpig (TE1) was monitored for a period of six months (July - November). During this period the

body mass of the animal remained stable at 88 kg. The mean daily food intakes for the six months averaged 1,99 kg (1,87; 2,28; 2,24; 1,94; 1,80; 1,81). The pelleted ration contained 14% crude protein, 8% crude fibre, 6% fat, 16% ash and 56% nitrogen-free extract. It consisted of 88% dry matter. The mean daily DM intake of this ration was thus 1,75 kg.

Scaled allometrically according to metabolic weight, a 70 kg bushpig would have consumed 1,47 kg DM of the pelleted ration. Based on digestibility coefficients derived for the domestic pig (ex Briedermann 1986) and the energy content of the food fractions (cf Schmidt-Nielsen 1979), the energy content of this daily intake is approximated for a 70 kg bushpig as 4 404 kcal, which is $\approx 1,6$ RMR or $\approx 2,6$ BMR (7.3.5: Table 7/27).

| | Digestibility | | Energy content |
|---------------------------------------|---------------|--------|-------------------------------------|
| PCP | 0,14 x | 0,80 x | 4,3 kcal/g x 1 470 g = 708 |
| PCF | 0,08 x | 0,43 x | 4,2 kcal/g x 1 470 g = 212 |
| PEE | 0,06 x | 0,70 x | 9,4 kcal/g x 1 470 g = 580 |
| NFE | 0,56 x | 0,84 x | 4,2 kcal/g x 1 470 g = <u>2 940</u> |
| Energy content of daily intake (kcal) | | | = <u>4 404</u> |

In this approximation, digestible energy is taken to be equivalent to metabolisable energy. According to Drennan and Maguire (1970), the mean ME of commercial rations was 95,5% of the DE and this assumption is therefore not considered to result in large-scale bias.

(c) Food requirements of free-ranging bushpigs

Based on an assumed total energy requirement of 4 235 kcal/day for a 70 kg bushpig (2,5 x basal metabolic rate; 7.4.6), the daily food requirement is approximated below (data from 8.3.3.2; 8.3.3.5).

One gram DM of the mean bushpig diet contains 2,72 kcal.

| | Content proportion | | Estimated digestibility | | Energy content | |
|-----|--------------------|---|-------------------------|---|----------------|-------------------------------------|
| PCP | 0,141 | x | 0,618 | x | 4,3 kcal/g | = 0,37 kcal/g |
| PCF | 0,202 | x | 0,581 | x | 4,2 kcal/g | = 0,49 kcal/g |
| PEE | 0,060 | x | 0,810 | x | 9,4 kcal/g | = 0,46 kcal/g |
| NFE | 0,472 | x | 0,704 | x | 4,2 kcal/g | = <u>1,40</u> kcal/g <u>2,72</u> |

The required energy may accordingly be obtained by $4\ 235\ \text{kcal} \div 2,72\ \text{kcal/g} = 1,55\ \text{kg DM}$ of the mean bushpig diet. Estimated daily dry matter food intake requirement for adult European wild boar ranged between 1,7 and 2,4 kg (Briedermann 1986). At a mean dry matter content of 25% of the bushpig diet (estimated from DM values of various food items given by McDonald *et al.* 1973), daily food intakes of 4,8 and 6,2 kg wet weight are derived for 50 and 70 kg bushpigs respectively.

8.3.4 Discussion

8.3.4.1 Adequacy of the diet

Diet quality may be evaluated primarily from the parameters of energy, protein and mineral content. Bushpig energy requirements were calculated above (8.3.3.6), but the actual food intake would have to be known for an assessment of energy available to individual animals. This information was not available, but energy balance was indirectly assessed from the condition of the animals (9.3). The lower apparent digestibility of energy substrates in the diets of bushpigs in low condition, noted above (8.3.3.5b), is relevant here. Starving animals appear to be less discriminating in their diet than satiated ones (Calow 1977). Individuals in poor condition were mostly solitary and presumably of low social rank. They may have suffered from poor digestion as a result of psychosocial stress.

Juvenile bushpigs have a higher dietary fat content (8.3.3.2). Dietary fat supplies essential fatty acids and young domestic pigs given diets adequate in energy, but deprived of fat, fail to grow (McDonald *et al.* 1973). Also, fat has a high energy content and digestibility (Schmidt-Nielsen 1979; 8.3.3.5a) and under negative energy balance, protein is used as an energy substrate and lost for growth (Comberg *et al.* 1978). A diet high in fat therefore makes good sense in the face of conflicting demands for protein (growth) and energy for thermoregulation (unfavourable surface to volume ratio in juveniles: 7.4.4).

The pregnant sow requires a dietary crude protein content of 13 - 14%, whereas growing individuals and lactating sows need 15 - 16% of crude protein (dry matter of diet; Groenewald and Boyazoglu 1980). For early growth, 22% crude protein is recommended (Maynard *et al.* 1979), while McDonald *et al.* (1973) even recommend 17% for lactating females. The generally recommended crude protein maintenance level is 14% (McDonald *et al.* 1973, Maynard *et al.* 1979). Dietary crude protein levels of only 12% were invariably found inadequate (Chamerlain 1972, Irvin *et al.* 1975).

Protein availability is especially important for the breeding sow. Lactating sows on a 12,5% crude protein diet had a lowered milk production and litter growth rate (Elsley and MacPherson 1972). Milk production is not solely dependent on the dietary level during lactation, but also on the entire nutritional regimen of the sow during her reproductive life (Mahan 1977). The level of crude protein and lysine in the lactation diet is also critical in relation to the rebreeding interval after the gilt is weaned (English *et al.* 1977).

On face value, the average crude protein content of bushpig diets (14,1%) appears to be adequate. Lactating females were apparently not capable of obtaining diets with significantly higher crude protein contents, nor did they have higher stomach fill masses (8.3.3.2; 8.3.3.7). This could be the result of a reduced foraging radius during lactation (6.3.2). Lactating bushpig females presumably rely on protein body reserves. Throughout the year, females select food items of animal origin significantly more than do males (8.1.2.2).

The crude protein content of Eastern Cape bushpig diets is only 1% higher than the Southern Cape average and the difference is not statistically significant (8.3.3.2). However, more of the Eastern Cape dietary protein is of animal origin (8.1.2) and therefore presumably of higher average biological value (cf McDonald *et al.* 1973). A high quality protein with a biological value of 90% meets the animals' requirements at a feed level of 12%, but with a biological value of only 60%, a 16% crude protein level is required (Groenewald and Boyazoglu 1980). Animal matter is the best source of essential amino acids, although fresh forbs, particularly legumes, provide reasonably high quality protein (Rérat 1972 ex Barrett 1978).

Evaluation of the adequacy of the diet in terms of digestible protein is discussed in section 8.3.4.2.

Calcium and phosphorus levels in bushpig diets were investigated (8.3.3.3). Both minerals are important in reproduction, but phosphorus deficiencies are more commonly associated with reproductive failure. Higher levels are required in the diets of lactating sows and growing animals (McDonald *et al.* 1973, Groenewald and Boyazoglu 1980). The calcium and phosphorus requirements of adult domestic pigs are given as 0,6% and 0,4% of dry matter intake respectively, while lactating females require 0,8% calcium and 0,6% phosphorus (Comberg *et al.* 1978). Other authors recommend somewhat higher levels (Maynard *et al.* 1979, Groenewald and Boyazoglu 1980).

Desirable Ca/P ratios range between 0,5 - 2,0 units of Ca/unit of P (Groenewald and Boyazoglu 1980) although there is evidence that domestic ruminants can tolerate much higher ratios (McDonald *et al.* 1973). Phosphorus, but not calcium, can be absorbed from the large intestine of the horse. This is believed to explain why excess dietary phosphorus greatly decreases calcium absorption, but excess calcium has a less dramatic effect on phosphorus absorption. Much of the excess Ca is absorbed in the small intestine and it is therefore not available to hinder P absorption from the large intestine (Hintz *et al.* 1978).

Mineral levels in bushpig stomach ingesta do not indicate Ca deficiencies, but phosphorus appears to be deficient in the Southern

Cape (0,203%). P levels in the diets of lactating females were significantly higher than in the case of other adults (0,62%; 8.3.3.3). The suggestion of Koen *et al.* (1988) that the P-deficiency in the diet, as well as a Ca/P imbalance, are possible population limiting factors for the Knysna elephants, is relevant. Most studies indicate that a P intake of 0,18% of an air-dried ration is near the minimal P requirement for growing cattle and lambs (Preston and Pfander 1964). According to Aibel *et al.* (1936 ex Maynard *et al.* 1979), the P requirement for growing pigs lies above 0,18%, but adequate levels are below 0,33%. We may tentatively conclude that P levels in the diets of Southern Cape bushpigs are very close to being limiting and that deficiencies are probably encountered under unfavourable nutritional circumstances.

8.3.4.2 Nutrient retrieval

The apparent digestibility of crude fibre was determined by the indicator method, mainly from Southern Cape samples. The value of 58% is relatively high compared with the apparent digestibility coefficient of crude protein (ca 62%) and with values of crude fibre of between 30 - 40% in the domestic pig (Schneider and Kirchgessner 1978). However, the digestibility coefficient for crude fibre is probably an overestimate. A part of the undigested residue may be broken down sufficiently to appear in the NFE of the faeces, instead of in the CF portion (Maynard *et al.* 1979). The digestibility coefficient of the nitrogen free extract is also unreliable because it may contain variable and unknown amounts of hemicellulose and lignin (Schneider and Kirchgessner 1978).

The apparent digestibility coefficient for crude protein is rather low and numerous factors may be involved. The most significant feature of nutrient retrieval is the apparent difference between the Southern and Eastern Cape, as shown by the feed to faeces crude protein ratios (Southern Cape: 1,00; Eastern Cape: 1,39; 8.3.3.5). This suggests greater protein availability per unit of dry matter intake in the Eastern Cape. It is paralleled by a high cell contents to lignin ratio in the Eastern Cape, estimated as follows (Tables 8/6 and 8/8):

% CRUDE PROTEIN + % ASH
% LIGNIN

The resultant ratio's are 1,79 for the Eastern Cape and 1,05 for the Southern Cape. Also, two of the ash components normally concentrated in fast-growing plant tissues, namely phosphorus and potassium (Weier *et al.* 1974), exhibit significantly higher concentrations in the Eastern Cape (8.3.3.3). A similar ratio, i.e. that between protein and fibre contents of leaves, has been found to be a better predictor of food selection by various primate species than either parameter on its own (Waterman 1983). Waterman *et al.* (1980) also found highly significant positive correlations between N-content and P-content and ash, and between ash and *in vitro* dry matter digestibility in food items from African rainforest vegetation. The overall impression is that of a higher mean tissue turnover and nutrient availability in food items consumed by Eastern Cape bushpigs (8.3.4.3).

Poor apparent digestibility of nitrogen associated with substances such as fibre, tannins and lignin is commonly reflected in increased faecal N concentrations (this study; Cornelius *et al.* 1977, Rérat 1978, Bryant and Kuropat 1980, Mould and Robbins 1980, 1981, Waterman *et al.* 1980, Sinclair *et al.* 1982, Sinclair *et al.* 1988). The interpretation of regional differences in feed to faeces crude protein ratios is somewhat problematic. Faecal nitrogen levels are influenced *i.a.* by dry matter digestibility, nondigestible fibre bound protein, metabolic faecal protein and tannin-bound protein (Robbins *et al.* 1987).

There are three possible causes for the regional differences, especially differences in the ratio of feed to faeces nitrogen:

- A high faecal N content may be the result of much undigestible N in the diet (a).
- Certain features of the diet may result in the increased production of microbial nitrogen (b).
- A link between metabolic rate and the rate of digestion may underly variable diet digestibilities. A low rate of digesta turnover may lead to disproportionately improved dry matter digestibility compared to that of nitrogen (c).

All three factors may be involved in the regional differences established in the study.

(a) Effects on true nitrogen digestibility

There is a well-established negative correlation between dietary fibre and digestibility (Waterman *et al.* 1980, Choo *et al.* 1981, Van Soest 1982, Stanogias and Pierce 1985a), and particularly the digestibility of protein (Bergner *et al.* 1975 *op. cit.* Rérat 1978, Shah *et al.* 1982, Low 1985). Fibre consists primarily of cellulose and lignin, which appear to have different effects on digestibility. Whereas cellulose induces increased microbial fermentation, thereby reducing apparent digestibility (b below), lignin and related substances (tannins) appear to affect true nitrogen digestibility. The source and level of fibre ingested, and primarily its degree of lignification, determines the value of feeds (Van Soest 1982) by affecting the rate or the amount of apparent absorption of nutrients (Comberg *et al.* 1978, Rérat 1978, Shah *et al.* 1982, Low 1985, Stanogias and Pierce 1985a). This may affect amino acids particularly because any which are not absorbed by the end of the small intestine appear to play no further role in the nutrition of the animal (Zebrowska 1973).

Crude fibre levels, which represent cellulose (Van Soest 1985), cannot explain the regional difference in relative faecal N in the bushpig populations studied since there is no difference in crude fibre levels between the Southern and Eastern Cape. Lignin levels are however significantly higher in the diet of Southern Cape bushpigs and presumably underly this difference. Per unit of dietary N, the bacterial caecal N in the two regions is similar and the additional faecal N in Southern Cape samples appears to be from undigested dietary nitrogen (8.3.3.5f). This interpretation is in line with the findings of Shah *et al.* (1982) which indicate that cellulose increased the excretion of endogenous faecal N per unit of food intake, whereas the excretion of dietary faecal N remained the same. Lignin on the other hand decreased the biological value of the dietary nitrogen. This interpretation is further supported by Milne and Bagley (1976) who found that as increasing amounts of grass (high cellulose content) were fed to sheep at the expense of heather (high in phenols like tannins and

lignins), the excretion of undigested dietary N in the faeces decreased, but the quantity of non-dietary N (mainly of microbial origin) in the faeces increased.

The effect here attributed to lignin is most often reported to be associated with non-lignin phenolics, mainly condensed tannins. However, the chemical boundary between tannins and lignins is not distinctly defined. Tannin and lignin levels are often correlated and are reported to exert similar effects on the availability of both dietary carbohydrates and protein (Swain 1979). Tannins tend to depress the nutritive value of the diet by reducing voluntary intake and digestibility. This is attributed to complex binding of the tannins with the nutrients, mainly proteins, and inhibition of digestive enzymes (McLeod 1974, Waterman *et al.* 1980, Choo *et al.* 1981, Robbins *et al.* 1987). This effect is often associated with increased faecal nitrogen excretion (e.g. Mould and Robbins 1980). Various researchers have found that variation in nutritional value and polyphenol content influence the performance of the growing pig (Harris *et al.* 1970, Tanksley 1975, Ford 1977, Sharp *et al.* 1977, Almond *et al.* 1979, Cousins *et al.* 1981, Kemm *et al.* 1981, Noland *et al.* 1981, Kemm *et al.* 1984, Mitaru *et al.* 1984).

No differences were detected in the levels of total soluble phenolics or condensed tannins in the stomach ingesta of bushpigs from the two regions. Regional differences in apparent or true digestibility cannot therefore be attributed to these substances. Total soluble phenolic levels did however inhibit microbial fermentation in bushpigs of both regions, thereby presumably limiting the intake of common dietary items high in these substances. This is in agreement with what an increasing number of authors are finding, namely that soluble phenolics often do not inhibit digestion, but rather reduce intake through their toxicity to digestive microbes (e.g. Robbins *et al.* 1987, Meyer and Karasov 1989).

It was suggested above that the regional difference in feed to faeces N ratio may be due to the divergent nutrient: lignin ratio of the dietary cell contents. Lignin may play a role in rendering nutrients unavailable for assimilation. Reviews on the occurrence, formation, structure and reactions of lignin are given by Brauns and Brauns (1960)

and Sarkanen and Ludwig (1971). The negative impact of lignin on digestibility is well known (Comberg *et al.* 1978, Parra 1978, Shah *et al.* 1982, Van Soest 1982, 1985). Lignins, when degraded to a soluble form, can act like tannins (Van Soest 1982). Lignins interfere with digestion through their propensity to bind to a variety of nutritional substances and digestive enzymes (e.g. Hoyt and Goheen 1971, Leitzmann *et al.* 1979, Swain 1979, Kritchevsky 1986, Howe and Westley 1988). In particular, lignin has been found to decrease the biological value of dietary nitrogen (Shah *et al.* 1982). In altering the dietary amino acid composition it may reduce the utilization of digestible protein (cf Comberg *et al.* 1978).

Lignin levels increase with maturation of plant tissues (Brauns and Brauns 1960, Sarkanen and Ludwig 1971) while nitrogen and ash levels decrease (Phillips and Goss 1935, 1939). Nutrient retrieval by herbivores must be influenced by more than lignin levels *per se* and should be viewed in the wider context of plant life history strategies and environmental interactions, involving growth rates, tissue turnover and longevity (8.3.4.3).

It appears that plants growing under nutrient poor conditions tend to produce polyphenolic substances (tannins, lignins) which form complexes with other plant constituents that are not readily broken down. These give rise *i.a.* to the formation of mor humus (Handley 1961). Sarkanen and Ludwig (1971) reported that plants growing under low Ca-levels tended to be more heavily lignified than when Ca-levels were high. Lignin concentration is an excellent index for the prediction of the rate of disappearance of forest litter samples. Litter which decomposers break down slowly tends to have high carbon/nitrogen ratios (Meentemeyer 1978). The high lignin content of bushpig food in the nutrient poor Southern Cape and the limited availability of food there in comparison to the Eastern Cape, are in agreement with these findings.

(b) Microbial faecal nitrogen excretion

Diets rich in relatively poorly digestible carbohydrates (e.g. cellulose, certain starches) result in enhanced microbial fermentation in the lower digestive tract and thus increased excretion of microbial

nitrogen (Mason and Palmer 1973, Mason *et al.* 1976, Rérat 1978, Gargallo and Zimmermann 1981, Shah *et al.* 1982, Low 1985). The higher proportion of faecal N/unit of intake in the Southern Cape (8.3.3.5f) could be attributable to a relatively lower apparent digestibility of the bushpig diet in this region. Although not reflecting true N digestibility, the increased faecal N losses are nevertheless inevitable and therefore meaningful in respect of the nitrogen economy of the animals concerned (cf McDonald *et al.* 1973).

(c) Digestive turnover and relative efficiency

The concentration of faecal N is related to the amount of N lost and the extent of its dilution by undigested dry matter (Arman *et al.* 1975). For example, the change from restricted to *ad lib* feeding, for a given level, brings about a reduction in dry matter digestibility through its influence on the rate of passage of the digesta (Rérat 1978). The digestibility of cellulose increases with retention time (Van Soest 1985) and its efficient use would result in a high faecal N concentration (Arman *et al.* 1975). It appears that any dietary factor which increases retention of digesta leads to improved dry matter digestibility and thus an increased proportion of faecal nitrogen. This could partly explain the differences in relative faecal N concentrations between bushpigs from the Eastern and Southern Cape.

8.3.4.3 Nutritional consequences of plant/environment interactions

The availability of nitrogen and phosphorus most frequently limit growth rate. Due to the inefficiency with which the limiting resources critical for growth are withdrawn from leaves and subsequently re-utilized, prolonged tissue life is a major mechanism by which the efficiency of resource use is maximized in resource-poor environments (Bloom *et al.* 1985). Long-lived tissues are therefore advantageous in such environments where scarce resources are expensive to acquire and rapid growth rates cannot be supported (Bloom *et al.* 1985). Habitats of high and moderate fertility are most effectively exploited by competitive and ruderal species which have high relative growth rates. Photosynthetic rates decline with leaf age and nutrient absorption capacity declines with root age, so that maintenance of both processes

depends upon rapid tissue turnover (Chapin 1980). Rates of tissue turnover are highest in species adapted to resource-rich environments because these species are selected to maximize rates of acquisition and growth even at the expense of efficiency in resource use (Bloom *et al.* 1985). Infertile soils are accordingly most successfully exploited by stress-tolerant plant species whose inherently low growth rates can be adequately maintained by their low capacities for photosynthesis and nutrient absorption. Compared to rapidly growing plants in fertile habitats, such plants require a longer period of growth before accumulating sufficient reserves for reproduction (Chapin 1980).

These interactions have profound effects on the composition of plant material as food for herbivores. Since nutrient stress has a greater effect upon growth than on photosynthesis and net assimilation rate, nonstructural carbohydrate concentrations rise above levels immediately needed for growth (Chapin 1980). The long-lived tissues produced by species adapted to infertile soils commonly have low nitrogen and mineral contents, i.e. nutrients associated with rapid tissue turnover, but accumulate higher concentrations of carbon-rich compounds, such as lignin, lipids or resins (Chapin 1980, Bloom *et al.* 1985). Plant tissues from infertile sites are often associated with more structural material, more accumulated non-structural carbohydrate and lower protein contents i.e. they have low N/C ratios (Chapin 1980, Muller *et al.* 1987). In addition, plants grown where little nitrogen is available have a larger proportion of leaf protein associated with tissue maintenance and structure than those on fertile sites that have high concentrations of photosynthetic enzymes (Bloom *et al.* 1985). Also phosphorus and potassium accumulate in tissues that are growing rapidly (Weier *et al.* 1974).

These patterns are reflected by the nature of bushpig diets in the two regions (8.2.3, 8.2.4, 8.3.3, 8.3.4). Diet in the base-rich Eastern Cape is characterized by comparatively high levels of mineral nutrients associated with fast plant tissue turnover. The Eastern Cape diet also includes a higher proportion of vertebrate animal protein. The Southern Cape bushpig diet, on the other hand, has higher levels of non-structural carbohydrates and lignin and a lower apparent digestibility, as manifested by the relatively high faecal N levels (8.3.4.2). It is

now also clearer why Waterman *et al.* (1980) found the gross energy content of leaves from African rainforest vegetation to be persistently negatively correlated with digestibility.

These fundamental differences in herbivore diets may be summarized and quantified by a turnover potential ratio (TPR) as defined below. This ratio is linked to plant tissue turnover capacity as determined by adaptation for optimal interplant competition under the environmental conditions of the area in question.

$$\text{TPR} = \frac{\text{Production nutrients in diet}}{\text{Maintenance nutrients in diet}}$$

Production nutrients are those critical for plant growth and reproduction, namely protein and ash minerals. For the purpose of the ratio, nutrients originating from animal material in the diet are included. Maintenance nutrients are those related to structure and energy storage. They are metabolically more inert and typically associated with lower levels of plant tissue turnover, denoting tissue longevity (non-structural carbohydrates and lignin). TPR values (Percentage crude protein + percentage ash ÷ percentage total soluble carbohydrates + percentage lignin) calculated for Eastern and Southern Cape bushpig diets were 1,11 and 0,64 respectively.

McNab (1980) suggested that a fundamental relationship existed between the rate of metabolism of a mammal and its body size, as well as the temporal and spatial quantity and quality of its food. He showed that animals living on the leaves of woody plants (folivores), fruit and invertebrates had low basal metabolic rates. Those that fed on grasses, herbs, nuts and vertebrates had high basal metabolic rates (McNab 1986). What is immediately apparent is that food items high in production nutrients are associated with high metabolic rates while those high in structural and non-structural carbohydrates (sugars, starches, lipids) are associated with low metabolic rates. It thus appears that the TPR of the diet as defined above is an excellent predictor of metabolic turnover rate. This has implications for longevity and turnover in the herbivores analogous to those applicable to the plants serving as prey

for the herbivores. These interactions are further explored in subsequent chapters, with a synthesis in Chapter 12.

McNab (1986) was not sure whether particular food habits lead to high basal rates of metabolism or whether animals with high basal rates select particular food habits. It appears that it works either way. Circumstantial evidence indicates that the dietary TPR is continuously monitored and cumulatively cues the appropriate metabolic rate setting. For example, Sherry *et al.* (1981) found in domestic pig trials that increased fibre levels, particularly in combination with an antibiotic, resulted in lowered metabolic rates and increased feed efficiency. Segregation of protein and starches in human diets for weight loss purposes (Grant and Joice 1984) presumably works according to the same principles. The undiluted dietary protein probably cues the body to a higher metabolic rate, leading to a reduction in fat storage.

On the other hand, depending on whether the storage or production mode is appropriate, as in pregnancy (for maximum nutrient retention) or lactation (for maximum milk production), animals may select a diet in accordance with the metabolic requirements. During pregnancy a low metabolic rate favours nutrient storage. A low TPR would be appropriate and it is noteworthy that pregnant bushpigs select a diet high in crude fibre/cellulose (8.3.3.2). Several studies on gestating sows have suggested that the digestion of dietary fibre increases during gestation (Low 1985). A high TPR and metabolic rate would favour maximum milk production and lactating bushpig sows select a diet high in ash minerals, especially phosphorus (8.3.3.2; 8.3.3.3) in accordance with this. Production nutrients are most effectively obtained from fast-growing plant tissues where nitrogen and phosphorus, among other elements, are concentrated (cf Joubert *et al.* 1969, McDonald *et al.* 1973). Concurrence of lactation with the growing season in spring thus makes good sense (10.3.5).

The turnover potential ratio (TPR) of plant material reflects the ratio of tissue expansion (growth) to tissue consolidation (storage, cell wall thickening, lignification, polymerization). Photosynthesis is required for both tissue expansion and consolidation, but growth is more critically affected by soil nutrients whereas photosynthesis is

dependent on temperature and water. The TPR thus indicates the growth/unit of photosynthesis and the dietary TPR serves as an index of resources available for reproduction of the herbivores concerned. It does not serve as an index for maintenance or energy balance. The low TPR of the diet of Southern Cape bushpigs is associated with relatively high levels of energy storage (9.3.2), but comparatively low reproductive turnover when compared with Eastern Cape bushpigs (10.3.6).

Like the TPR, it appears that carbon isotope ratios reflect the degree of plant tissue expansion in relation to tissue consolidation.

- (I) The carbon isotope composition of the plant material formed is highly correlated with the type of photosynthetic cycle followed by the organism (Deines 1980). Plants following the C_4 -pathway of carbon fixation have higher $\delta^{13}C$ values compared to plants following the C_3 -pathway. The productivity of C_4 plants is also higher than that of C_3 plant species (Schrader 1976). The isotopic composition of CAM plants covers the whole range of C_3 and C_4 plants, depending on environmental conditions. CAM plants under environmental conditions favouring the C_4 photosynthetic pathway have high $\delta^{13}C$ isotope values.
- (II) Well-nourished plants have higher carbon isotope values than plants deficient in nitrogen or potassium (O'Leary 1981).
- (III) Carbon isotope ($\delta^{13}C$) values decline over plant fractions according to the sequence below (Deines 1980).

Amino acids, hemicellulose, sugars > cellulose > lignin >> lipids.

Fat tissues are by far the most depleted of $\delta^{13}C$ (De Niro and Epstein 1977, 1978b, O'Leary 1981, Tieszen *et al.* 1983). In CAM plants, Lerman (1975) found the insoluble fraction (mainly carbohydrates) to be more depleted of $\delta^{13}C$ than water extracts of the same plants (mainly malate). The insoluble fraction of older leaves had even more negative $\delta^{13}C$ values (Lerman 1975).

- (IV) As the growing season progressed, the $\delta^{13}C$ values of maple leaves and a grass species at the same locality decreased (Lowdon and Dyck 1974).

This pattern parallels the expected trend in the turnover potential ratio. It is concluded that carbon isotope values ($\delta^{13}\text{C}$ values) of herbivore collagen may directly and reliably predict the TPR of the diet available to the herbivores involved.

Using the nutritional indices of crude protein feed to faeces and collagen isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), the same regional dichotomy is evident for both bushpigs and elephants (Table 8/14).

| TABLE 8/14: BUSHPIG AND ELEPHANT FEED TO FAECES CRUDE PROTEIN RATIOS AND COLLAGEN ISOTOPE RATIOS FOR THE SOUTHERN AND EASTERN CAPE | | | |
|--|----------------|----------------|---|
| INDEX | Southern Cape | Eastern Cape | SOURCE |
| <u>Feed to faeces crude protein ratio</u> BUSHPIG ELEPHANT | 1,00 1,27 | 1,39 1,65 | This study From data of Koen <i>et al.</i> (1988) |
| $\delta^{13}\text{C}$ (‰) BUSHPIG ELEPHANT | -21,0 -23,6 | -16,0 -17,0 | This study Largely ex Van der Merwe <i>et al.</i> (1988) |
| $\delta^{15}\text{N}$ (‰) BUSHPIG ELEPHANT | + 7,9 + 2,1 | + 9,1 +11,9 | This study Vogel <i>et al.</i> (1990) |
| Turnover Potential Ratio (TPR): Bushpig | 0,64 | 1,11 | This study |

The differential availability of production nutrients compared to maintenance nutrients, as documented *inter alia* by the indices in Table 8/14, has definite implications in terms of bushpig reproduction, energy economy and population dynamics. Southern Cape bushpigs have a lower reproductive turnover, greater levels of energy storage and increased longevity, as outlined in subsequent chapters. The patterns are paralleled by the life history tactics of the prey plants (Chapter 12). Similar nutritional constraints and regional differences apparently apply to elephants, throwing new light on the poor performance of the Knysna elephant population.

8.4 Ecological impacts of bushpig foraging

Foraging impacts of suids relate to:

- (I) the edaphic environment (soil layers; ground exposure),
- (II) the disturbance of plant communities,
- (III) seed predation, and
- (IV) predation on invertebrate and vertebrate animals.

These effects are usually limited in extent due to comparatively low population densities. However, specific ecological consequences, although important, may be less obvious and difficult to elucidate or quantify. Gross negative and lasting impacts commonly result when suids are introduced into foreign environments (Wood and Barrett 1979, Tisdell 1982).

The rooting action of European wild boar during foraging exposes and loosens the soil surface and affects the structure of the upper soil strata. This results in aeration and mixing of the raw humus or humus layer with the A horizons and in reduced litter cover (Bratton 1974, Bratton 1975, Howe and Bratton 1976, Hennig 1981, Singer *et al.* 1984, Briedermann 1986). Through this mixing of ground surface and soil layers or the removal of patches of litter, plant seeds may be buried and suitable conditions created for germination (Briedermann 1986).

Levels of soil organic matter, cation exchange capacity and acidity increased on rooted sites, whereas percentage base saturation declined (Lacki and Lancia 1983). These changes suggested that rooting stimulated organic matter decomposition and soil nutrient mobilization. The greater intensity and duration of the impact, the greater were the effects (Lacki and Lancia 1983). According to Singer *et al.* (1984) wild boar rooting accelerated the leaching of Ca, P, Zn, Cu and Mg from leaf litter and soil. Nitrate concentrations were higher in the soil, soil water and stream water from the rooted stands, suggesting alterations in the nitrogen transformation process. These effects resulted from high densities of up to 7 - 9 animals/km² (Singer *et al.* 1984). The findings of Lacki and Lancia (1983) and Singer *et al.* (1984) relate to introduced

European wild boars in foreign environments (USA) and were therefore probably particularly pronounced. However, removals of boars from native habitats are suspected to have decreased the rate of nutrient cycling, thereby affecting the stability of some European forests (Grodzinski 1975 ex Lacki and Lancia 1983).

The role of suid rooting as a soil disturbing agent should however not be overestimated. Except under mast fruiting conditions, rooting action is localized and population densities are relatively low (Briedermann 1968). Attempts to quantifying the effect yielded estimates of ca 4 ha of soil surface moved per annum and individual (Kozlo 1975 ex Briedermann 1986) or 4% of the forest area/annum (Jezierski and Myrcha 1975). However, on areas seemingly entirely rooted over, only about 20% was in fact really mixed through (Briedermann 1986).

Foraging by European wild boar in newly occupied environments is reported to have substantial impacts on ground vegetation. Rooting activities have severely damaged the herbaceous understoreys of several types of forest in the Great Smoky Mountains National Park in the United States of America. Selective feeding directly reduced the populations of a number of plant species, with certain species being more affected than others. Modifications of the normal successional processes were postulated (Howe and Bratton 1976). Generally Howe *et al.* (1981) concluded that wild boar significantly reduced herbaceous and subterranean forages in mesic herb communities within northern hardwood forests.

Where suids occur in their native habitats, the effects on the vegetation are apparently much less spectacular. An exception here is the patchwise removal of bracken (*Pteridium aquilinum*) through extensive foraging on its rhizomes (Hone 1980, Hennig 1981, Briedermann 1986). In this process a smothering vegetation cover is often removed and the soil exposed, favouring the regeneration of other species (Briedermann 1968, 1986). Other vegetation communities seldom have the same value as bracken rhizomes as a staple diet and are therefore not affected extensively. The effects of seed consumption appear to be mainly destructive, plant propagules being substantially, but seldom totally eliminated (Briedermann 1986).

Two vertebrates that depend largely on leaf litter for habitat, the red backed vole (*Clethrionomys gapperi*) and short-tailed shrew (*Blarina brevicauda*) were nearly eliminated from intensely rooted stands in the Great Smoky Mountains National Park (Singer et al. 1984). In Europe, Hennig (1981) suggested a regulatory effect of wild boar foraging on ground breeding birds, certain reptiles and rodents under particular conditions. Consumption of insect pests by wild boars is not considered effective in the control of outbreaks (Briedermann 1976, Hennig 1981). Even with relatively high population densities, the European wild boar is not capable of reducing insect populations below the critical levels required to prevent eruptions (Briedermann 1968, 1986).

Foraging effects of bushpigs

(I) Disturbance of the edaphic environment

The localized effects of rooting on soil discussed above are probably also brought about by bushpig foraging. Mixing of soil layers, aeration and exposure is presumably responsible for the creation of favourable conditions for germination of various plant seeds (cf Phillips 1926a and b). For example, Geldenhuys (1975) found that covering *Podocarpus falcatus* seeds with soil increased their probability of germination.

The extent of soil disturbance per 24 h period in the study enclosure was visually estimated. The part of the enclosure under indigenous forest covered approximately 3 000 m². Any square meter of surface area which had some rooting disturbance was taken as "disturbed". On average 32% of the 0,3 ha was disturbed within any 24-hour period (n = 35); i.e. a ground surface disturbance rate of 0,1 ha/day/family group of 4 animals applied. This amounts to 36 ha/annum, disregarding overlap in rooted areas and corresponds to about 5% of the average home range area per annum (720 ha: 6.2.1.1). The technique overestimated disturbance so that in reality only about 1 - 2% may be considered truly affected. The meaningfulness of these calculations is uncertain. Although the area affected by surface disturbance is probably insignificant, it may have special ecological significance in local habitat types where concentrations of bushpig food occur. Examples are below suitable fruiting trees, in senescent bracken stands (Plate 11a, page 410), at

mesic or phreatic sites or in patches with concentrations of *Rhizopogon* fruiting bodies.

(II) Impacts on plant communities

Due to the difficulty of studying the possibly subtle influences of bushpig disturbance on plant communities, virtually nothing is known about them. Extensive rooting in bracken stands is an exception (Plate 11a, page 410). Bracken is widespread on suitable sites in large gaps or at the forest edge. Soil disturbance tends to accentuate the competitive ability of pioneers by removing established, rooted plants and bringing seeds to the surface or allowing opportunities for fresh seed to germinate in bare soil (Fox 1976). Bushpig rooting in bracken stands is therefore likely to favour the continuation of succession towards scrub or forest.

(III) Seed predation and propagule dispersal

In most cases the seeds consumed by bushpigs were destroyed by chewing or digestion. However they have been reported to act as seed dispersing agents (Phillips 1926a, 1928, 1931, Breytenbach 1979, Breytenbach and Skinner 1982, Ghiglieri *et al.* 1982). During this study uncrushed seeds of *Olea capensis* ssp *macrocarpa* and *Podocarpus latifolius* were observed in bushpigs faeces. Some of these seeds also germinated (Plates 10a and 10d, page 406). Only a very small percentage of intact *Podocarpus latifolius* seeds germinated after passage through the digestive tract of the bushpig. The process was monitored on two occasions; 2 of 372 and 5 of 124 seeds had germinated, in contrast to high germination percentages of uneaten seeds. However, the ecological importance of dispersal may be greater than these findings suggest. Bushpigs tend to defecate preferentially in open patches or patches devoid of ground vegetation (5.1.2.1), thus selectively depositing seeds in favourable regeneration sites. They also move far and thereby may contribute to gene flow of otherwise relatively heavy and immobile propagules. Phillips (1926a) listed many more species of which the seeds were believed to be dispersed by bushpigs in the Southern Cape but this requires further verification.

The role of mycophagists in fungal spore dispersal is well established (Trappe and Maser 1977, Kotter and Farentinos 1984). Hypogeous micorrhizal fungi, such as *Rhizopogon*, depend on mammal mycophagists for dispersal (Trappe and Maser 1977). Spore dispersal may enhance the invasion of non-forested vegetation types by ectomicorrhizal tree species. Seeds of micorrhizal hosts that germinate near the spore-containing faeces are provided with micorrhizal inoculum (Maser, Trappe and Nussbaum 1978). Bushpigs in the Southern Cape may play a role in this regard.

(IV) Predation on invertebrate and vertebrate animals

Bushpig population densities are very low and the ingestion of live vertebrates and invertebrates is opportunistic. Effects on animal populations are therefore considered negligible. Predation on rain frogs (*Breviceps fuscus*) in the Southern Cape may be an exception, since considerable numbers are apparently consumed (8.1.2.2) and this may constitute a significant mortality factor for this frog species.

8.5 Synopsis

- (I) The bushpig diet was composed of 40% subterranean plant parts (mainly tubers and rhizomes), 30% herbage, 13% fruit, 9% animal matter and 8% fungi. In the Southern Cape relatively higher proportions of herbage, fruit and fungi were found. In the Eastern Cape the proportions of subterranean plant organs and animal matter were comparatively higher.
- (II) The most important dietary items in the Southern Cape were underground fungal bodies of *Rhizopogon*, bracken rhizomes and *Blechnum punctatum* fronds. In the Eastern Cape tubers of Vitaceae (*Rhoicissus* and *Cyphostemma*), vertebrate animal matter and foliage of *Aloe ciliaris* predominated.
- (III) With its bunodont dentition, monogastric digestive system and adaptations for rooting the bushpig is adapted to an omnivorous diet. Dietary items are procured from a feeding stratum of $\pm 0,5$ metre above and below ground surface. Suitable dietary items

generally occur in woody vegetation types and are typically scattered in space and time.

- (IV) The average bushpig stomach ingesta contained 14,1% crude protein, 20,2% crude fibre, 6,0% ether extract, 12,4% ash minerals and 47,2% nitrogen-free extract. Eastern Cape bushpig diets and those of lactating females of both regions exhibited higher ash, phosphorus and calcium percentages. The crude fibre contents of the diets of pregnant females was higher than that of non-reproductive or lactating females. Eastern Cape diets had lower lignin levels than those of the Southern Cape (22,3% versus 17,0%) while the reverse was found for soluble carbohydrate levels (10,3% 14,2%). Liver trace element levels were comparable to those of other suids.
- (IV) Using acid-insoluble ash as marker substance in the indicator method revealed the following mean digestibilities (for Southern Cape bushpigs): 61,8% for crude protein, 58,1% for crude fibre, 81,0% for ether extract and 70,4% for nitrogen-free extract. A significantly higher crude protein feed to faeces ratio in Eastern Cape as against Southern Cape bushpigs suggests a higher protein digestibility in the Eastern Cape.
- (VI) Staple foods (bracken rhizomes, *Blechnum* fronds and Vitaceae tubers) contained relatively high levels of polyphenols which were shown to inhibit microbial fermentation.
- (VII) Differences in the nutritional content of the diets between the two regions were characterized by the turnover potential ratio (TPR). This ratio quantified nutritional differences with causal significance in respect of life history features of the populations concerned (8.3.4.3, 12).

9. GROWTH, ENERGY STORAGE AND CONDITION EVALUATION

9.1 Introduction

The general level of well-being of an animal is usually termed "condition" and is taken to be linked to the individual animal's chances of living or dying. Condition is an important factor in respect of mortality and reproduction (Caughley 1971, Hanks 1981). Condition of an individual or a population may be indexed by a variety of parameters, including fat reserves, blood haematology and chemistry and aspects of body growth (Hanks 1981).

The ability of animals to maintain a positive energy balance largely determines their productivity and genetic contribution (Hudson 1985). Tissue accumulation as growth or storage is central to animal condition and thus to survival and reproduction. Storage implies the ingestion and deposition in body tissues of any nutrient for which there is no immediate metabolic demand, but which may be utilized later for maintenance, growth or reproduction (Pond 1981). Few organisms have a food supply which is so regularly available in sufficient quantity that no storage is necessary. Mammals typically employ fat as an energy reserve due to its high energetic density per unit of weight or volume (Pond 1981). Reserve materials are important in supporting the individual through periods of hardship, and failure to accumulate or to maintain reserves as a result of reproduction might contribute to a reduction in survival and subsequent fecundity (cf Calow 1979).

The trade-off between maternal storage and subsequent reproduction is clearly shown by the preweaning growth rates of offspring. Growth rates of sucking young are proximate determinants of the demands of lactation, which may influence the frequency of reproduction and other population phenomenon (Calow and Townsend 1981, Hudson 1985). A more direct trade-off appears to exist between the early onset of breeding, resulting in a reduction in growth rate and adult size, and survival risks or a lowered subsequent reproductive rate (cf Calow 1981).

The patterns of body tissue accumulation or mobilization may be viewed as the overt expression of energy and matter balances, representing the

integration of animal adaptations to optimize resource accumulation in a variable physical and biotic environment (Robbins and Robbins 1979). It has accordingly been suggested that reproductive effort, growth rates, parental dependence periods, age of sexual maturity and many other processes dependent on tissue accumulation or growth represent short- and long-term feedback systems whose balancing capabilities determine species survival (cf Case 1978a). Some of these interacting phenomena in the bushpig are investigated in this chapter. They form the basis for interpreting reproductive tactics (10) and life history strategies (12).

9.2 Methods

Morphometric data (body mass, total body length and hind foot length) were obtained from captive and free-ranging bushpigs captured or shot in the Southern and Eastern Cape (1.3.1.3, 1.3.1.4, 1.3.2.1, 1.3.2.3, 1.3.4). The body mass of each whole bushpig was measured using a Salter spring balance of 100 kg capacity. Juveniles below 10 kg were weighed with a similar balance of 10 kg capacity. In some cases the carcass mass, i.e. without head, skin, entrails and lower foot limbs, was also determined. The body measurements followed Ansell (1965):

- (I) Head and body length: measured along the contours of the body from the tip of the snout to the junction of the tail with the body;
- (II) Hind foot length: the linear measurement from the point of the hock to the tip of the hoof.

Age was determined from tooth eruption and wear patterns according to Seydack (1983), with expected levels of accuracy of 1-3 months for 1-2 year olds, 3-6 months for 3-4 year olds and 0,5-3,0 years for animals 4 years and older.

After skinning the animal, a visual assessment was made of the condition based on body coverage with subcutaneous fat. It was allocated to one of three classes: "fat", "average" or "lean". The thickness of the subcutaneous fat layer was measured or estimated at 3 different localities on the body surface: shoulder, back and thorax (1.3.2.3). In

addition, the thickness of the peritoneal fat layer was determined by slicing perpendicularly through the layer at various places and recording the maximum measurement obtained.

Between 2-10 g of marrow was taken from the combined humerus and femur bones of each animal (1.3.2.3). Only the marrow from the central section of each bone was used so as to avoid the haemopoietic tissue at the ends. Bone marrow collections were made from 189 culled bushpigs. Sampling was concentrated on animals 2 years and older, since bone marrow is considered to be of limited use as a measure of condition in younger animals (Hanks *et al.* 1976). Only 34 yearling samples were collected for comparisons within this age class. The marrow samples were oven-dried at 105°C for 4 days to constant mass. Dry mass was then expressed as a percentage of fresh mass. The dried samples were transferred to a Soxhlet apparatus for fat extraction with petroleum ether (b.p. 30-60°C) for 4-6 hours. The results allowed the calculation of the percentage fat where fat mass was expressed as a percentage of the fresh mass of bone marrow.

Blood samples, both for haematology and blood chemistry, were collected from immobilized, captured free-ranging animals (1.3.1), from free-ranging shot individuals (1.3.2) and from periodically immobilized captive animals (1.3.4). Blood samples were not taken from bushpigs killed during hunts where dogs were used because uncontrollable effects were expected to influence blood parameters. The blood collection procedure is described in section 1.3.1.3. During 1981, only the haemoglobin, packed cell volume, total protein, albumin and globulin were analysed by a private laboratory. In the subsequent years, improved logistics allowed a fuller complement of blood parameters to be investigated, including haemoglobin, packed cell volume, MCHC, MCV, red and white blood cell counts, glucose, protein, albumin, globulin, triglycerides and cholesterol. The analyses were performed by the George Hospital Laboratory (George) using standard clinical methods.

9.3 Results

9.3.1 Growth and body size

Body mass in adult bushpigs (3 years and older), separated by sex and region, was as follows:

| | | n | \bar{X} (kg) | s |
|-----------------|---------|----|----------------|-------|
| Southern Cape : | Males | 84 | 70,0 | 8,949 |
| | Females | 82 | 68,6 | 7,944 |
| Eastern Cape : | Males | 21 | 72,0 | 8,763 |
| | Females | 32 | 62,7 | 8,654 |

Body mass differs significantly between males and females in the Eastern Cape ($t = 3,81$ $df = 51$, $P < 0,001$), but not in the Southern Cape ($t = 1,07$ $df = 164$, NS). Male body mass is similar in both regions ($t = 0,92$ $df = 103$, NS), but females in the Eastern Cape are lighter, on average, than those in the Southern Cape ($t = 3,47$ $df = 112$, $P < 0,001$). No trend in body mass over season is evident in bushpig males (Table 9/1).

| | | SUMMER Dec - Feb | AUTUMN March - May | WINTER June - Aug | SPRING Sept - Nov |
|---|-----------|---------------------|-----------------------|----------------------|----------------------|
| MALES | \bar{X} | 67,8 | 72,0 | 69,9 | 71,3 |
| | s | 7,192 | 10,734 | 8,727 | 8,622 |
| | n | 28 | 22 | 25 | 36 |
| FEMALES | \bar{X} | 64,3 | 64,8 | 67,8 | 69,1 |
| | s | 8,393 | 8,211 | 7,762 | 8,976 |
| | n | 24 | 18 | 40 | 34 |
| Data for animals 3 years and older, pooled over regions | | | | | |

The average body mass of females in summer is lower than in spring ($t = 2,06$ $df = 56$, $P < 0,05$: Table 9/1). Since pregnancies are concentrated in spring and lactations in summer (10.3.5), female body mass was investigated in relation to reproductive state.

| | n | \bar{X} (kg) | s |
|----------------------------------|-----|----------------|-------|
| All adult females (both regions) | 114 | 66,9 | 8,147 |
| Pregnant females | 36 | 70,8 | 8,480 |
| Lactating females | 11 | 59,9 | 8,868 |

The average body mass of pregnant females is significantly higher than the female average ($t = 2,48$ $df = 148$, $P < 0,05$), whilst lactating sows are significantly lighter ($t = 2,70$ $df = 123$, $P < 0,01$).

The available linear morphometric data is summarized in Table 9/2.

| SEX | AGE CLASS | n | \bar{X} | s | RANGE |
|---|-----------|----|-----------|-------|---------------|
| TOTAL BODY LENGTH (Head and body) in cm | | | | | |
| Males | Juveniles | 26 | 84,4 | 14,50 | 48,0 - 104,0 |
| | Yearlings | 33 | 109,7 | 8,56 | 96,0 - 129,0 |
| | Subadults | 25 | 120,9 | 6,59 | 109,0 - 134,0 |
| | Adults | 80 | 125,6 | 6,51 | 110,0 - 154,0 |
| Females | Juveniles | 30 | 84,2 | 14,83 | 52,5 - 102,0 |
| | Yearlings | 33 | 110,5 | 6,47 | 101,0 - 125,0 |
| | Subadults | 21 | 117,8 | 7,22 | 109,0 - 130,5 |
| | Adults | 74 | 120,7 | 14,09 | 109,0 - 141,0 |
| HIND FOOT LENGTH in cm | | | | | |
| Males | Juveniles | 18 | 19,7 | 2,15 | 15,0 - 23,0 |
| | Yearlings | 25 | 23,4 | 1,49 | 19,5 - 26,5 |
| | Subadults | 17 | 24,0 | 1,44 | 19,5 - 25,5 |
| | Adults | 59 | 24,7 | 1,10 | 22,5 - 29,0 |
| Females | Juveniles | 26 | 19,0 | 2,84 | 12,3 - 23,5 |
| | Yearlings | 29 | 23,4 | 1,12 | 21,5 - 25,5 |
| | Subadults | 18 | 23,7 | 1,09 | 22,0 - 25,2 |
| | Adults | 53 | 24,1 | 1,10 | 21,7 - 27,0 |

A consistent tendency for males to have somewhat higher means in all three parameters investigated, namely body mass, body length and hindfoot length, is evident.

On average, 53,8% ($s = 4,65$ $n = 121$) of the body mass was carcass mass, defined as body mass after removal of the skin, head, all entrails and lower limbs. The percentage carcass mass represents the average for the

data pooled over sex and age classes, because differences between male and female and over age classes were found to be small.

Post-natal growth was described by identifying and estimating the best-fit regression equations for the available body mass at age data. A standard, iterative, non-linear regression computer programme was used (OXFORD, NONLIN procedure *vide* Guest 1961). The model resulting in the best fit for the full data set, for males and females separately, was

$$Y = a(1 - e^{-bx})^c$$

where Y = body mass in kg and x = age in years or months (Table 9/3). This model was also selected to describe growth in more detailed analyses of the juvenile and yearling body mass to age data (Table 9/3; Figures 9/3 and 9/4). Alternative models of the 12 options provided by the OXFORD nonlinear regression analyses program were either inferior or only slightly superior judged by their R² values. In view of this, it was deemed desirable to stick to a single model for all growth descriptions. The model selected represents the "mono-molecular" curve and should not be confused with the Von Bertalanffy model (cf Fabens 1965).

The growth in mass with age for free-ranging male and female bushpigs is illustrated in Figures 9/1 and 9/2 (*vide* Table 9/3). The regression curves show asymptotic body masses of 71,9 and 67,9 kg for males and females respectively. Just over 50% and 80% of the asymptotic body masses are, on average, attained at one and two years of age (38,3 and 36,7 kg; 57,2 and 55,7 kg for males and females 1 and 2 years old respectively).

FIG.9/1: BODY MASS TO AGE : MALE BUSHPIGS

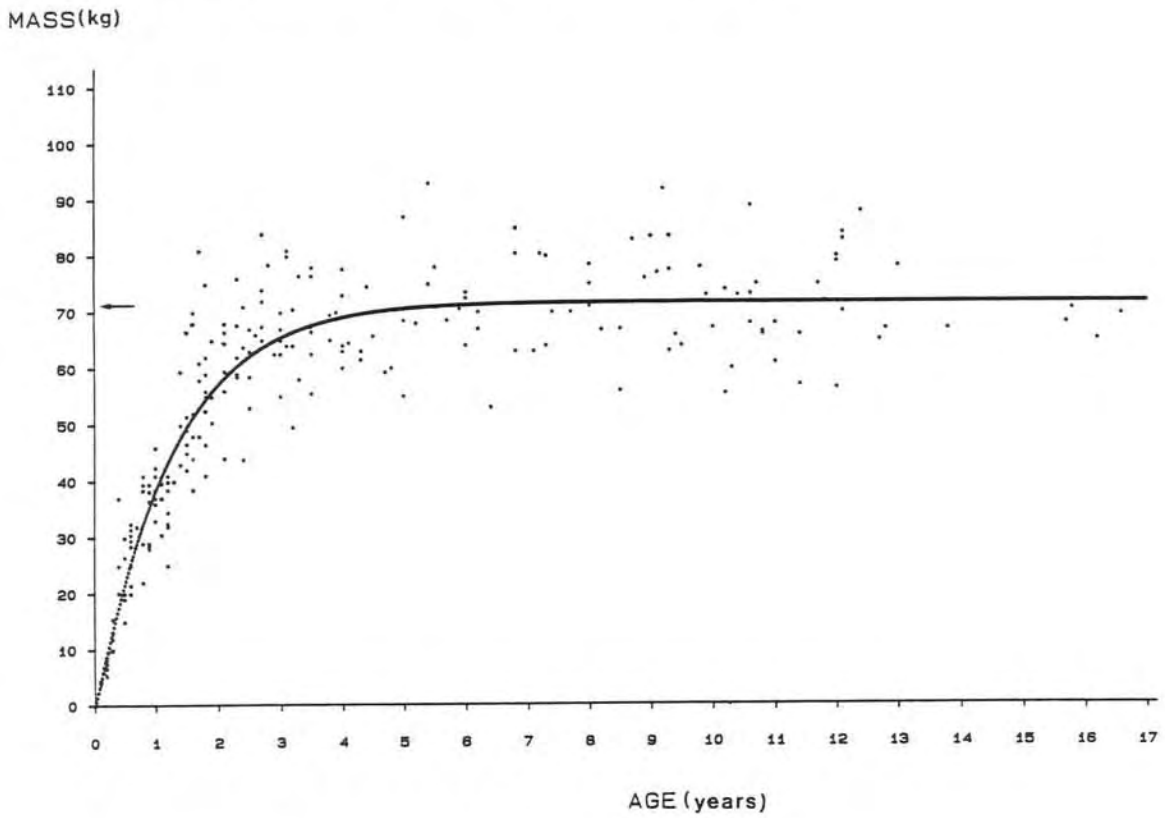


FIG.9/2: BODY MASS TO AGE : FEMALE BUSHPIGS

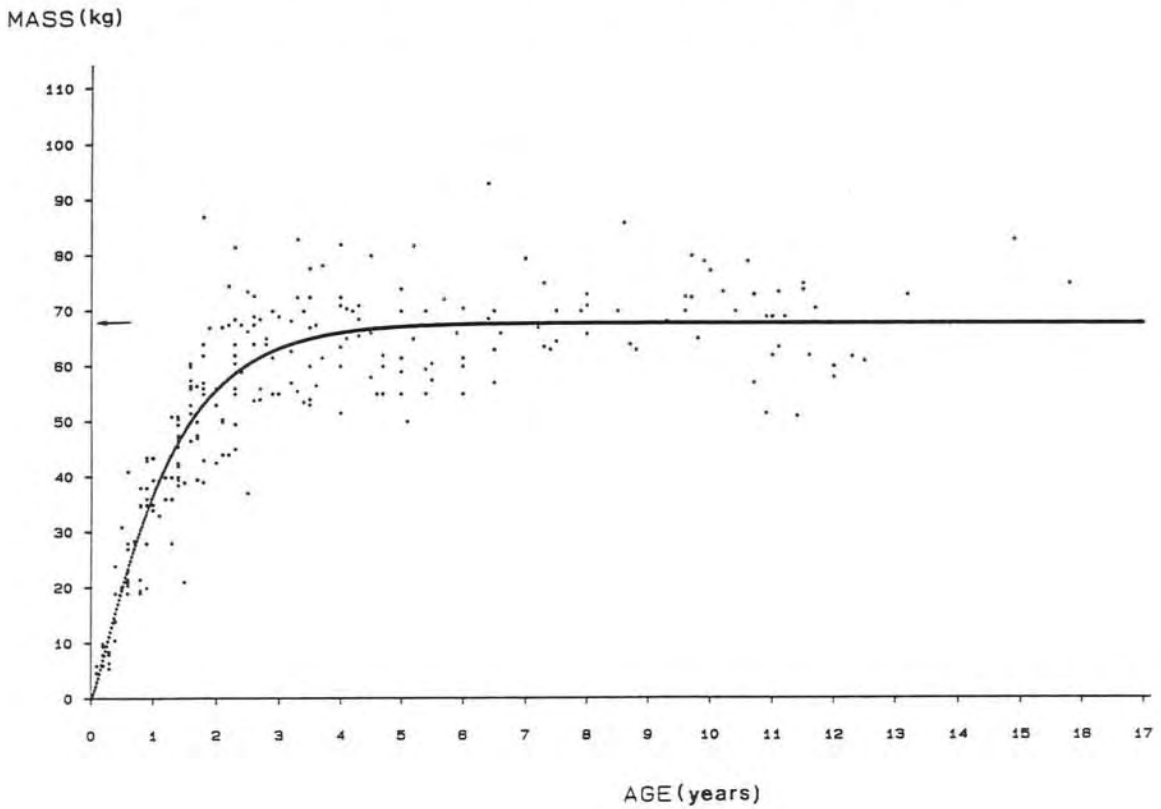


FIG.9/3: BODY MASS TO AGE : JUVENILE BUSHPIGS

MASS (kg) (--- equivalent regression curve for captive bushpigs)

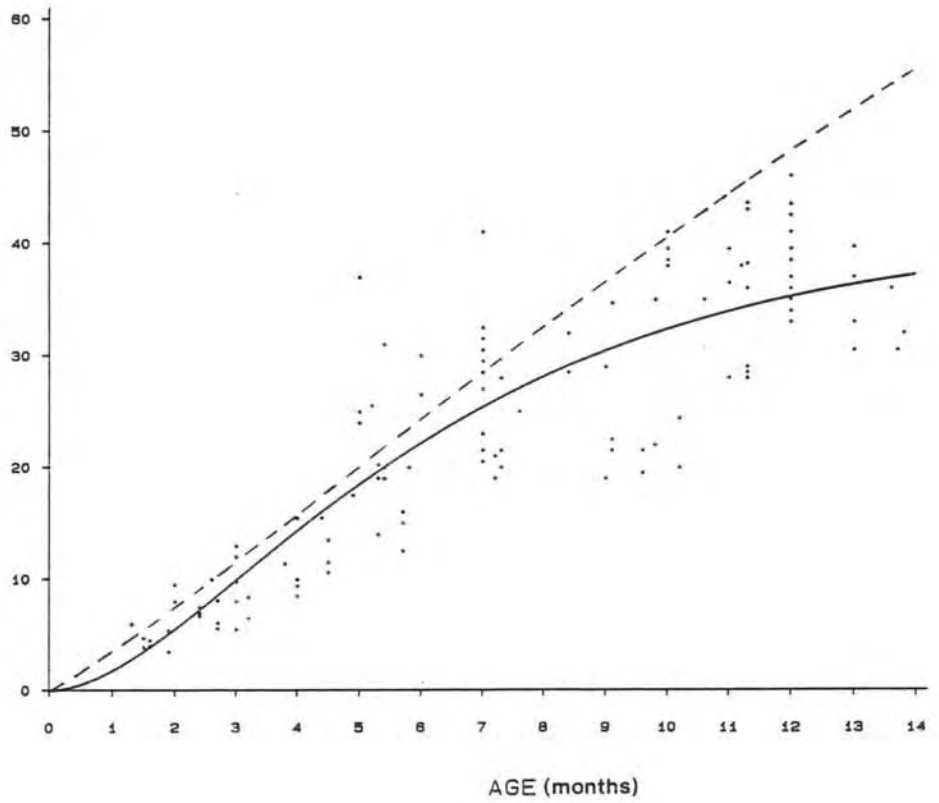


FIG.9/4: BODY MASS TO AGE : YEARLING BUSHPIGS

MASS (kg) (--- equivalent regression curve for captive bushpigs)

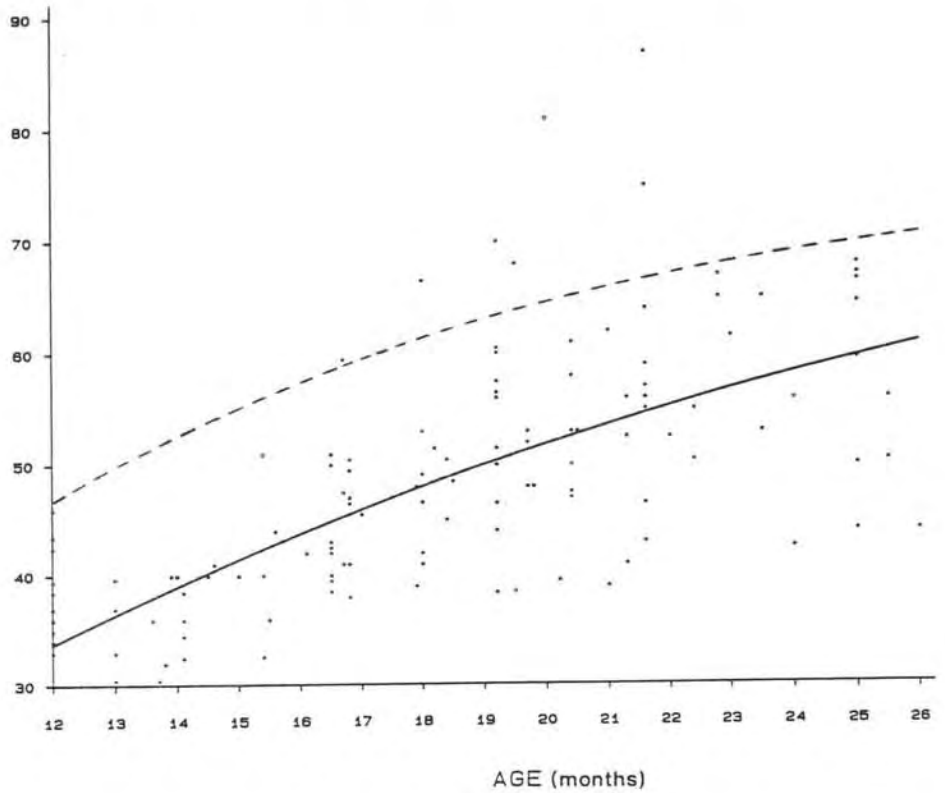


TABLE 9/3: REGRESSION MODEL PARAMETERS FOR BUSHPIG BODY MASS AT AGE*

| | n | R ² | a | b | c |
|---|-----|----------------|---------|---------|--------|
| <u>Full age range:</u> | | | | | |
| Males | 240 | 0,83 | 71,874 | 0,85233 | 1,1346 |
| Females | 250 | 0,81 | 67,938 | 0,98169 | 1,3141 |
| <u>Juveniles:</u> | | | | | |
| Free-ranging males | 61 | 0,79 | 38,358 | 0,29773 | 2,5963 |
| Free-ranging females | 56 | 0,75 | 51,025 | 0,12129 | 1,4007 |
| Free-ranging (sexes combined) | 117 | 0,78 | 42,293 | 0,19931 | 1,8217 |
| Captives (sexes combined) | 181 | 0,91 | 201,129 | 0,02727 | 1,1277 |
| <u>Yearlings:</u> | | | | | |
| Free-ranging males | 64 | 0,52 | 78,132 | 0,08977 | 2,1143 |
| Free-ranging females | 66 | 0,37 | 81,325 | 0,05454 | 1,1754 |
| Free-ranging (sexes combined) | 130 | 0,43 | 79,519 | 0,07049 | 1,5294 |
| Captives (sexes combined) | 100 | 0,35 | 76,479 | 0,12178 | 1,8758 |
| * $Y = a(1 - e^{-bx})^c$ Y in kg; x in years, or months for juvenile and yearling curves. | | | | | |

In the second half of their first year, captive juveniles grow substantially faster than their free-ranging counterparts (Fig. 9/3). This size differential is largely maintained through the yearling phase (Fig. 9/4). The average growth rate of free-ranging juvenile bushpigs is 100g/day. That of captives is 126g/day, which is similar to that recorded by Sows and Phelps (1968). The average yearling growth rate, i.e. between 1 and 2 years of age, (52g/day) was only about half that of the juveniles. There is a tendency for free-ranging yearlings to catch up (Fig.9/4) and ultimate adult body mass differences are not expected to be as disparate as suggested by subadult values.

In order to test differences in body mass at age between the sexes, regions or the free-ranging versus captive state statistically, individual body masses were contrasted with the average expected body masses over the two parameters under investigation. For example, when testing for regional differences, individual body masses were compared with the average for the data of the respective regions pooled. Two-way frequency tables were accordingly created, denoting the number of individuals above or below the pooled parameter average (Table 9/4).

The ages of slower growing free-ranging individuals were somewhat underestimated (cf Seydack 1983). Thus, differences in growth between individuals subject to two nutritional levels would likely be underestimated using tooth eruption ages instead of true age. Any statistically significant differences found can therefore safely be taken as real.

| TABLE 9/4: FREQUENCIES OF BUSHPIG INDIVIDUALS ABOVE OR BELOW AVERAGE BODY MASS FOR THEIR RESPECTIVE AGES IN RELATION TO SEX, REGION AND CAPTIVE VERSUS FREE RANGING STATE | | | |
|---|-------------|-------------|--------------------------|
| | < \bar{X} | > \bar{X} | Statistical significance |
| JUVENILES | | | |
| Males | 15 | 22 | G = 1,388 |
| Females | 17 | 14 | NS |
| Southern Cape | 15 | 18 | G = 0,007 |
| Eastern Cape | 17 | 18 | NS |
| Captives | 8 | 12 | G = 5,297 |
| Free-ranging | 69 | 33 | P < 0,05 |
| YEARLINGS | | | |
| Males | 21 | 24 | G = 2,102 |
| Females | 29 | 18 | NS |
| Southern Cape | 44 | 44 | G = 0 |
| Eastern Cape | 22 | 22 | NS |
| Plateau zone | 16 | 30 | G = 9,086 |
| Foothill zone | 28 | 14 | P < 0,005 |
| Southern Cape subregions: Plateau zone = Indigenous forest and agricultural lands; Foothill zone: Indigenous forest, pine plantations and fynbos. | | | |
| Captives | 2 | 13 | G = 23,798 |
| Free-ranging | 93 | 28 | P < 0,001 |

Although not statistically significant, a consistent tendency for males to be heavier both as juveniles and yearlings was evident. This conforms to data of bushpig growth reported by Sows and Phelps (1968). Sizes at age were similar in the Southern and Eastern Cape. On average, captive juveniles and yearlings were significantly heavier for their ages than free-ranging animals (Table 9/4).

An investigation of male/female intralitter sibling pair size differences revealed a tendency for male siblings to be heavier ($t = 2,636$ $df = 19$ $P < 0,02$). Size variability amongst surviving litter mates, which was recorded up to group break-up, i.e. up to about 2 years of age, was found to be substantial. Body mass of litter mates was expressed as a percentage of the heaviest sibling. In 80% of the comparisons, mass deviation varied between zero and 20%. In the remaining 20% of comparisons, siblings had masses between 50 and 80% of the heaviest sibling. Intralitter body mass variability thus exhibited nearly the same magnitude as in the case of pre-natal litters (10.3.3).

9.3.2 Energy storage

Energy storage was recorded for one year and older bushpigs with visual assessment of the incidence of subcutaneous fat (Plate 12) and three metric fat depot parameters : subcutaneous fat index, maximum peritoneal fat layer thickness and femur marrow fat percentage. The subcutaneous fat index consisted of the sum of the subcutaneous fat layers, in millimeters, measured at three localities (shoulder, thoracic and back; *vide* 9.2).

These indicators of fat storage and body mass were subject to principal component analysis (Jeffers 1978) with respect to sex, age, region, season and female reproductive state. An analysis of variance was carried out on the scores of individuals on the principal components. The first principal component positively weighted all four parameters. The second principal component contrasted subcutaneous and peritoneal fat layer thickness with femur marrow fat percentage and body mass. The analysis revealed highly significant effects of sex ($P < 0,0001$) and female reproductive state ($P < 0,005$). Females have more subcutaneous and peritoneal fat, relative to marrow fat percentage and body mass, than males. Pregnant females had more adipose tissue than non-reproductive or lactating individuals. No significant differences were detected regarding season, age or region. However, more specific analysis revealed significant regional differences in peritoneal fat thickness.

PLATE 12

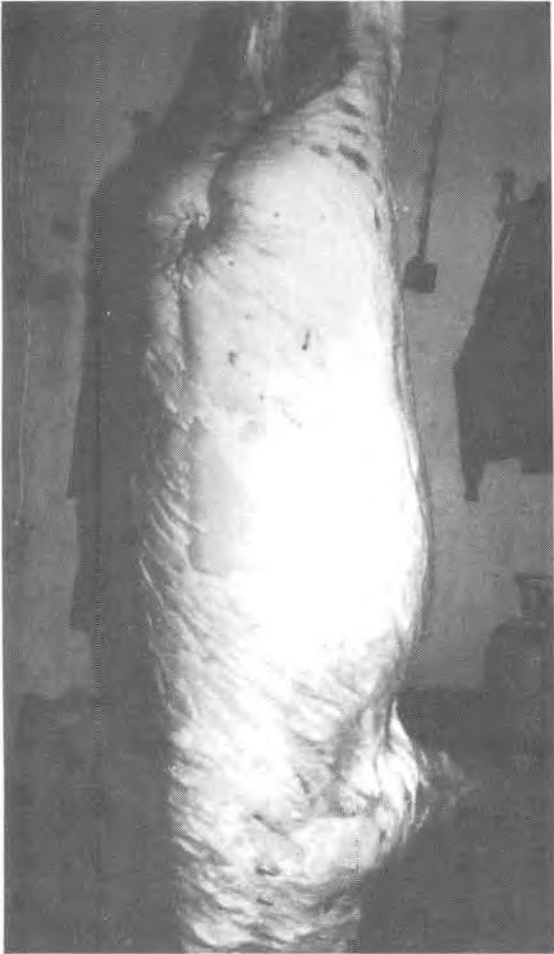
- a. Pregnant bushpig female OKC 52: very fat. Shot 4.08.1984 (Alicedale district). Live mass: 83 kg.

- b. Bushpig male OKC 54: very lean. Shot 11.08.1984 (Alicedale district) Live mass: 55 kg.

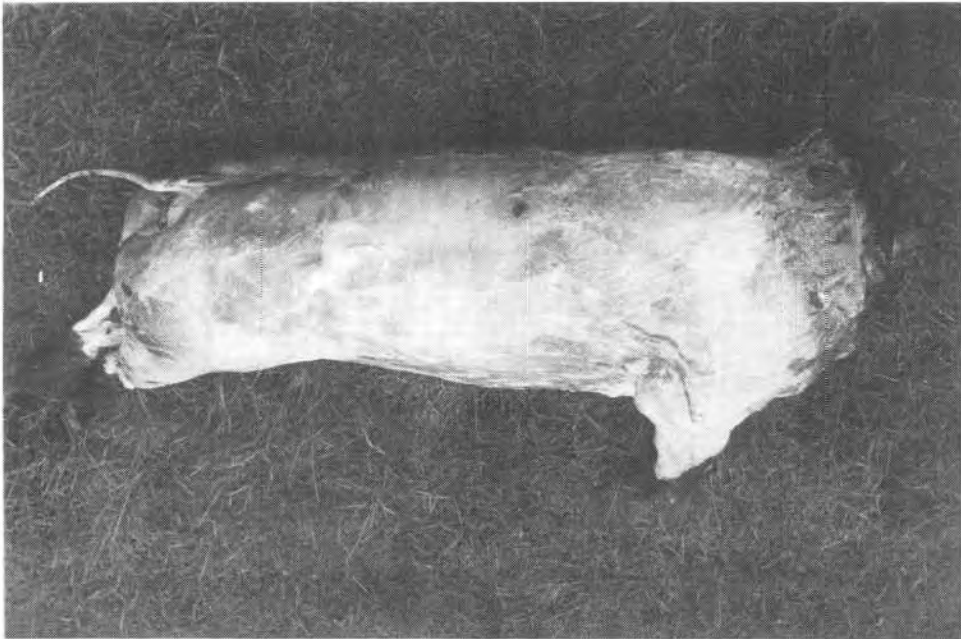
- c. Bushpig male CU8: relatively little subcutaneous fat (lean) but good in meat. Live mass: 71 kg (Goudveld).

PLATE 12

a



b



c

(a) Visual assessment of subcutaneous fat

The spread of subdermal fat over the body surface of skinned animals was assessed and subjectively classified as either "fat", "average" or "lean". The resultant frequencies were grouped according to sex, region, female reproductive state and season (Table 9/5). The seasonal frequency distribution was only investigated for males, since seasonality in female breeding biased the results in females.

| TABLE 9/5: FREQUENCY DISTRIBUTIONS OF SUBCUTANEOUS FAT ASSESSMENT IN SOUTHERN AND EASTERN CAPE BUSHPIGS | | | | |
|---|-----|---------|------|--|
| | FAT | AVERAGE | LEAN | STATISTICAL SIGFICANCE |
| <u>MALES</u> | | | | |
| Eastern Cape (a) | 3 | 10 | 16 | ab : G=8,10 P<0,05 cd : G=2,54 (NS) |
| Southern Cape (b) | 4 | 32 | 12 | |
| <u>FEMALES</u> | | | | |
| Eastern Cape (c) | 15 | 16 | 11 | ac : G=8,67 P<0,05 bd : G=15,95 P<0,001 |
| Southern Cape (d) | 24 | 27 | 8 | |
| <u>REPRODUCTIVE STATE</u> | | | | |
| Pregnant | 28 | 15 | 1 | G = 34,21 P < 0,001 |
| Non-reproductive | 16 | 43 | 24 | |
| Lactating | 3 | 4 | 5 | |
| <u>SEASON (MALES)</u> | | | | |
| Summer | 1 | 10 | 9 | G = 0,95 (NS) |
| Autumn | 1 | 5 | 5 | |
| Winter | 3 | 12 | 10 | |
| Spring | 2 | 15 | 14 | |

Females had more subdermal fat than males and this difference was less pronounced in the Eastern Cape. Proportionately more males were lean in the Eastern Cape. Only about 2% of pregnant females were classed as lean, whereas 29% of the non-reproductive sows and 42% of lactating sows were considered lean.

(b) Subcutaneous fat index

A one-way ANOVA indicated highly significant effects on subcutaneous fat related to female reproductive condition ($P < 0,001$) and sex ($P < 0,0001$). Pregnant sows had more subcutaneous fat than non-reproductive females ($t = 3,59$ $df = 55$, $P < 0,001$) and the latter had

more subcutaneous fat than males ($t = 3,06$ $df = 87$, $P < 0,01$) (Table 9/6). Regional differences are not statistically significant, although clearly discernable. Yearling and reproductively active bushpigs of the Eastern Cape tend to have less subcutaneous fat (Table 9/6).

| | \bar{x} | n | s | Range |
|-----------------------|-----------|----|-------|---------|
| <u>Males (2y +)</u> | | | | |
| Males | 7,54 | 57 | 6,29 | 0 - 23 |
| Southern Cape | 7,56 | 39 | 6,20 | 0 - 17 |
| Eastern Cape | 7,50 | 18 | 6,49 | 0 - 23 |
| <u>Females (2y +)</u> | | | | |
| Non-reproductive | 13,53 | 32 | 12,18 | 0 - 45 |
| Southern Cape | 13,41 | 19 | 10,30 | 0 - 40 |
| Eastern Cape | 15,25 | 13 | 15,36 | 2 - 45 |
| Pregnant | 23,84 | 25 | 8,59 | 6 - 37 |
| Southern Cape | 25,50 | 14 | 7,79 | 15 - 37 |
| Eastern Cape | 21,73 | 11 | 9,45 | 6 - 37 |
| Lactating | 11,50 | 6 | 12,93 | 1 - 28 |
| Southern Cape | 17,50 | 2 | 14,85 | 7 - 28 |
| Eastern Cape | 8,50 | 4 | 13,00 | 1 - 28 |
| <u>Yearlings</u> | | | | |
| Males | 11,12 | 17 | 8,73 | 1 - 27 |
| Southern Cape | 14,75 | 8 | 8,24 | 5 - 26 |
| Eastern Cape | 7,89 | 9 | 8,25 | 1 - 27 |
| Females | 11,82 | 22 | 8,93 | 0 - 31 |
| Southern Cape | 14,40 | 15 | 9,96 | 0 - 31 |
| Eastern Cape | 9,86 | 7 | 9,08 | 0 - 25 |

Within the Southern Cape, the average subcutaneous fat indices for bushpigs presumed to have access to agricultural crops, compared to those without, were 14,7 and 9,9 respectively ($t = 1,86$ $df = 47$, NS). Access to food resources from agricultural crops was assessed from locality or stomach contents. A larger sample size would probably confirm the presumption that the ready availability of carbohydrate-rich food is responsible for enhanced energy storage.

(c) Peritoneal fat

The average thickness of the peritoneal fat layer of bushpigs in the Eastern Cape (5,5 mm) was less than that (9,3 mm) for the Southern Cape ($P < 0,005$). The regional difference was particularly pronounced in females ($t = 3,02$ $df = 72$ $P < 0,01$). Pregnant females had more peritoneal fat than non-reproductive females ($t = 4,19$ $df = 48$, $P < 0,001$), but the difference between the latter and males was not statistically significant ($t = 0,91$ $df = 74$, NS) (Table 9/7).

| TABLE 9/7: MAXIMUM PERITONEAL FAT LAYER THICKNESS (mm) OF SOUTHERN AND EASTERN CAPE BUSHPIGS | | | | |
|--|-----------|----|-------|--------|
| | \bar{X} | n | s | Range |
| <u>Males (2y +)</u> | | | | |
| Males | 5,88 | 53 | 4,66 | 0 - 20 |
| Southern Cape | 6,18 | 38 | 4,84 | 0 - 20 |
| Eastern Cape | 5,13 | 15 | 4,16 | 1 - 15 |
| <u>Females (2y +)</u> | | | | |
| Non-reproductive | 7,13 | 23 | 7,06 | 0 - 25 |
| Southern Cape | 9,14 | 14 | 8,32 | 0 - 25 |
| Eastern Cape | 4,22 | 9 | 3,70 | 2 - 12 |
| Pregnant | 13,52 | 27 | 8,60 | 5 - 30 |
| Southern Cape | 15,76 | 17 | 9,26 | 5 - 30 |
| Eastern Cape | 9,70 | 10 | 5,95 | 5 - 20 |
| Lactating | 6,83 | 6 | 9,37 | 0 - 25 |
| Southern Cape | 15,00 | 2 | 14,14 | 5 - 25 |
| Eastern Cape | 2,75 | 4 | 3,59 | 0 - 8 |
| <u>Yearlings</u> | | | | |
| Males | 6,40 | 15 | 5,53 | 1 - 22 |
| Southern Cape | 8,13 | 8 | 5,74 | 2 - 22 |
| Eastern Cape | 4,43 | 7 | 4,93 | 1 - 13 |
| Females | 9,18 | 17 | 7,45 | 1 - 30 |
| Southern Cape | 10,69 | 13 | 7,71 | 2 - 30 |
| Eastern Cape | 4,25 | 4 | 4,03 | 1 - 10 |

Whereas sex differences were pronounced and regional differences less so for subcutaneous fat, the reverse was true for peritoneal fat. Although not statistically significant in all cases, both types of fat depots showed the same pattern: lower fat reserves in the Eastern Cape, leaner males and substantial fat reserves in pregnant females.

(d) Bone marrow fat percentage

Seventy-seven percent of male and 70% of female bushpigs had bone marrow with a fat content of at least 70% (Figure 9/5 and Table 9/8).

FIG.9/5: PERCENTAGES OF BUSHPIGS WITH BONE MARROW FAT RESERVES OF 70% OR MORE

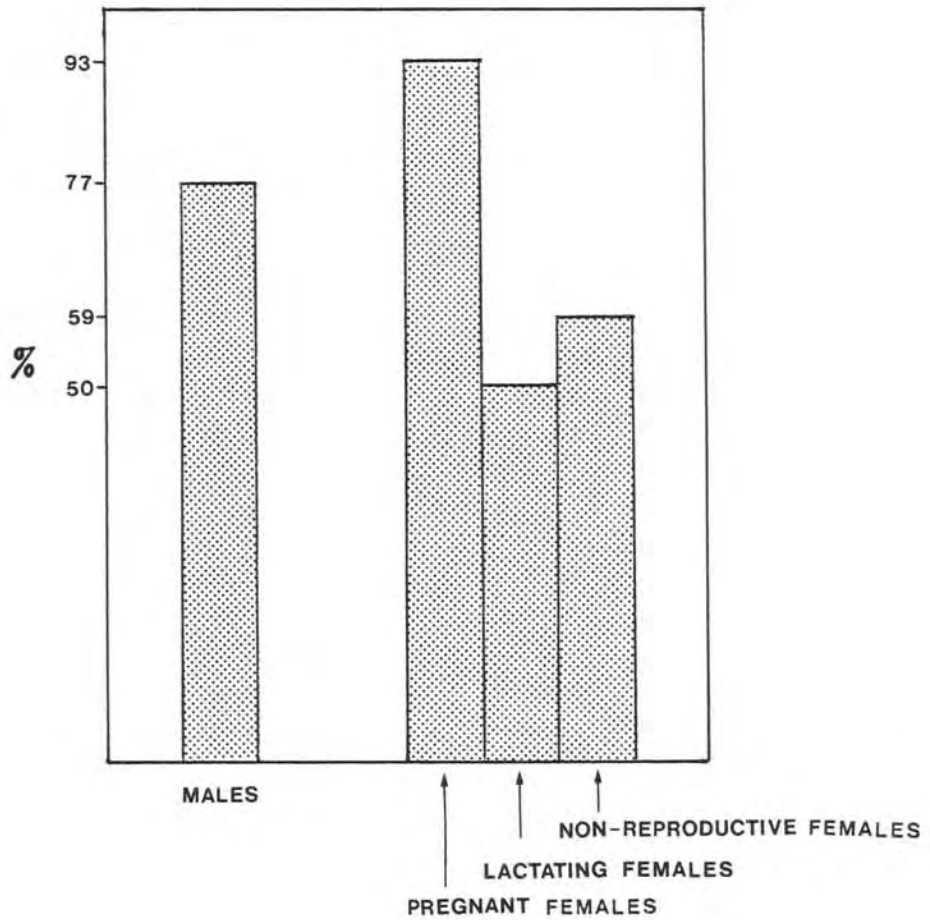


TABLE 9/8: FREQUENCIES OF BUSHPIG FEMUR MARROW FAT PERCENTAGES (YEARLINGS AND 2 YEARS +)

| | <40% | 40-60% | 60-70% | 70-80% | 80-100% |
|--------------------------|------|--------|--------|--------|---------|
| Yearlings | 2 | 2 | 2 | 12 | 16 |
| Males | 3 | 8 | 6 | 13 | 43 |
| Non-reproductive females | 5 | 3 | 6 | 1 | 19 |
| Pregnant females | 0 | 0 | 2 | 4 | 21 |
| Lactating females | 4 | 2 | 0 | 1 | 5 |

No seasonal trends were evident. It is noteworthy that the 4 records of marrow fat percentages for lactating sows below 40% originated from the Eastern Cape and the 2 in the class 40 - 60% were from the Southern Cape.

For adult bushpigs proportionately more males had values exceeding 70% than non-reproductive and lactating females ($G = 4,03$ $df = 1$, $P < 0,005$), once again reflecting the energetic costs of reproduction in females. Disproportionately few pregnant females had bone marrow fat percentages below 70% ($G = 10,00$ $df = 1$, $P < 0,005$). Very low values were associated with starvation (CHI: 0,7%), sociospatial conflict or encroachment in females (CFI: 0%, CEI: 33,2%, CL2: 0%) or lactation (EC 22: 21,4%; OKC 16: 14,8%; OKC 13: 9,9%). Most adult bushpigs for which group composition was known and which had less than 60% marrow fat, were solitary (9 out of 13). This comparison excluded lactating females.

From Table 9/9 it can be seen that marrow fat is mobilized only after peritoneal fat reserves have largely been depleted.

| Peritoneal fat layer thickness (mm) | Femur marrow fat percentage classes | | | | |
|-------------------------------------|-------------------------------------|--------|--------|--------|---------|
| | 0 - 20% | 20-40% | 40-60% | 60-80% | 80-100% |
| 0 - 2 | 4 | 3 | 7 | 4 | 7 |
| 3 - 5 | | | 1 | 5 | 12 |
| 6 - 10 | | | | 2 | 21 |
| 11+ | | | | 2 | 18 |

The depletion/replenishment pattern of subcutaneous relative to marrow fat is identical to that for peritoneal fat indicated in Table 9/9. Individuals with femur marrow fat percentages below 60% are very unlikely to have substantial subcutaneous or peritoneal fat reserves left and this percentage may therefore be considered a condition threshold value.

9.3.3 Conditions evaluation indices

9.3.3.1 Body mass to age or size

(a) Body mass at age

An analysis of an animals growth may provide objective criteria for assessing physiological condition, based on the concept that a reduction in weight at age or a reduction in growth rates can be equated with poor condition (Hanks 1981). Mammals do show differences in rates of growth and ultimate body size in relation to the nature of available food resources (Franzmann 1985). However, the largest animals with the most rapid growth rates are not necessarily found in the nutritionally best areas (cf Klein and Strandgaard 1972). There may be confounding trade-offs between growth and size versus reproduction. The information content of body size at age depends on these interactions and whether condition is defined in relation to maintenance or reproduction.

Body size changes of individuals in the same area have been used successfully for the detection of changing population condition, i.e. in habitat quality over time (eg. for European wild boar in certain areas in Germany by Briedermann, 1986).

Differences in the food resource base for the bushpig between areas may be investigated by comparing body mass at age with the predicted values, making use of the regression equations for male and female bushpigs in Table 9/3. Using this approach, significant differences in population condition between the montane and plateau subregions of the Southern Cape were demonstrated (9.3.1; Table 9/4). The body masses at age of individuals from the fast-growing age classes, namely juveniles and yearlings, are the most sensitive and appropriate to use.

(b) Body mass to size ratio

Body mass corrected for skeletal size may be used as a means of comparing animals from different habitat types (Hanks 1981). The resultant condition indices describe the slenderness or heaviness of an animal, i.e. serve as a measure of "skeletal fill" with flesh and fat

reserves. In the mass to size ratio, the effect of size is corrected for and the index should therefore reflect the current state of energy and protein reserves.

The condition index has the following basic formula:

$$I = \frac{1000 W^a}{L}$$

where W = mass in kg, a = preselected exponent and L = body length in mm.

Beukes (1984) and Briedermann (1986) used an exponent of $a = 1$ and Bailey (1968), Brand *et al.* (1975) and Malpas (1977) used a cubic relationship between body mass and their measure of skeletal size, i.e. $a = 1/3$. The latter exponent is appropriate since it results in a condition index independent of body size.

The condition index applied to the bushpig data was thus

$$I = \frac{1000 W^{0,33}}{L}$$

Total body or hindfoot length is generally used as measure of skeletal size for this correction. Any subcutaneous fat would tend to increase the total body length measurement (cf Barrett 1978). This effect is considered insubstantial and if present, would make the M/S ratio a somewhat more conservative index of condition. Stomach fill mass could substantially alter individual comparisons if one animal had an empty stomach and another a full one. Variability due to stomach fill can be avoided by subtracting its mass in culled animals. This is particularly important if differences in hunting technique result in most animals being shot at different times of day in different areas.

The available body length data is presented below (in mm):

| | n | \bar{X} | s |
|-----------------------|----|-----------|-------|
| Southern Cape males | 46 | 1257 | 58,05 |
| Southern Cape females | 39 | 1247 | 68,16 |
| Eastern Cape males | 19 | 1247 | 52,44 |
| Eastern Cape females | 30 | 1198 | 57,65 |

The skeletal size estimated from body length was smaller in Eastern Cape than in Southern Cape females ($t = 3,16$ $df = 67$, $P < 0,01$).

From the available data on adult bushpigs, the M/S condition indices ranged between 2,94 and 3,71, with an overall average of 3,290 ($n = 133$ $s = 0,1536$). The results are summarized in Table 9/10.

| Region/Sex | n | \bar{X} | s | | Statistical significance |
|----------------|----|-----------|--------|---|--|
| Eastern Cape | 49 | 3,319 | 0,1555 | a | a vs b: $t = 3,08$ $df = 70$ $P < 0,01$ |
| Southern Cape: | 84 | | | | |
| Foothill zone | 23 | 3,205 | 0,1236 | b | b vs c: $t = 2,64$ $df = 82$ $P < 0,05$ |
| Plateau zone | 61 | 3,299 | 0,1528 | c | |
| Southern Cape: | | | | | d vs f: $t = 0,44$ $df = 62$ NS |
| Males | 45 | 3,260 | 0,1492 | d | |
| Females | 39 | 3,286 | 0,1508 | e | |
| Eastern Cape | | | | | e vs g: $t = 0,78$ $df = 67$ NS |
| Males | 19 | 3,320 | 0,1609 | f | |
| Females | 30 | 3,315 | 0,1547 | g | |

The poorer condition in the foothill versus the plateau subregions of the Southern Cape is in agreement with the findings in sections 9.3.1.

9.3.3.2 Indices of fat reserves

Fat reserves represent stored energy and they have been widely used to assess condition in wild animals (Hanks 1981, Franzmann 1985). Four condition indices related to fat reserves were investigated in this study: visual assessment of subcutaneous fat, a subcutaneous fat index,

maximum peritoneal fat layer thickness and femur marrow fat percentage (9.2; 9.3.2).

(a) Visual assessment of subcutaneous fat

During visual assessment of subcutaneous fat, each individual was classified subjectively as either fat, average or lean. This visual assessment of subdermal fat provided a reasonable indication of fat storage when compared with the metric fat reserve indices (Table 9/11). An analysis of variance showed differences for the 3 assessment classes, fat, average and lean to be significant for all the parameters presented in Table 9/11 ($P < 0,0001$).

| TABLE 9/11: VISUAL ASSESSMENT CLASSES OF SUBCUTANEOUS FAT AND THEIR ALTERNATIVE FAT RESERVE CONDITION INDEX VALUES (BUSHPIGS 1YEAR AND OLDER) | | | | |
|---|----|-----------|-------------------------|---------|
| Visual Assessment Classes | n | \bar{X} | 95% Confidence Interval | Range |
| <u>Subcutaneous fat index</u> | | | | |
| FAT | 43 | 25,2 | 23,34 - 26,98 | 9 - 45 |
| AVERAGE | 63 | 11,0 | 9,53 - 12,53 | 2 - 25 |
| LEAN | 44 | 2,4 | 0,61 - 4,21 | 0 - 8 |
| <u>Peritoneal fat thickness (mm)</u> | | | | |
| FAT | 43 | 14,2 | 12,54 - 15,88 | 4 - 30 |
| AVERAGE | 56 | 7,1 | 5,63 - 8,55 | 2 - 25 |
| LEAN | 39 | 2,3 | 0,58 - 4,09 | 0 - 12 |
| <u>Marrow Fat percentage</u> | | | | |
| FAT | 33 | 83,6 | 77 - 90 | 61 - 92 |
| AVERAGE | 85 | 77,3 | 73 - 82 | 21 - 92 |
| LEAN | 60 | 64,7 | 59 - 70 | 0 - 89 |

What is meant by "fat", "average" and "lean" is difficult to standardize over different observers and over time for the same observer. This approach is thus inherently subjective. Neither does this approach provide for the fact that males are less predisposed to fat storage than females (9.3.2). Sex differences increase the problem of standardization.

(b) Subcutaneous and peritoneal fat indices

These involve the sum of three subcutaneous fat layer measurements and the maximum peritoneal fat layer thickness respectively, as described in sections 9.2 and 9.3.2. Quantitatively, subcutaneous and peritoneal fat make up most of the fat reserves in the bushpig and are progressively mobilized long in advance of imminent starvation (9.3.2). The subcutaneous and peritoneal fat indices should therefore be the most meaningful and sensitive indices of "fat storage" condition. The two parameters are strongly contingent ($G = 103,46$ $df = 4$ $P < 0,0001$) (Table 9/12).

| Subcutaneous fat index (mm) | Maximum peritoneal fat layer thickness (mm) | | |
|------------------------------------|---|-------|----|
| | 0 - 2 | 3 - 5 | >5 |
| 0 - 3 | 28 | 6 | 1 |
| 4 - 10 | 8 | 17 | 12 |
| > 10 | 2 | 8 | 58 |
| $G = 103,46$ $df = 4$ $P < 0,0001$ | | | |

If the peritoneal fat layer is ≤ 5 mm, or the subcutaneous fat index ≤ 10 , then the femur marrow fat percentage is $< 60\%$, i.e. the animal is clearly in a marginal to poor condition (Table 9/9, 9.3.2). These two fat reserve condition indices were contrasted with the condition index based on the body mass/size ratio (Table 9/13).

Fat reserve condition indices were not significantly related to the M/S ratio condition index (Table 9/13).

Fat depots were found to be very variable in individual animals within a population, depending on reproductive state, age, sex and condition. Particularly large sample sizes are thus required in order to establish whether area differences in population condition exist.

| TABLE 9/13: FAT RESERVES CONDITION INDICES COMPARED WITH THE BODY MASS/SIZE RATIO CONDITION INDEX IN EASTERN AND SOUTHERN CAPE BUSHPIGS (FREQUENCIES) | | | |
|---|--------------------------------------|-------------|--------|
| Peritoneal fat condition index | Body mass/size ratio condition index | | |
| | < 3,20 | 3,20 - 3,40 | > 3,40 |
| 0 - 5 | 7 | 22 | 2 |
| > 5 | 12 | 12 | 4 |
| Subcutaneous fat condition index | | | |
| 0 - 10 | 12 | 18 | 1 |
| > 10 | 7 | 18 | 6 |
| Peritoneal fat : | G = 4,843 | df = 2 | NS |
| Subcutaneous fat: | G = 5,294 | df = 2 | NS |

(c) Percentage bone marrow fat index

Bone marrow tissue is a three-component system, comprised of water, fat and non-fat residue, in which the water and the fat are linearly and inversely related (Neiland 1970). The tedious process of ether extraction and determination of percentage fat may be avoided in future by using the relationship of percentage dry mass to percentage fat established for the bushpig. The marrow sample only requires to be oven-dried to constant weight, expressed as a percentage of the wet weight and used in the formula below (n = 189, r = 0,991).

$$\text{Percentage fat} = 1,048 (\text{Percentage dry mass}) - 8,7.$$

This relationship is reasonably close to the general formula derived for African ungulates: Percentage marrow fat = percentage dry mass - 7 (Brooks *et al.* 1977).

An individual with a femur marrow fat percentage below 60% is most likely in a poor condition, since marrow fat is the last of the fat reserves to be mobilized. The reverse does however not necessarily hold; i.e. an individual with a bone marrow fat content above 60% does not have to be in a good condition, but it will probably be. This conclusion (cf Mech and Delgiudice 1985) is supported by the frequency

distribution in a comparison with body mass to size condition (Table 9/14).

| TABLE 9/14: BUSHPIG CONDITION AS REFLECTED BY FEMUR MARROW FAT VERSUS BODY MASS/SIZE RATIO | | |
|--|------------------|-------|
| Body mass/size ratio condition index | Femur marrow fat | |
| | < 60% | > 60% |
| > 3,40 | 2 | 14 |
| 3,20 - 3,40 | 5 | 39 |
| < 3,20 | 7 | 12 |

Although not sensitive in the initial stages of nutritional deficiencies, bone marrow fat is a very useful condition index when studying causes of death (Sinclair and Duncan 1972).

9.3.3.3 Blood profile parameters

Two separate data sets are involved (9.2). Data set I involves the initial blood sampling during 1981, whereas data set II includes all subsequent blood sampling data. The two were kept separate and analyzed separately because it became apparent that set I averages were consistently lower than those of set II, for both wild and captive bushpigs. Different institutions were involved and it is suspected that the analyses of the two data sets were not comparably standardized. Detailed statistical analysis was only applied to data set II and condition evaluation criteria were then developed.

Data set I

The blood parameter values of haemoglobin (Hb) and packed cell volume (PCV) of free-ranging bushpigs were significantly lower than those of captive animals (Table 9/15). Parameter averages, when pooled over culled and immobilized free-ranging individuals, were 12,0 for Hb (n = 63, s = 2,94 and 95% confidence intervals: 11,26 - 12,74) and 38,5 for PCV (n = 63, s = 8,41 and 95% confidence interval: 36,4 - 40,6).

| TABLE 9/15: BLOOD PARAMETER STATISTICS FOR SOUTHERN CAPE BUSHPIGS (DATA SET I: 1981) | | | | |
|---|----|-----------|-------|-----------------------------------|
| | n | \bar{X} | s | Statistical significance |
| <u>HAEMOGLOBIN (Hb) *</u> | | | | |
| Free-ranging (culled) | 44 | 11,7 | 3,194 | a a vs b : t = 1,09 df = 61 NS |
| Free-ranging (immobilized) | 19 | 12,6 | 2,333 | b b vs c : t = 3,71 |
| Captive (immobilized) | 37 | 14,7 | 1,820 | c df = 54 P < 0,001 |
| <u>PACKED CELL VOLUME (PCV)*</u> | | | | |
| Free-ranging (culled) | 44 | 38,0 | 9,271 | a a vs b : t = 0,77 df = 61 NS |
| Free-ranging (immobilized) | 19 | 39,8 | 5,950 | b b vs c : t = 4,10 |
| Captive (immobilized) | 37 | 46,1 | 5,245 | c df = 54 P < 0,001 |
| <u>ALBUMIN/GLOBULIN RATIO</u> | | | | |
| Free-ranging (culled) | 46 | 1,00 | 0,623 | a a vs b : t = 1,07 df = 65 NS |
| Free-ranging (immobilized) | 21 | 0,84 | 0,418 | b b vs c : t = 1,27 |
| Captive (immobilized) | 37 | 1,01 | 0,527 | c df = 56 NS |
| <u>NON-ESTERIFIED FATTY ACIDS*</u> | | | | |
| Free-ranging (culled) | 46 | 0,57 | 0,085 | a a vs b : t = 0,38 df = 64 NS |
| Free-ranging (immobilized) | 20 | 0,56 | 0,124 | b b vs c : t = 0,82 |
| Captive (immobilized) | 37 | 0,53 | 0,135 | c df = 55 NS |
| * UNITS: Hb (g/dl) PCV: % NEFA: meq/100 ml | | | | |

Data set II

The blood parameters were subjected to principal component analysis (cf Jeffers 1978). The four identified principal components and their variates were as follows (percentage variance explained in brackets).

- PC1 (29,6%) : + Hb, + PCV, + Albumin (A), + RBC, -Glucose.
- PC2 (19,6%) : + Globulin (G), - A/G ratio, - Protein, - MCV.
- PC3 (10,9%) : + Triglycerides, + Glucose, - MCV.
- PC4 (9,7%) : + MCHC, - Cholesterol, - Leucocytes.

Significance of effects are shown in Table 9/16 below:

| TABLE 9/16: SIGNIFICANCE TABLE OF EFFECTS ON THE PRINCIPLE COMPONENTS (P <) | | | | | |
|---|--------|-------------------------|-----|------|---------------------|
| | Season | Free-ranging vs captive | Sex | Age | Reproductive status |
| PC 1 | NS | 0,0001 | NS | 0,01 | NS |
| PC 2 | NS | NS | NS | NS | NS |
| PC 3 | NS | 0,01 | NS | NS | NS |
| PC 4 | 0,005 | NS | NS | NS | NS |

Tested in isolation, only the variate cholesterol of PC 4 showed a significant seasonal effect ($P < 0,01$). The seasonal means were as follows: 2,27 mmol/l in summer; 2,17 mmol/l in autumn; 2,47 mmol/l in winter and 1,69 mmol/l in spring. The only other strongly significant effect was that of the free-ranging versus captive condition on PC 1 variates. Refer to Table 9/17 for a detailed analysis of variance. No effects of sex or female reproductive status (pregnant, lactating, non-reproductive) were evident on any of the blood parameter values.

Averages of captives clearly exceeded those of free-ranging bushpigs for the red blood cell parameters haemoglobin, packed cell volume and erythrocyte count. Captives also had a higher albumin/globulin ratio (Table 9/17). These differences are probably due to the fact that captives received balanced rations *ad libitum*.

Glucose and triglycerides were significantly lower in captive animals (Table 9/17). Blood glucose levels are very sensitive to excitement during capture and immobilization and are virtually always increased in proportion to the degree of excitement experienced (Seal *et al.* 1972a, Franzmann and Le Resche 1978, Karns and Crichton 1978, Wesson *et al.* 1979a). Among collared peccaries, serum levels of glucose were considerably higher in trapped as opposed to shot animals (Lochmiller and Grant 1984). The higher glucose levels in free-ranging bushpigs may have been the result of higher excitement levels during capture and immobilization compared with similar handling of the captive animals. Immobilization may result in lowered blood parameter values due to hemodilution (Seal *et al.* 1972) and this effect may be more pronounced in the more excited individuals. According to this reasoning, the lower

blood parameter values in immobilized, more excited free-ranging bushpigs may be an artefact of handling. If this were the case, haemoglobin values for example, should be lower for animals with above average glucose levels. This was tested for free-ranging animals and

| TABLE 9/17: BLOOD PARAMETER VALUES OF FREE-RANGING VERSUS CAPTIVE SOUTHERN CAPE BUSHPIGS | | | | | | |
|--|---------|----------|--------------|----------------|-----------------------------|-----------------------------------|
| Blood parameter (units) | F* or C | n | \bar{X} | s | 95% Confidence Intervals | Significance testing: F vs C; P < |
| Haemoglobin (g/dl) | F C | 62 74 | 14,1 17,6 | 1,97 1,63 | 13,7 - 14,6 17,2 - 18,1 | 0,0001 |
| PCV (%) | F C | 62 74 | 41,4 50,9 | 5,86 5,37 | 40,0 - 42,8 49,7 - 52,2 | 0,0001 |
| MCHC (g/dl) | F C | 62 74 | 34,0 34,7 | 1,71 1,47 | 33,6 - 34,4 34,3 - 35,0 | 0,05 |
| Erythrocytes $\times 10^{12}/l$ | F C | 62 74 | 6,3 7,3 | 0,87 1,02 | 6,0 - 6,5 7,0 - 7,5 | 0,0001 |
| MCV (fl) | F C | 81 84 | 26,3 49,6 | 69,9 55,2 | 12,5 - 40,1 36,1 - 63,2 | 0,05 |
| Leucocytes ($\times 10^9/l$) | F C | 62 74 | 9,7 10,5 | 2,78 3,16 | 8,9 - 10,5 9,8 - 11,2 | NS |
| Glucose (mmol/l) | F C | 78 75 | 9,3 5,2 | 4,88 1,25 | 8,5 - 10,2 4,4 - 6,0 | 0,0001 |
| Protein (g/l) | F C | 81 84 | 64,0 64,3 | 20,00 32,14 | 58,1 - 69,9 58,5 - 70,1 | NS |
| Albumin (A) (g/l) | F C | 81 84 | 29,2 31,3 | 15,23 25,61 | 24,6 - 33,9 26,7 - 35,8 | NS |
| Globulin (G) (g/l) | F C | 81 84 | 33,5 29,8 | 17,10 25,78 | 28,7 - 38,4 25,0 - 34,5 | NS |
| A/G ratio | F C | 80 81 | 0,9 1,1 | 0,25 0,31 | 0,86 - 0,98 1,03 - 1,116 | 0,0005 |
| Triglycerides (mmol/l) | F C | 78 80 | 1,2 0,8 | 0,80 0,57 | 1,01 - 1,32 0,67 - 0,98 | 0,005 |
| Cholesterol (mmol/l) | F C | 78 81 | 2,3 2,1 | 1,18 1,29 | 1,98 - 2,54 1,81 - 2,35 | NS |
| * F: Free-ranging bushpigs C: Captive bushpigs | | | | | | |

found not to be the case (haemoglobin average for individuals with below-average glucose levels: 14,1 as against 14,5 g/dl for those with above-average glucose levels; $t = 0,74$; $df = 61$ NS). Lower red blood cell parameters in free-ranging bushpigs were therefore considered meaningful. The lack of significant differences in Hb and PCV levels of culled versus immobilized free-ranging bushpigs (Table 9/15) further supported this conclusion.

Together with erythrocyte counts, haemoglobin and packed cell volume most consistently reflected condition (as represented by values of captive vs free-ranging animals: cf Table 9/17). The latter two parameters were selected for further investigation of their potential as condition indicators of free-ranging bushpigs. Both are largely correlated and only respond to changes in food resource availability with some delay, as the following examples show.

(I) On 18.3.1986 captive TD14(M) had been without food for the preceding 9 days. This relatively short period of fasting had no effect on Hb (19,9 g/dl) or PCV (59%) levels.

(II) TD7(M) was recaptured on 12.1.1986 after having been outside of the study enclosure for 6 weeks and placed back into the enclosure:

| | Hb (g/dl) | PCV(%) |
|-----------|-----------|--------|
| 12.1.1986 | 11,2 | 33 |
| 31.1.1986 | 14,0 | 43 |
| 9.7.1987 | 17,1 | 47 |

(III) The body mass of the free-ranging female CC9 was 66 kg on 3.6.1984. When captured on 17.11.1985 she had been entangled in the radio-collar (her front leg was stuck between the throat and the collar) and was extremely lean (53 kg). The entanglement presumably occurred as a result of lactational mass loss when rearing CC10 and CC11, then 7,5 months old.

| | Hb (g/dl) | PCV (%) |
|------------|-----------|---------|
| 17.11.1985 | 9,5 | 30 |
| 10.12.1985 | 12,1 | 36 |

When recaptured after 23 days CC9(F) was on the way to recovery and weighed 55 kg.

The lower limits of the 95% confidence intervals of free-ranging animals were chosen to define the boundary between poor and average to good condition. Animals with haemoglobin levels below 13,7 g/dl and PCV values below 40% were accordingly classified as being in a poor condition. When compared with a condition classification based on the body mass differential at age (Body mass - expected mass, Table 9/3), the condition of 68% and 70% of the individuals was correctly classified by the Hb and PCV criteria respectively (Table 9/18).

| Mass (at age) differential (kg) | Haemoglobin (g/dl) | | |
|---------------------------------|------------------------|----------|------------------------|
| | <13,7 | ≥13,7 | |
| ≤ - 5 > - 5 | 17 9 | 15 35 | G = 7,41 P < 0,01 |
| Mass (at age) differential (kg) | Packed cell volume (%) | | |
| | <40 | ≥40 | |
| ≤ - 5 > - 5 | 18 9 | 14 35 | G = 8,91 P < 0,0005 |

It is noteworthy that 5 of the 9 relatively heavy animals classified as being in poor condition by blood parameter criteria, were lactating females. Those that were relatively light, but in good condition according to blood parameter criteria (15 and 14 individuals in Table 9/18), were presumably smaller-sized individuals, but with sufficient "skeletal fill."

The final adult skeletal sizes of individuals differ and changes in body mass are considered to be more closely related to the current condition of the animal than could be derived from a single measurement of body mass. The recapture programme provided the opportunity of assessing the condition of individual animals by changes in body mass and of relating the resultant condition classification to haemoglobin and packed cell volume levels. An absolute or relative decrease in body mass of two kilograms or more was taken to denote poor condition. The condition classification derived in this way was compared with the condition classification based on Hb and PCV levels. Animals with less than 13,7 g/dl Hb and with PCV values below 40% were considered to be in poor condition (Table 9/19).

Compared with the condition classification from body mass changes, 81% and 78% of the 27 cases in Table 9/19, were correctly classified using Hb and PCV levels as criteria.

9.4 Discussion

9.4.1 Growth pattern comparisons

Juvenile European wild boar growth rates may be as low as 50g/day in a poor oak mast year (Pine and Gerdes 1973) or as high as 123 g/day (Pépin *et al.* 1987). Intermediate rates of 89 g/day (Pine and Gerdes 1973) and 96 g/day (Mauget 1980) are similar to the growth rate of 100g/day determined for juvenile bushpigs in this study. Unlike the pattern in the bushpig, sexual differences in growth rates become pronounced in the second year of life in the European wild boar (Pépin *et al.* 1987) and in the subadult age class in the warthog (Mason 1982, 1985 and Rodgers 1984). Growth rates during the yearling phase appear to be similar in European wild boar and bushpig (cf Jezierski and Myrcha 1975), but lower compared to the juvenile phase.

Juvenile and, to a lesser extent, yearling warthogs apparently grow considerably more slowly than European wild boars and bushpigs. Warthog juvenile growth rates of approximately 55 and 47 g/day were derived from the data of Mason (1982) and Rodgers (1984) respectively. Warthog growth rates were much reduced during the dry season (Mason 1985).

TABLE 9/19 : BODY MASS DYNAMICS AND CONDITION ASSESSMENT WITH HEMOGLOBIN AND PACKED CELL VOLUME LEVELS IN SOUTHERN CAPE BUSHPIGS

| Identification Number | Sex | RS * | Age (yrs) | Body mass (kg) * | Mass differential * | Body Mass Condition * | Hemoglobin level (g/dl) | | Packed cell volume level (%) | | | | |
|-----------------------|-----|------|-----------|------------------|---------------------|-----------------------|-------------------------|---|------------------------------|---|---|----|---|
| OC1 | F | N | 1,3 | 42,0 | -3,1 | P | 14,9 | P | 44 | P | | | |
| | | N | 1,4 | 38,0 | -8,3 | | 12,8 | | 38 | | | | |
| OC3 | M | | 7,9 | 61,0 | -10,8 | G | 13,7 | G | 41 | G | | | |
| | | | 10,3 | 60,0 | -11,9 | | 17,7 | | 50 | | | | |
| OD1 | F | N | 1,8 | 43,0 | -10,1 | G | 15,3 | G | 42 | G | | | |
| | | N | 2,6 | 64,0 | +2,9 | | | | | | | | |
| OD3 | M | | 2,7 | 70,0 | +6,2 | P | 16,4 | P | 46 | G | | | |
| | | | 3,7 | 55,0 | -13,5 | | 13,2 | | 40 | | | | |
| OE1 | F | N | 3,2 | 57,0 | -7,1 | P | 16,1 | P | 49 | P | | | |
| | | N | 3,8 | 57,0 | -8,8 | | 13,9 | | 41 | | | | |
| | | N | 4,7 | 50,0 | -17,4 | | 13,3 | | 38 | | | | |
| OF1 | F | N | 1,4 | 42,5 | -3,3 | G | 15,4 | G | 43 | G | | | |
| | | N | 1,5 | 48,0 | -0,1 | | 17,8 | | 52 | | | | |
| OG1 | M | | 11,4 | 57,0 | -14,9 | G | 12,6 | P | 37 | P | | | |
| | | | 13,5 | 60,5 | -11,4 | | 13,0 | | 38 | | | | |
| OG2 | F | N | 3,7 | 62,5 | -3,1 | P | 11,4 | P | 31 | P | | | |
| | | N | 3,9 | 60,0 | -6,0 | | | | | | | | |
| OI4 | M | | 1,5 | 66,5 | +16,9 | P | 15,5 | G | 50 | G | | | |
| | | | 1,9 | 60,0 | +8,3 | | 16,3 | | 47 | | | | |
| OI8 | F | N | 1,5 | 53,0 | +4,8 | P | 15,8 | G | 49 | G | | | |
| | | N | 1,9 | 53,0 | -2,2 | | | | | | | | |
| OK1 | F | N | 12,0 | 58,0 | -9,9 | P | 9,9 | P | 34 | P | | | |
| | | N | 12,1 | 50,5 | -17,4 | | | | | | | | |
| OL2 | F | L | 2,3 | 60,5 | +1,7 | P | 10,9 | P | 31 | P | | | |
| | | N | 3,0 | 50,0 | -13,3 | | 10,9 | | 32 | | | | |
| OP2 | M | | 3,9 | 70,0 | +1,0 | G | 15,1 | G | 46 | G | | | |
| | | | 4,6 | 80,5 | +10,2 | | 16,2 | | 45 | | | | |
| OR1 | M | | 8,3 | 75,0 | +3,2 | P | 11,4 | P | 34 | P | | | |
| | | | 9,3 | 58,5 | -13,2 | | | | | | | | |
| OT3 | F | N | 1,8 | 59,0 | +5,4 | G | 19,1 | G | 55 | G | | | |
| | | N | 2,3 | 66,0 | +7,7 | | 14,6 | | 42 | | | | |
| OT4 | M | | 3,3 | 63,0 | -4,0 | G | 12,4 | G | 36 | G | | | |
| | | | 3,7 | 66,5 | -1,9 | | 16,4 | | 44 | | | | |
| OT7 | M | | 2,1 | 68,0 | +9,8 | G | 15,3 | G | 47 | G | | | |
| | | | 2,9 | 73,0 | +7,9 | | | | | | | | |
| OU3 | F | N | 9,9 | 79,0 | +11,1 | P | 15,4 | P | 45 | P | | | |
| | | N | 10,4 | 77,0 | +9,6 | | 11,1 | | 32 | | | | |
| OU8 | M | | 8,7 | 83,0 | +11,2 | P | 13,5 | P | 37 | P | | | |
| | | | 8,8 | 65,0 | -6,8 | | 11,4 | | 34 | | | | |
| | | | 9,3 | 89,5 | +17,7 | | P | | 16,0 | | G | 45 | G |
| | | | 9,6 | 84,0 | +12,1 | | | | | | | | |
| OV1 | M | | 4,0 | 64,0 | -5,2 | P | 11,8 | P | 33 | P | | | |
| | | | 4,1 | 57,0 | -12,4 | | | | | | | | |
| OW1 | M | | 1,4 | 40,0 | -7,2 | G | 14,9 | G | 46 | G | | | |
| | | | 1,7 | 53,0 | -0,2 | | | | | | | | |
| OW2 | M | | 1,5 | 49,1 | -0,5 | G | 16,0 | G | 45 | G | | | |
| | | | 1,9 | 61,5 | +5,3 | | | | | | | | |
| OW3 | F | N | 1,5 | 41,0 | -7,2 | G | 17,6 | G | 46 | G | | | |
| | | P | 2,2 | 66,0 | +8,5 | | | | | | | | |
| CZ1 | F | L | 7,4 | 63,0 | -4,9 | G | 11,6 | G | 35 | G | | | |
| | | N | 8,1 | 69,0 | +1,1 | | 14,4 | | 42 | | | | |
| DD1 | M | | 6,5 | 74,0 | +2,5 | P | 14,1 | G | 44 | G | | | |
| | | | 6,7 | 67,5 | -4,1 | | | | | | | | |
| DK1 | M | | 3,3 | 58,0 | -9,0 | P | 15,3 | P | 49 | G | | | |
| | | | 3,5 | 55,0 | -12,8 | | 13,3 | | 43 | | | | |

*RS : Female reproductive state (Non-reproductive, Pregnant, Lactating)

*Mass differential : Body mass - expected body mass for age (kg)

*Body mass condition : defined in text : P = Poor G = Average go good

It is noteworthy that prenatal growth rates are also much lower in warthog than in wild boar and bushpig. This follows from a 6 month gestation period in the warthog compared to 4 months in the other two species, while birth weights of all three are similar (10.4.1.2). Pregnancy in the warthog coincides with the dry season (cf Mason 1982). It appears that the rate of protein procurement for growth is particularly limiting during the dry season for the non-ruminant warthog.

In many species studied, it is possible to identify a definite break in the growth curve, or change in the form of growth, which coincides with weaning (Pond 1977). Post-weaning growth checks in pigs are especially associated with conditions of restricted food availability (Mount and Ingram 1971, Barrett 1978, Blackshaw 1981). When associated with limited food availability, retardation of winter growth is common in zones with pronounced cold winters (Briedermann 1986). Where European wild boars live under conditions of mild winters and sufficient food, winter growth checks are absent (Schnorrenberg 1979). Seasonal influences on growth or post-weaning growth checks were not evident in the bushpig. This is not unexpected since weaning is a relatively gradual process in free-ranging suids (10.4.1.4).

Pre- and postnatal size variation within litters was found to be substantial in bushpigs (10.3.3; 9.3.1), as it is in domestic and feral *Sus scrofa*. In the European wild boar birth mass of littermates varied within 30% (Briedermann 1986). Factors responsible for within-litter weight variation in domestic piglets at 8 weeks of age were quantified by McBride *et al.* (1965) as follows: due to birth mass (19%), teat order (5%), weight at 3 weeks (29%) and social rank (17%). There was a continuing association and interaction between social rank and growth (McBride *et al.* 1965). Pigs dominant during nursing weighed more at birth, were involved in more fights, won more of their fights, tended to gain control of the anterior teats and exhibited lower mortality and greater gains to 21 days than did subordinates (Scheel, Graves and Sherritt 1977). As suggested by Geist (1978a), juvenile aggression and specialized weapons may pay off in larger body size and higher dominance with benefits extending into adulthood. Specialized weapons are found in suckling suids in the form of short, sharp temporary canines, which are presumably used in agonistic encounters determining access to the

most favourable suckling positions (teats). Possible implications of intralitter size variability in terms of maternal fitness are discussed in section 10.4.1.3.

As may be expected in species with pronounced sexual dimorphism in body size, European wild boar and warthog males continue to grow for longer than females. Measurements by Briedermann (1970) on European wild boar in Germany indicate that male growth is essentially completed by 5 years of age, that in females at 3 to 4 years. Body dimensions of European wild boar in Russia increased up to the ages 8 and 6 years in males and females respectively (Kozlo 1975). However, 95% of the final body dimensions were reached in the 5th year in males (body mass excluded) and in the 4th year in females. At 5 years the average male body mass was only 75% of the final mass. According to Hell and Paule (1983 ex Briedermann 1986), growth in European wild boar in Slovakia is still relatively strong in the third and fourth years of life and may only be finally completed within the eighth and ninth years of life. In the bushpig, both sexes exceed 90% of their final body masses at 3 years of age, 95% at 4 years and 98% at 5 years of age.

9.4.2 Juvenile growth and breeding season

Comparison of the growth rates of free-ranging and captive bushpig juveniles (Fig. 9/3) shows that a significant difference only develops after weaning. This suggests that free-ranging sows attempt to maintain maximum growth rates in their offspring even in the face of food shortages which they may experience during lactation. This is presumably of critical importance for the viability and survival of the progeny and therefore for reproductive success. The uncompromising provisioning of the young is at the cost of the maternal body reserves (10.3.4). Thereafter they require replenishment before the next reproductive venture can take place. In this section the possible relevance of these patterns in influencing the breeding seasonality of the bushpig (10.3.5), is discussed.

Bushpigs and other suids have young which are comparatively small at birth (5.3.2). This has thermoregulatory implications (7.4.4). The studies of Moen (1968) on white-tailed deer *Odocoileus virginianus*

indicated that small body size increases the difficulty of maintaining body temperature, but that adequate food could substantially extend the thermoneutral zone under cold conditions (also Picton 1979 and Searcy 1980). Where two groups of pigs received the same amount of food each day, animals kept under warm conditions grew faster (Baldwin and Ingram 1968a). This is in accord with higher summer gains reported for domestic pig weanlings (Noland and Scott 1960). Sainsbury (1972) found that growth rates of pigs fed on a low plane were most adversely affected during the winter months. Several authors have reported reduced fat and protein deposition in growing domestic pigs when food is limited under cold conditions (Bianca and Blaxter 1961, Close and Mount 1971, Verstegen *et al.* 1973).

There is thus good evidence that pigs, and other homeotherms, require additional food to compensate for temperature regulation requirements at ambient temperatures below the thermoneutral zone (Verstegen *et al.* 1982). Bushpig juveniles would often experience such conditions during the winter months in the study area (7.4.3.2). Where resources are limited a trade-off is postulated between maternal condition (and ultimately the chances of rebreeding in the subsequent year; i.e. life time reproductive success) and juvenile energetics (and thus their growth and survival). The energy needs for juvenile thermoregulation entail an added load which may be minimized if lactation is confined to the season of the year with the lowest thermoregulatory demand, i.e. summer.

9.4.3 Growth and food resources

Pre-weaning growth rates appear to be well-buffered against food shortages, although maternal costs of maintaining them presumably vary with food availability (9.4.3). Pépin *et al.* (1987) found that the existence or absence of oak masts did not significantly affect the growth of European wild boar piglets up to the age of 6 to 8 months. Klein (1984 *ex Pépin et al.* 1987) reported that the growth rate in European wild boar juveniles up to 6 months of age did not vary from year to year. However, faster growth rates may mean a larger final size and thus possibly greater reproductive output (Calow and Townsend 1981). Since small offspring are often vulnerable to adverse physical

conditions and predation, fast growth is advantageous in that the length of the vulnerable stage is minimized (Callow and Townsend 1981). One may thus expect a strong positive link between food availability and growth rate.

A host of studies relate increased food availability or intake to increased growth (Schoener 1971). Growth rates of free-ranging baboons (*Papio cynocephalus*) were consistently one-half to one-third lower than those of well-provisioned captives and equivalent to those of captive baboons fed a low protein diet (Altmann and Alberts 1987). Differences in growth rates of captive and free-ranging juvenile bushpigs found in this study also fall in this category. Similar observations were recorded for warthog (Roth 1965) and collared peccary (Low 1970). European wild boar juveniles and yearlings in good mast years were significantly heavier than in poor years (Briedermann 1986, Pépin *et al.* 1987). Feral hogs with access to pastures made more rapid gains and were significantly heavier by about 25% than back-country hogs on Dye Creek Ranch, California (Barrett 1978).

Briedermann (1986) compared the performance of European wild boar between two areas in Germany. The one (Hakel) had nutrient-rich soils, mainly broad-leaved forests and much forest to agriculture interface, while the other (Nedlitz) was characterized by sandy soils, a predominance of conifer forests and much less forest to agriculture interface. Individuals from Hakel were substantially heavier, especially in the juvenile and yearling age classes. Briedermann (1986) related these differences to differences in the quantity and quality of food available. Analogous differences were found in age-specific body mass of bushpigs from the plateau and the foothill zones in the Southern Cape (9.3.1, Table 9/14). The plateau zone was primarily covered with a mosaic of indigenous forest and agricultural land, whereas in the foothill zone pine plantations, fynbos and some indigenous forest, generally on acid soils, predominated.

Faster gains are particularly dependent on dietary protein, as numerous studies *inter alia* in the domestic pig have shown. For example high protein rations (18 - 20%) produced significantly greater rates of body mass gain than low protein rations (10 - 12%) (Pond *et al.* 1960,

Chamberlain 1972, Atinmo, Pond and Barnes 1974). The effect of dietary protein on growth is however influenced by the level of dietary energy. Noland and Scott (1960) found a protein/energy interaction in domestic pigs during the period of gain from 18 - 34 kg. Rations with calorie/protein ratios of from 49 - 75 produced the fastest gains in the weight range from 18 - 57 kg. Thereafter a calorie/protein ratio of 100 resulted in the most rapid gains. Increasing levels of energy intake resulted in more efficient gains and lower daily feed intakes (Noland and Scott 1960). Bushpig growth rates do not differ between the Southern and Eastern Cape, but the degree of energy deposition apparently does (9.4.4). Divergent dietary calorie to protein ratios may be involved.

9.4.4 Body mass dynamics

Briedermann (1986) summarized the data available on European wild boar body mass in various regions of Europe and found a pronounced gradient of increasing size from west to east. Animals from western Europe had weights similar to those of bushpig, whereas adult males in Russia commonly averaged 145 to 200 kg, or even higher. Adult warthog body weights have the same order of magnitude (85 kg in males, 57 kg in females *vide* Kingdon 1979) as in the bushpig. Male giant forest hogs commonly weigh 230 kg, as against 180 kg for females (Kingdon 1979). The bushpig is the only one of these suid species which does not exhibit any pronounced sexual dimorphism in body size (4.4.3.3).

With increasing size the absolute food requirements increase, but those relative to unit of size decline. Thus, as food diminishes in an animal's environment, large consumers are selected against faster than small consumers (Belovsky 1978). However, the average energetically optimal body size is determined by the quantity and quality of the food resources and their availability over space and time. For "bulk" feeding herbivores, such as the giant forest hog and the warthog, quality of food is critical and body size reflects the optimum in terms of the quality to quantity ratio in procurable food (8.2.5.3). For omnivores, such as the European wild boar and the bushpig, food quantity and its spatiotemporal availability is critical (8.2.5). Margalef (1963) pointed out that body size of individuals is proportional not to

the productivity, but to the productivity pulse of an ecosystem. The ability to withstand starvation increases with size, because maximum fat stores increase faster with size than do metabolic costs (Searcy 1980). Lindstedt and Boyce (1985) view this allometry in the ability to endure fasting as a potentially strong selective pressure on body size in seasonal environments where animals must survive environmentally imposed fasts. Selection is considered to optimize the difference between foraging profit and maintenance cost, both per unit of time, scaled to body size. When the scaling function maximizes the length of time an individual can survive on the profit gained in a given period of foraging, optimum body size increases as ambient temperature decreases (Searcy 1980). This author thus identified the importance of allometry in survival-time and showed that this effect was amplified at colder temperatures. Eastern Europe has a more continental climate than western Europe, i.e. it is seasonally more pronounced with lower ambient temperatures. This may explain the west to east body size gradient in European wild boar previously discussed. Bushpig body mass would be expected to conform to that of European wild boar subjected to a climatic regime with the least seasonality, which is the case.

Whereas no seasonal trend is evident in body mass of male bushpigs, in females it changes with the seasonal reproductive cycle (10.3.5). Average female body mass is highest in winter and spring when most pregnancies occur and lowest in summer, when most lactations tend to occur (Table 9/1). The average body mass of pregnant females is higher than the overall female average and that of lactating females is lower (9.3.1). For species living in clearly seasonal environments, the effect of seasonality in food availability and reproduction on body mass and condition are superimposed. For example, in European wild boar males, body mass is high in summer, declining to late winter (Briedermann 1986). This is a direct reflection of food availability and storage (9.4.5). In females the seasonal body mass cycle is strongly modified by the reproductive cycle. Peak body mass is achieved in autumn and early winter (pregnancy), with minimum values in spring and early summer (lactation).

Body mass in both male and female adult warthogs reached low values during late winter and early spring although most females were pregnant

during this period. However, mean bone marrow fat content was highest then and was associated with pregnancy (Mason 1982). Such seasonal changes may involve 20 - 25% of body mass (Briedermann 1986), but Jezierski and Myrcha (1975) consider even losses of 30 - 50% quite normal in Polish winters.

Gestational anabolism is a well-documented phenomenon in domestic sows and numerous other mammals (Duncan and Lodge 1960). The mass of the normal sow is constantly changing as she gains during pregnancy, experiences a sudden drop at parturition and continues to lose weight during lactation as she mobilizes her body reserves for milk production (English *et al.* 1977). These changes essentially involve energy storage cycles, which are dealt with in greater detail in section 9.4.5.

The lower body mass of bushpig females in the Eastern Cape is not paralleled in males (9.3.1). It is associated with earlier and more frequent breeding and larger litter sizes in the Eastern Cape (10.3.6) and is probably causally related to it. Females breeding earlier in life often attain smaller size at maturity (e.g. in beavers *Castor canadensis*, Boyce 1981 and reindeer *Rangifer tarandus*, Skogland 1983). A population with a higher proportion of lactating females must be expected to have a lower average body mass.

Lactation retarded growth in domestic sows, and young sows, even when well-fed, but especially when poorly fed, were less tall at 18 months of age than litter mates not bred. Sows with small litters often gained weight throughout lactation, but those with large litters lost weight and only began to gain in the third week after weaning (Duncan and Lodge 1960). According to Iff (1976), early pregnancy in European wild boar sows resulted in delayed body and dental development. In collared peccaries (*Tayassu tajacu*) from western Texas, the body masses of males were slightly greater during wetter years, but females were slightly lighter. This was interpreted as the result of a higher breeding rate in the wetter years and consequently a greater energy drain due to lactation (Low 1970).

9.4.5 Patterns in energy storage

Organisms store materials for use during local or seasonal shortages, because they are temporarily unable to gather or synthesize food for themselves, or because the rate of growth or metabolism is temporarily so high that food intake cannot keep up with the demand (Pond 1981). Adipose tissue, primarily functioning as an energy reserve (Pond 1978), is particularly important for animals which may have to face times when food availability is uncertain or subject to the stresses associated with competition for mates, rearing, territorial defence or migrations (Young 1976). Storage strategies are clearly products of selection and evolve in response to the challenges presented by the trophic conditions of the environment (Calow 1977). Adiposity is accordingly favoured by predictable as well as unpredictable, but probable periods of trophic hardship (Calow 1977). Periodically increased trophic demands associated with the reproductive cycle also commonly favour adiposity, especially those related to early lactation (cf Spinage 1985).

Energy storage also involves costs. Additional food material has to be obtained, converted into storage molecules and carried around (Pond 1981). In view of this, organisms do not accumulate energy reserves in larger quantities or for longer periods than the circumstances of selection require. In many female mammals, therefore, the deposition of fat in order to meet the demands of lactation, does not begin to any measurable extent until gestation has begun and the timing seems unrelated to fluctuations in food supply (Pond 1981). Also, in environments with little variation in food supply, less reserves are stored. Large fat reserves are advantageous when foraging conditions are uncertain or predictably pulsed (cf Calow 1977; e.g. in elephants *Loxodonta africana*: Laws, Parker and Johnstone 1975, Malpas 1977).

Energy storage patterns in the bushpig differ according to sex, female reproductive state and region, but are apparently not affected by season (9.3.2).

(a) Season

In seasonal northern hemisphere environments, the European wild boar exhibits a seasonal fat storage cycle (Briedermann 1986). Adult

European wild boar in Russia have subcutaneous fat layers 35 - 50 mm thick on the back and flanks in autumn in regions of abundant food (Sludskii 1956). For example, in the Caucasus this may amount to 20 kg of internal and up to 30 - 40 kg of subcutaneous fat with a total body mass of 160 - 180 kg. Fat thus makes up approximately 30% of the live mass (Sludskii 1956). Seasonal changes in body fat content of feral pigs in North America were correlated with changes in dietary sources and their availability (Graves 1984). The lack of any pronounced seasonality in food availability for bushpigs in the study area (8.1.8.3) presumably explains the absence of a seasonal rhythm in energy storage.

(b) Sex

Adult male bushpigs have lower levels of fat reserves than females (9.3.2). Domestic boars are also usually leaner than gilts (Martin *et al.* 1972). Female mammals generally tend to have greater fat reserves than males (Pond 1978) and this is related to the requirements of reproduction in the female, as discussed below (c).

(c) Female reproductive status

In bushpig females, fat reserves followed the reproductive cycle, with much storage during pregnancy and mobilization during lactation (9.3.2). Pregnant females are generally in good condition, as evidenced by increased fat reserves (e.g. in the warthog, Mason 1985 and in elephants, Williamson 1975). A well-known characteristic of the pregnant domestic sow is the considerable greater efficiency in feed utilization than the non-pregnant female (Cole 1982). Pregnant sows still grow on a maintenance scheme for non-pregnant sows (Den Hartog and Van Kempen 1980). On the other hand, the accumulated fat reserves are used up rapidly during lactation (cf Clutton-Brock *et al.* 1982, Dunham and Murray 1982). Lactation was found to require from 3 to 5 times more energy than pregnancy in white tailed deer *Odocoileus virginianus* (Cothran *et al.* 1987). Baber and Coblenz (1986) observed a rapid decline in condition in feral pigs during lactation when the nutrition was poor and Breytenbach (1977) made similar observations in lactating or post-lactating bushpig females at St. Lucia, Natal.

By more equitably spreading the increased cost of lactation into pregnancy (through storage), time spent foraging during lactation is reduced. This is believed to facilitate suckling frequency and reduced movement of the young, which would lower the risk of predation (11.2.3) When resources are at chronically low levels throughout the breeding season, the high costs of lactation can only be met by supplementation from stored energy. In this way, females presumably maximize the utilization of overall low resource levels by accumulating the necessary amounts of energy (and protein) during pregnancy to meet the relatively high, pulsed demands of lactation (cf Mattingly and McClure 1982).

(d) Regional differences in fat storage

The degree and nature of fat storage is very much influenced by the nature of food resources: their temporal stability, quantity and composition (protein/energy ratio). Caughley (1970) considered the level of fat reserves as an indicator of an animal's well-being, its general state of nutrition and the favourability of its environment. Field observations showed that subcutaneous fat deposition of wild pigs in Hawaii varied according to the food resources available to them. Pigs shot at high elevations and feeding mainly on forest vegetation had less fat and were generally much thinner than those living near cultivated areas (Diong 1973).

Apart from food quantity, the composition of the diet exerts an influence on fat storage. Of the Carnivora, only the omnivorous species, like bear, badger and raccoon, lay down large quantities of fat (Pond 1978). The warthog, unlike the omnivorous bushpig and European wild boar, does not have a high proportion of fat in the body tissue, either subcutaneous, intramuscular or in the cavities (Smith 1970, Cumming 1975, Mason 1982). In contrast, a yearling female warthog which had been living in maize lands, had a subdermal fat layer of about 1 cm over most of the body (ex Mason 1985). A yearling bushpig (CU2) which had access to a lucerne field and was exceptionally large for its age, had no subdermal fat (this study).

The dietary protein to energy (P/E) ratio appears to be of importance in influencing the degree of fat storage. Energy, and energy and protein

restrictions result in reduced carcass fatness, while protein restrictions result in increased carcass fatness (Fowler and Livingstone 1972, Young and Sharma 1973, Carden and Goenaga 1977, Coffey *et al.* 1982). When the effects of food intake were taken into account, carcass fatness increased steadily with reductions in protein level down to 13% while the reduction from 13% to 10,5% produced a much greater increase in fatness (Fuller *et al.* 1976).

Fat storage cannot be merely a product of the quantity and composition (P/E ratio) of the food resources available, but must also be energetically advantageous. Benefits would be expected when food supplies are unreliable (as discussed above) or during period of high thermoregulatory demand (9.4.4). Graves and Graves (1977) found that although the digestible energy consumption of the subjects was approximately equal, feral pigs grew more slowly and were fatter than domestic pigs. They interpreted this as an adaptation to strongly seasonal availability of food. Lipid reserves contribute to sustaining high levels of thermoregulatory expenditure and must also have survival value (King and Farner 1966). We may conclude that the fat storage strategy of an animal is the result of a balance between the cost and benefits of storage under the prevailing circumstances of resource availability (quantity and P/E ratio). Apart from the costs of storage mentioned earlier (cf Pond 1978), fat deposits may also incur costs by interfering with efficient heat dissipation and with predator evasion in warm African savanna environments (Smith 1970, Owen-Smith 1982). These factors could explain the relatively sparse fat deposits in the warthog. However, an alternative explanation is based on the metabolic consequences of a high dietary TPR (8.3.4.3) and its life history consequences (12.2.3: Table 12/1).

Bushpigs in the Eastern Cape tend to have less fat reserves than those in the Southern Cape. This pattern is particularly pronounced in females and yearlings of both sexes. The higher fat reserves of Southern Cape animals are postulated to be the result of higher thermoregulatory demands (2.3, 7.3), particularly in juveniles and yearlings, and a lower dietary P/E ratio (8.3). In the process of procuring sufficient protein for reproduction and growth in the Southern

Cape, relatively large amounts of carbohydrates are ingested and retained as fat reserves, because they are energetically advantageous.

9.4.6 Interpretation of blood profile parameters

The red blood cell parameters (RBC, HB and PCV), and the albumin/globulin ratio showed promise as condition indicators in the bushpig (9.3.3.3, Table 9/17). The A/G ratio in Sinclair miniature pigs fed 16% and 4% protein diets *ad libitum* stabilized at ca 1,0 and ca 0,3 respectively after 20 weeks of treatment (Tumbleson, Burks and Hook 1972). Increasing dietary protein levels tend to result in an increase in albumin, but a decrease in the globulin fraction of serum protein (Hassan and Roussel 1975). Franzmann (1971 ex Malpas 1977) used the serum A/G ratio to detect differences in protein intake in bighorn sheep (*Ovis canadensis*). Although not statistically significant, the serum A/G ratio also tended to be consistently higher in elephants (*Loxodonta africana*) during the wet season than in the dry season in 3 different areas, thus reflecting diet quality at the time of sampling (Malpas 1977). The A/G ratio was significantly lower among peccaries (*Tayassu tajacu*) fed restricted diets (Lochmiller *et al.* 1985b). Given sufficient sample sizes, differences in the intake of protein between bushpig populations would presumably also be detectable (9.3.3.3, Table 9/15 versus Table 9/17). Haemoglobin and packed cell volume were however found to be more sensitive and consistent indicators of individual condition (9.3.3.3) and subsequent discussion is confined to these two parameters.

Haemoglobin is a complex, iron-containing conjugate protein, composed of a pigment and a protein. If whole blood is centrifuged, a mass of erythrocytes accumulates at the bottom, and this is referred to as packed cell volume (also hematocrit). In contrast to the few studies with inconsistent findings (Seal, Verme and Ozoga 1978, Warren *et al.* 1982, Algar, Arnold and Grassia 1988), there is clear evidence for a positive correlation of condition with high Hb and PCV levels (Table 9/20).

| TABLE 9/20: LIST OF STUDIES SHOWING A POSITIVE RELATIONSHIP BETWEEN HAEMOGLOBIN OR PCV VALUES AND CONDITION | | | |
|---|-----------|-----|-----------------------------------|
| Species | Parameter | | Authors |
| | Hb | PCV | |
| Euros (<i>Macropus robustus</i>) | x | | Ealey and Main (1967) |
| Mule deer (<i>Odocoileus hemionus</i>) | | x | Anderson et al (1970) |
| Bighorn sheep (<i>Ovis canadensis</i>) | | x | Franzmann (1972) |
| White-tailed deer (<i>Odocoileus virginianus</i>) | x | x | Seal et al (1972b) |
| Reindeer (<i>Rangifer tarandus</i>) | x | x | Bjarghov et al. (1976) |
| Sable antelope (<i>Hippotragus niger</i>) | | x | Wilson and Hirst (1977) |
| Roan antelope (<i>Hippotragus equinus</i>) | | x | Wilson and Hirst (1977) |
| Moose (<i>Alces alces</i>) | x | x | Franzmann and LeResche (1978) |
| Baboon (<i>Papio ursinus</i>) | x | | op. cit. Melton and Melton (1982) |
| Rabbit (<i>Oryctolagus cuniculus</i>) | x | x | Richardson and Wood (1982) |
| Bison (<i>Bison bison</i>) | x | x | Hawley and Peden (1982) |
| White-tailed deer (<i>O. virginianus</i>) | x | | Kie, White and Drawe (1983) |
| Oryx (<i>Oryx gazella</i>) | x | | Fourie and Van Ouwerkerk (1984) |
| Blue wildebeest (<i>Connochaetus taurinus</i>) | x | | Fourie and Van Ouwerkerk (1984) |
| Collared peccary (<i>Tayassu tajacu</i>) | x | x | Lochmiller et al. (1985a) |
| Western grey kangaroo (<i>Macropus fuliginosus ocydromus</i>) | x | | op. cit. Algar et al. (1988) |
| Black bear (<i>Ursus americanus</i>) | x | x | Franzmann and Schwartz (1988) |

Payne et al. (1970) observed a sharp increase of Hb in dairy cattle following access to spring pastures. They also found that PCV was related to milk yield of cows and was affected by season, being low at the end of winter and rising sharply when the animals came on to spring pasture. The lactating groups of cows had significantly lower levels of Hb and PCV than non-lactating groups at each sampling. Increased Hb levels were thought to indicate improved protein status (Rowlands et al. 1974). Based on research in the domestic pig, it was suggested that protein and not energy intake determines red blood cell characteristics. The effects were only evident after 10 weeks of feed restriction in pregnant sows and energy restriction had no effect (Atinmo et al. 1974). Burks, Evans and Tumbleson (1974) compared hematological responses to a 16% and 4% protein diet in Sinclair miniature swine. They found that

from 4 to 28 weeks of age, PCV and Hb concentrations were lower in individuals on the 4% diet.

Red blood cell parameters (RBC, PCV, Hb) fluctuated seasonally among wild peccaries (*Tayassu tajacu*) collected in southern Texas, coinciding with changes in range condition (Lochmiller *et al.* 1985a). These authors also reported that well-fed captives had higher red blood cell parameter values than free-ranging peccaries. Lactating females fed high protein diets had greater Hb and PCV levels than those fed low protein diets (Lochmiller 1984 *ex* Lochmiller *et al.* 1986b). In another part of the study, the highest Hb and PCV levels were associated with *ad libitum*-fed females, but these differences were not evident until the 56- and 84-day samples (Lochmiller *et al.* 1985b). Finally, Hb and PCV concentrations were found to be significantly greater among female peccaries fed the high quality diet (15,2% vs 6,3% crude protein diets: Lochmiller *et al.* 1986b):

| Treatment period | 10 Weeks | | 15 Weeks | |
|------------------|----------|------|----------|------|
| | High | Low | High | Low |
| Diet quality | | | | |
| PCV (%) | 41,9 | 36,0 | 44,1 | 36,0 |
| Hb(g/dl) | 14,7 | 12,3 | 15,2 | 12,3 |

Protein restriction for prolonged periods apparently results in depressed erythropoetic activity and Hb synthesis (Lochmiller *et al.* 1986b). The studies cited indicate that red blood cell parameters provide sensitive indices for the assessment of condition related to protein nutrition. The delayed response to changes in dietary quality suggests that these parameters reflect protein reserve status rather than the current protein intake. On the assumption that protein reserves are critical for reproduction, red blood cell condition indices should be directly linked to condition in terms of reproductive turnover.

9.4.7 Condition evaluation

A number of factors determine the usefulness of any particular parameter for assessing condition:

- (I) Purpose. Must the parameter be useful for assessing the condition of individuals or populations? What is the type of condition involved? If it is defined in relation to an animal's chances of living or dying (Hanks 1981), i.e. its survival, other condition indices may be appropriate than if the index is required to reflect reproductive turnover of the population. In the case of bushpigs in the Cape Province, animals are on average "fatter" in the population with the lower reproductive turnover (10.3.6).
- (II) Availability of biological material (from live or dead animals).
- (III) Logistics (ease of collection and analysis, type of personnel involved, laboratory facilities).
- (IV) Interpretation. The parameters selected should be sensitive to the phenomenon to be assessed, but robust in respect of other influences (e.g. handling stress or normal physiological variability). If it is not possible to sample enough animals to accommodate individual variation, data may be difficult to interpret. Baseline values from individuals or populations of known condition are necessary to interpret the data.

In this study, useful indices for assessing condition in the bushpig were found to be body mass, fat reserves and red blood cell population characteristics.

(a) Body mass relative to age or size

Whereas body mass at age in comparison to the mean expected mass, is the appropriate index for the juvenile and yearling age classes, for subadults and adults the ratio of body mass/size must be used (9.3.3.1). The required parameters (body mass, body length, age) are relatively easily obtainable from both dead and live animals. Standardized measurements are imperative for good results. Gut fill is a source of body mass variation which should be minimised by standardising data collection procedures.

These condition indicators reflect both muscle mass and energy reserves accumulated. They represent nutritional condition over a long period and are therefore particularly meaningful and robust.

(b) Fat reserve condition indices

Bone marrow fat percentages may be simply determined from the relationship of percentage fat to dry mass established for the bushpig (9.3.3.2). Studies of several wild ungulates have indicated that bone marrow fat reserves are the last to be mobilized in response to increasing nutritional stress (Ransom 1965, Brooks *et al.* 1977). Their concentration will therefore only be sensitive to severe, prolonged nutritional deficiencies. Because only a relatively small quantity is present, marrow fat itself possesses little total energy. In a deer-sized animal with 100% of its marrow fat, this contains energy reserves for only about 1 - 2 days (Mech and Delgiudice 1985). If the bone marrow fat percentage is below 60% in the bushpig, the individual is most likely in a poor condition (9.3.3.2). For higher fat percentages, all that can be concluded is that the animal is not necessarily in a poor condition, but even that is speculative.

Subcutaneous and peritoneal fat indices are more sensitive than bone marrow fat. Fluctuations in these reserves reflect physiological events related to reproduction which can obscure smaller differences in nutritional condition. Fat reserves are not only influenced by reproductive state, but also by the energy storage strategy and the availability of food (9.4.5). This makes interpretation difficult in the case of individuals. Fat reserve condition indices therefore reflect the degree to which the animals were able to convert surplus food into energy reserves.

A disadvantage is that condition indices based on fat reserves can only be obtained from culled animals.

(c) Red blood cell condition indices

Haemoglobin and packed cell volume levels seem to be sensitive indices of protein reserve status (9.3.3.3, 9.4.6). If this is critically

linked to reproduction as postulated (10.4.3), the indices are particularly biologically meaningful. Long response periods to changes in protein intake make them robust. However, the conditions under which blood is collected should be standardized as far as is possible in order to minimize sources of variation due to factors such as excitement and immobilization. Many bushpigs, mainly those from the Eastern Cape, were obtained on hunts where they were chased by dogs. Blood sampling was not undertaken. Whether red blood cell parameters are in fact rendered useless as a result of excitement and physiological stress should however be investigated. The alpha-globulin/beta globulin ratio, not determined in this study, was a sensitive indicator of protein intake in peccaries (Lochmiller *et al.* 1986b). The value of this parameter for condition assessment in bushpig, and its resilience to stress, should be investigated.

In conclusion, comprehensive condition assessment in bushpig research or management should involve the following: determination of age, body mass and length, thickness of subcutaneous and peritoneal fat layers; whole blood collection for haemoglobin and packed cell volume determinations. A minimum programme may be confined to the parameters body mass, body length, age for juveniles and yearlings and haemoglobin.

9.5 Synopsis

- (I) Mean body mass of the adult bushpigs studied was 71,8 kg for males and 67,9 kg for females. At one and two years of age approximately 50% and 80% respectively of adult body mass is attained under average conditions.
- (II) Eastern Cape bushpig females are smaller than those from the Southern Cape in terms of body mass and length. Female body mass tends to fluctuate with reproductive state, being highest during pregnancy and lowest during lactation.
- (III) At any particular age, juvenile and yearling bushpigs in captivity were considerably heavier than their free-ranging counterparts. The growth rate of free-ranging bushpig juveniles averaged

100g/day and 52g/day in yearlings. Within litter size variability was high, with male siblings tending to be slightly heavier.

- (IV) No growth rate differences were evident between animals from the Southern and Eastern Cape. Growth rates from the Southern Cape foothill zone were lower than those of animals from the plateau zone. Observed patterns in growth rate reflected assumed differences in availability of food resources.
- (V) Energy was mainly stored in the form of subcutaneous and peritoneal fat. Energy reserves in Eastern Cape bushpigs were generally lower than in the Southern Cape. Females, especially when pregnant, tended to store more fat. The metabolic costs of lactation were commonly reflected in severe depletion of energy reserve.
- (VI) Energy storage patterns were interpreted as adaptations to cope with unpredictable food shortages or energetically demanding periods and pulsed requirements (lactation). They were influenced by the quantity of the food resources and the dietary protein/energy ratio.
- (VII) A number of potential condition indicators were investigated and found useful for condition assessment in the bushpig: body mass at age, body mass to size ratio, subcutaneous fat layer index, maximum peritoneal fat layer thickness and haemoglobin or packed cell volume levels. Although all were correlated, they tended to express different facets of condition.

10. REPRODUCTION

10.1 Introduction

A great deal of variation among life histories relates to aspects of reproduction (Begon *et al.* 1986). The lifetime productivity of a female depends on her reproductive life span (age at first breeding; survivorship), the interbirth interval and litter size (Eisenberg 1983, Hudson 1985). Natural selection favours those individuals with the greatest fitness, i.e. those that make the greatest proportionate contribution to the future of the population to which they belong. All life history components affect this contribution (Begon *et al.* 1986). They do so through the media of fecundity and survivorship, both of which are linked to food availability and the resultant body condition.

The central theme of this chapter is the interaction of resource use (Chapters 6, 7, 8 and 9) and social factors (Chapter 4) with reproduction. The objective is *i.a.* to develop a better understanding of population regulation (Chapter 11). The benefits of maximizing reproductive output must balance the costs of concomitant reductions in parental survivorship and long-term fecundity, as well as the associated lower individual fitness of smaller offspring (Calow 1981). These interactions are interpreted within the framework of life history strategies in Chapter 12.

10.2 Methods

A variety of information relating to reproduction became available from post-mortem sampling (1.3.2), the capture programme (1.3.1) and enclosure studies (1.3.4). The capture programme provided data over a number of consecutive breeding cycles. Enclosure studies made it possible to monitor sequential reproductive events and associated physiological parameters of the study group over a period of 7 years. The biological sampling programme included male and female gonads, conceptuses, milk samples and blood samples for hormone determinations. The ages of all sampled individuals were determined according to Seydack (1983).

Male reproductive tracts were dissected out of freshly shot animals and stored in formol saline (1.3.2). Testis and epididymis weights were determined in the laboratory. Slices of tissue were taken from the mid-portion of one testis of each animal and stored in formol saline for subsequent histological examination. Preparation by sectioning and staining of specimens was carried out by staff at the Department of Physiology, University of Stellenbosch. Each section was examined microscopically for the presence of spermatogenesis. Mean seminiferous tubule diameter was calculated from 25 circular tubules measured in cross-section with a Zeiss micrometer eyepiece. Blood serum testosterone concentrations were determined by radio-immunoassay at the Department of Chemical Pathology (University of Cape Town), making use of a more specific antiserum exhibiting less than 10% cross-reactivity with 5 α -dihydrotestosterone (Millar and Kewly 1976).

Both ovaries were removed during evisceration of the sows and stored in formol saline. Individual ovaries were later weighed, cut sagittally into 2 mm slices and examined macroscopically for the presence of *corpora lutea*, *corpora albicantia* and follicles of particular size classes. Follicles were counted and those 2mm and larger measured in two dimensions at right angles. The number of *corpora lutea* and *corpora albicantia* were recorded. All embryos and foetuses from 51 litters were labelled and preserved in formol saline. The stage of development of the foetuses was described in the laboratory (cf Henry 1968, Diong 1973). The following measurements were taken according to Ansell (1965): sitting height (SH) of small foetuses, replaced for older ones by crown rump length (CR), dorsal curvature length (DCL) and also head, hind foot, ear and tail lengths.

Progesterone and estradiol 17- β levels in bushpig peripheral blood serum were determined by radioimmunoassay procedures at the Departments of Chemical Pathology and Obstetrics and Gynaecology (Medical School, University of Cape Town).

It was possible to collect a total of 18 milk samples, 5 from free-ranging sows and 13 from 3 captive individuals. It was difficult to extract sufficient quantities of milk and sample volumes varied between 5 and 20 ml. Oxytocin was injected in the case of immobilized captured

and captive sows. This only marginally improved milking output. The milk samples were preserved with 1-2 drops of undiluted formalin. Milk composition was analyzed at the Dairy Laboratory, Elsenburg (Department of Agriculture), using standard methods employed for milk analysis in the domestic sow.

10.3 Results

10.3.1 Sexual maturation

10.3.1.1 Sexual maturity in the male

Multiple range analysis according to the 95% confidence interval method, revealed significant differences in paired testis mass, paired epididymis mass and seminiferous tubule diameter between juveniles and yearlings, and yearlings and subadults. These parameters were similar for subadults and adults (Table 10/1).

| TABLE 10/1: DEVELOPMENT OF TESTES, EPIDIDYMIS AND SEMINIFEROUS TUBULE DIAMETER WITH AGE IN BUSHPIGS (CAPE PROVINCE) | | | | |
|---|----|-----------|-------|-------------------------|
| | n | \bar{X} | s | 95% Confidence interval |
| <u>Paired testis mass (g)</u> | | | | |
| Juveniles | 25 | 4,76 | 1,61 | 1,08 - 8,44 |
| Yearlings | 46 | 16,45 | 9,24 | 13,74 - 19,16 |
| Subadults | 22 | 33,46 | 12,30 | 29,54 - 37,38 |
| Adults | 86 | 37,63 | 9,77 | 35,65 - 39,61 |
| <u>Paired epididymis mass (g)</u> | | | | |
| Juveniles | 25 | 1,46 | 0,69 | 0,87 - 2,06 |
| Yearlings | 45 | 3,63 | 1,61 | 3,19 - 4,08 |
| Subadults | 22 | 5,75 | 1,98 | 5,11 - 6,39 |
| Adults | 86 | 6,65 | 1,49 | 6,33 - 6,97 |
| <u>Seminiferous tubule diameter (μm)</u> | | | | |
| Juveniles | 18 | 70,4 | 17,39 | 59,5 - 81,4 |
| Yearlings | 42 | 117,5 | 26,13 | 110,4 - 124,7 |
| Subadults | 23 | 156,7 | 23,31 | 147,1 - 166,4 |
| Adults | 87 | 170,8 | 23,20 | 165,9 - 175,8 |

FIG. 10/1 : VARIATION IN TESTES MASS WITH AGE IN BUSHPIGS

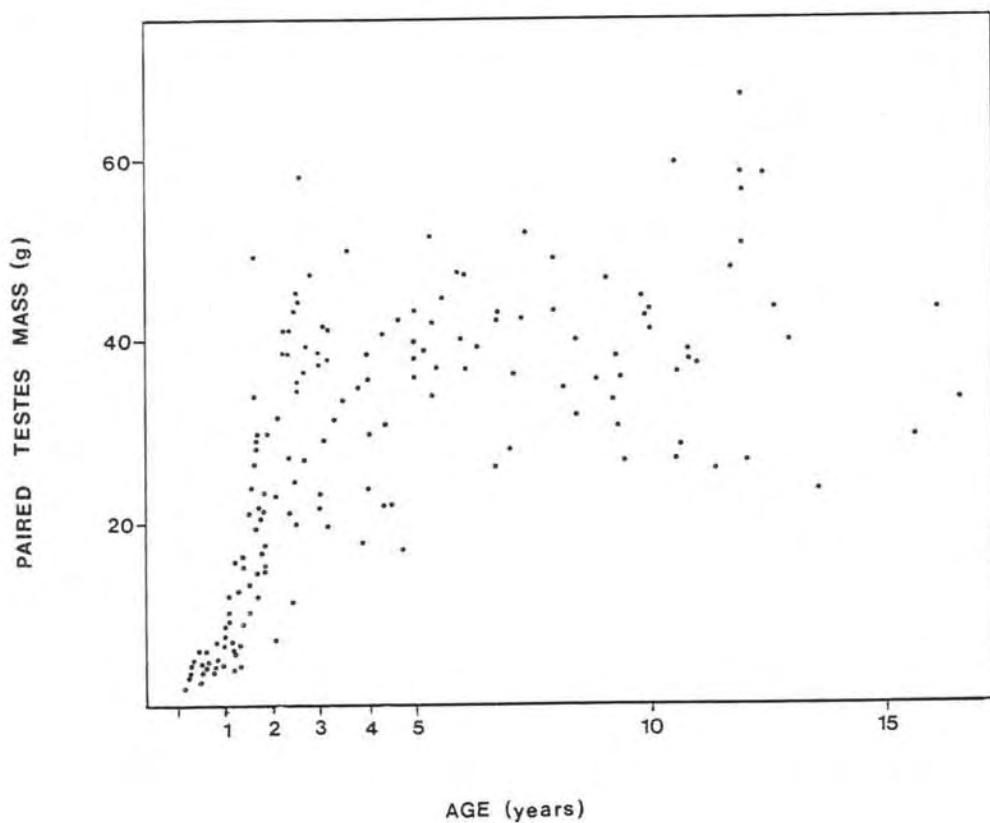
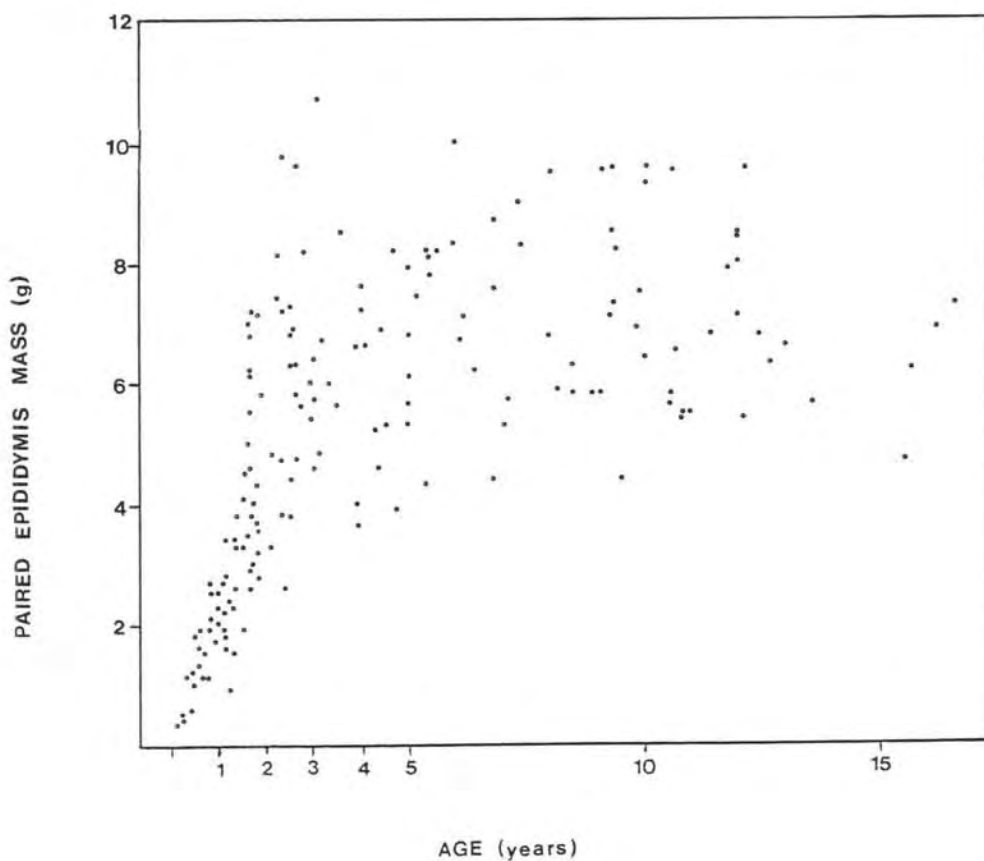


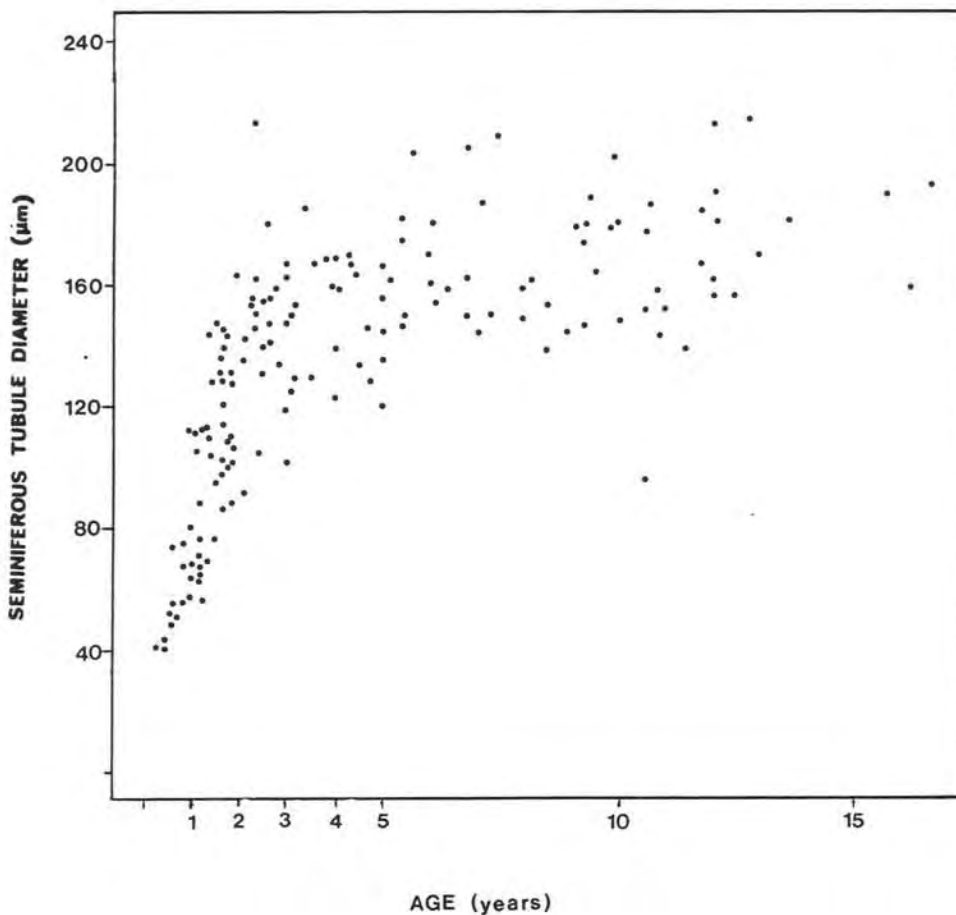
FIG. 10/2: VARIATION IN EPIDIDYMIS MASS WITH AGE IN BUSHPIGS



Paired testes and epididymis mass both approach adult values around the age of 20 months (Figures 10/1 and 10/2). Both these parameters tend to increase up to about 3 years of age and wide variation is exhibited among animals of the yearling, subadult and adult age classes.

The available data on seminiferous tubule diameter in relation to age are plotted in Figure 10/3.

FIG. 10/3: VARIATION IN MEAN SEMINIFEROUS TUBULE DIAMETER WITH AGE IN BUSHPIGS



Seminiferous tubule diameters tend to increase up to the age of 5 years. Minimum values of seminiferous tubule diameters of adults were however already attained by some yearlings at 16-18 months of age (Fig. 10/3).

The testis sections of each animal were investigated for and classified according to the presence or absence of elongating spermatids or spermatozoa or both (Table 10/2). Spermatozoa and elongating spermatids were first observed in the seminiferous tubules of yearling bushpigs 16-17 months of age. Spermatogenesis was evidently undiminished in the specimens of the oldest individuals. The oldest individual in the data set was approximately 16 years old.

| TABLE 10/2: INCIDENCE OF ELONGATED SPERMATIDS OR SPERMATOZOA IN THE BUSHPIG (n = 167) | | | |
|---|--------|---------|-------|
| AGE CLASSES (MONTHS) | ABSENT | PRESENT | TOTAL |
| ≤ 12,0 | 17 | 0 | 17 |
| 12,1 - 13,0 | 3 | 0 | 3 |
| 13,1 - 14,0 | 3 | 0 | 3 |
| 14,1 - 15,0 | 5 | 0 | 5 |
| 15,1 - 16,0 | 2 | 0 | 2 |
| 16,1 - 17,0 | 2 | 2 | 4 |
| 17,1 - 18,0 | 1 | 0 | 1 |
| 18,1 - 19,0 | 1 | 2 | 3 |
| 19,1 - 20,0 | 1 | 8 | 9 |
| 20,1 - 21,0 | 1 | 3 | 4 |
| 21,1 - 22,0 | 2 | 3 | 5 |
| 22,1 - 23,0 | 1 | 2 | 3 |
| 23,1 - 24,0 | 0 | 0 | 0 |
| 24,1 - 36,0 | 2 | 21 | 23 |
| 36,1 - 180 | 3 | 79 | 82 |
| 181 - 200 | 0 | 3 | 3 |

From the foregoing it is concluded that most male bushpig yearlings reach physiological sexual maturity between 16 and 20 months of age.

Blood serum testosterone determinations were available from bushpig males 0,8 years and older. Mean testosterone values, in nMol/l, were 2,67 (s = 2,73; n = 35); 2,39 (s = 2,11; n = 96) and 2,02 (s = 1,82; n = 17) for the age groups 0,8 - 2,0 years, > 2 years and > 10 years respectively. These means did not differ significantly. The wide variation in values is illustrated in Fig. 10/5 (10.3.5).

10.3.1.2 Sexual maturity in the female

According to Sowls and Phelps (1968) a captive female bushpig farrowed at 23,8 months of age; i.e. conception occurred at 19,8 months. This is in accord with records in this study. The 3 earliest conception ages were 18, 24 and 24 months, determined by back-dating with the aid of foetal age.

Follicles of 6 mm in diameter or larger, i.e. believed to approach ovulation, were recorded in females 14,4; 16,8 and 16,8 months old. *Corpora lutea* of ovulation were observed in females as young as 19 - 22 months (n = 4). In the ovaries of one individual of 18 months *corpora albicantia* were found. The captive female TD12 had a serum estradiol value of 267 pMol/l on 18.7.1985, presumably indicating oestrous. The animal then was 19,2 months old.

From the above it may be safely concluded that most female bushpigs reach sexual maturity between 17 and 22 months of age. Depending on date of birth, this age range is reached during the second mating season. However, due to factors such as social position and nutrition, successful breeding may only occur much later (10.3.6.2.b).

10.3.2 Female reproductive cycles

10.3.2.1 Ovarian dynamics

Follicles

In contrast to *corpora lutea*, which were opaque and light yellow in colour, ripe follicles were clear and semi-transparent and protruded from the surface of the ovary.

Follicles destined to ovulate in the domestic sow reached an average diameter of 6,5 mm two days before oestrus (Burger 1952 ex Mason 1982) Clough (1969) rated 7-8 mm as the diameter of follicles at ovulation in the warthog. Follicle diameters in the bushpig ovary varied between 1 and 8 mm. Follicles with diameters of 6 mm or more were taken to be approaching the stage of ovulation. Of 39 females without *corpora*

lutea, i.e. not ovulating, pregnant or lactating, 12 had follicles of this size. They were spread over most months of the year, suggesting that ovulation may occur at any time of the year. Actual follicular rupturing was visible in two cases.

Corpora lutea

Following rupture, the development of a *corpus luteum* commences at each site of ovulation. *Corpora lutea* of the oestrus cycle regress again in the absence of fertilization of the ova. During the first two weeks, i.e. prior to regression in the absence of fertilization, *corpora lutea* of pregnancy are indistinguishable from those of the oestrus cycle.

Corpora lutea of ovulation or pregnancy in the bushpig may measure between 6 and 10 mm in diameter. *Corpora lutea* in the domestic sow measure 8 - 9 mm in diameter within a week of ovulation, increasing to 10 mm or more if pregnancy follows, compared with 4 - 6 mm for newly formed *corpora haemorrhagica* (Anderson and Melampy 1967). *Corpora haemorrhagica*, which are newly formed *corpora lutea* with a central blood clot, of similar dimensions were noted in the bushpig (n = 6).

Corpora lutea remain present throughout pregnancy and presumably remain functional as endocrine glands secreting progesterone, thereby playing a crucial role in the maintenance of pregnancy. No macroscopically visible indications were found that *corpora lutea* regress prior to parturition. Ovulation apparently does not occur during pregnancy or lactation in the bushpig and no active *corpora lutea* were present in any lactating females (lactational anoestrous).

Corpora albicantia

After parturition the *corpora lutea* degenerate rapidly to form small, brown-pigmented masses of scar tissue, the *corpora albicantia*. Two weeks post-partum, the *corpora lutea* of pregnancy had regressed to 2 - 3 mm in diameter (n = 3). This initial rapid regression is reflected in the rapid decline of ovarian mass (Table 10/4). As in the warthog (cf Mason 1982), by one month postpartum *corpora albicantia* had darkened from light yellow in very early post-partum females to light brown.

They subsequently darkened further. Older *corpora albicantia* were usually 0,1 - 2 mm in diameter and often irregularly shaped with diffuse margins. Some occurred as thin crescent-shaped lines on the rims of large follicles or *corpora lutea* of pregnancy.

Corpora albicantia from successive pregnancies apparently did not accumulate in the bushpig ovary. The numbers observed in lactating animals ranged between being equal to litter size and that expected from the ovulation rate, i.e. originated from the preceding generation of *corpora lutea* of ovulation or pregnancy (Table 10/3).

The mean ovulation rate in the bushpig, i.e. number of ova shed per female during ovulation, was determined by counting *corpora lutea* (cf Perry and Rowlands 1962) and was found to be 4,20 (s = 1,141; n = 59; range: 2 - 7). Ovulation peaks occurred during the months of June to August (10.3.5). Instances were observed of the combined presence of large follicles or *corpora lutea* of ovulation and *corpora albicantia* in animals which had not lactated within the preceding year. This suggests that the bushpig female may be seasonally polyoestrous.

| Identification No. | Age (yrs) | Date shot | Litter size | Age of litter | <i>Corpora albicantia</i> count |
|---|-----------|------------|--|--|---------------------------------|
| 07 | 9,8 | 4.4.1978 | 1* | ? | 0 |
| TD 4 | 10,7 | 1.1.1981 | 2 | 6 weeks | 3 |
| B34 | 7,0 | 11.11.1981 | 1 | 2 weeks | 2 |
| TD 3 | 12,5 | 6.1.1982 | 2 | 3 weeks | 4 |
| OKW 48 | 5,0 | 30.10.1982 | 3 | 2 weeks | 3 |
| OKC 12 | 3,5 | 16.12.1982 | 2* | ? | 2 |
| OKC 13 | 6,0 | 15.1.1983 | 3* | ? | 3 |
| OKC 51 | 3,3 | 16.6.1984 | 2 | 2,4 months | 3 |
| OKC 58 | 5,1 | 1.9.1984 | 2 | 1,5 months | 3 |
| OKC 69 | 10,9 | 2.2.1985 | 1* | ? | 4 |
| EC 22 | 6,0 | 18.1.1986 | 4* | 2,6 months | 5 |
| | | | $\bar{X} = 2,1$ s = 0,944 n = 11 | $\bar{X} = 2,9$ s = 1,300 n = 11 | |
| *Estimate from number of active mammae. | | | | | |

Ovarian dynamics is also reflected by paired ovarian mass of the various phases in the reproductive sequence (Table 10/4).

| TABLE 10/4: PAIRED OVARIAN MASS (in grams) IN BUSHPIG FEMALES (SOUTHERN AND EASTERN CAPE) | | | | | | | | |
|---|-----------|-------|----|-----|-----------|----|------|-------|
| | \bar{X} | s | n | | | df | t | P< |
| Immature age groups | | | | | | | | |
| 0,4 - 0,8 years | 0,58 | 0,310 | 9 | | | | | |
| 0,9 - 1,3 years | 1,02 | 0,364 | 10 | | | | | |
| 1,4 - 1,7 years | 1,52 | 0,484 | 20 | | | | | |
| Mature individuals | | | | | | | | |
| May - August* | 2,52 | 1,154 | 12 | I | VI vs I | 26 | 1,25 | NS |
| Ovulation/early undetected pregnancy | 3,20 | 1,124 | 23 | II | I vs II | 43 | 1,70 | NS |
| Pregnancy | 4,15 | 1,036 | 42 | III | II vs III | 63 | 3,43 | 0,01 |
| Lactation* | 2,03 | 0,695 | 13 | IV | III vs IV | 53 | 6,89 | 0,001 |
| Sept. - Dec.* | 1,81 | 0,650 | 13 | V | IV vs V | 24 | 0,83 | NS |
| Jan. - April* | 2,10 | 0,610 | 16 | VI | V vs VI | 26 | 1,21 | NS |
| *Ovaries without <i>corpora lutea</i> | | | | | | | | |

There was no evidence of reproductive senescence. Pregnancies were recorded in females between 12 and 16 years of age.

10.3.2.2 Hormone concentrations

It was not possible to differentiate between ovulation and pregnancy on the basis of peripheral blood serum concentrations of progesterone, since these values overlapped considerably (Table 10/5).

Estradiol - 17β (E_2) concentrations during early pregnancy, lactation and anoestrous were below 200 pMol/l (n = 55). E_2 -concentrations between 200 and 500 pMol/l may possibly be indicative of oestrous (n = 11). Estradiol concentrations (in pMol/l) tend to increase progressively during pregnancy (Fig. 10/4). The mean E_2 concentration for the last 3 weeks of pregnancy was 1 109 pMol/l or 302 pg/ml (s = 497, n = 6). No

trend between progesterone values and stage of pregnancy was detected (Fig. 10/4)

| Reproductive State | \bar{X} nMol/l (ng/ml) | n | s | Range |
|------------------------|-----------------------------|----|-------|-------------|
| Ovulation | 24,3 (7,6) | 3 | 21,19 | 6,7 - 47,8 |
| Pregnancy or Ovulation | 31,2 (9,8) | 10 | 17,80 | 6,8 - 56,3 |
| Pregnancy | 39,1 (12,3) | 20 | 16,55 | 13,5 - 65,6 |
| Lactation | <3 (<1) | 15 | - | - (-) |
| Non-reproductive | <3 (<1) | 34 | - | - (-) |

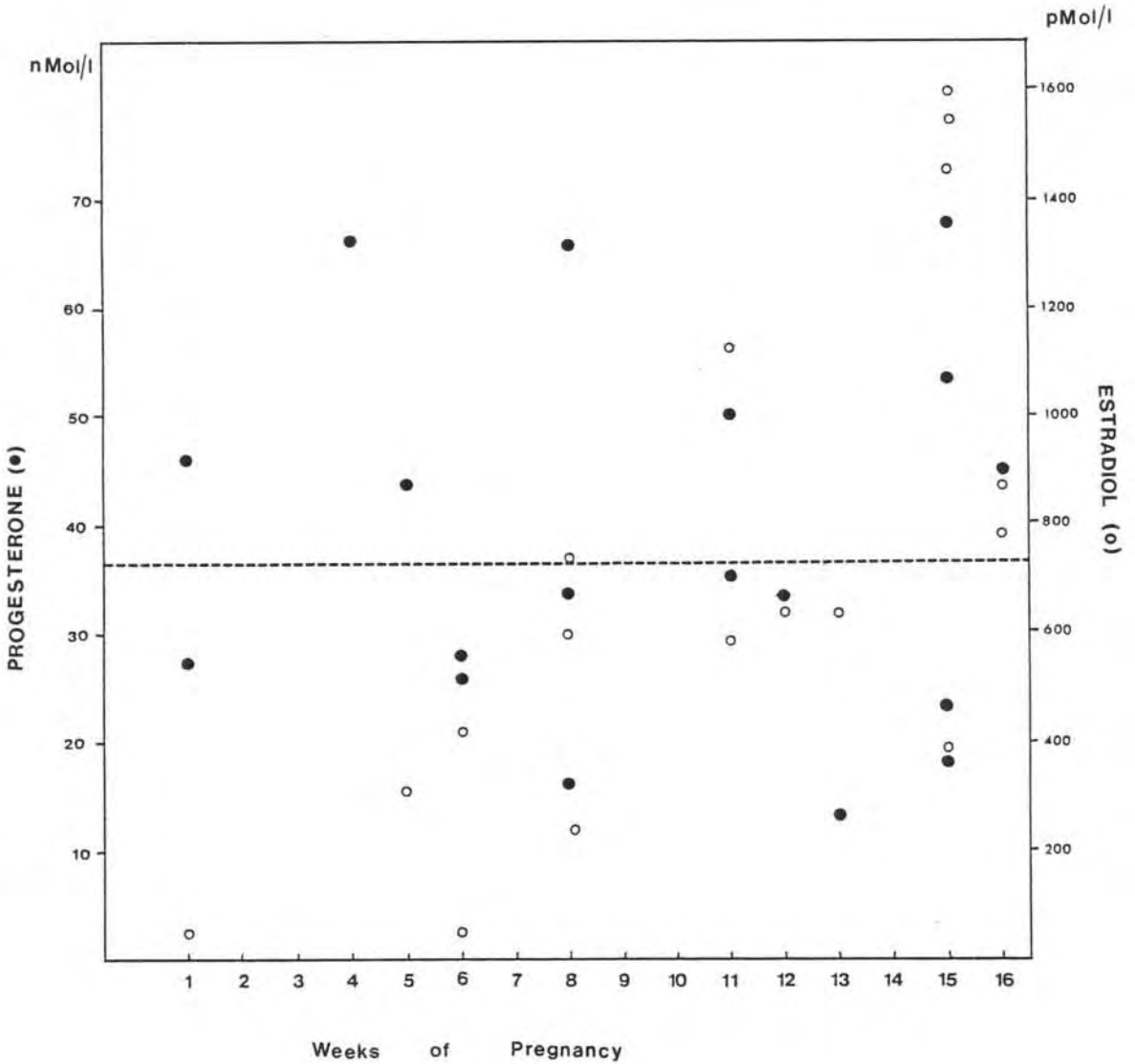
Progesterone values during pregnancy exhibit considerable variability, but are not subject to any trend related to stage of pregnancy. In contrast, estradiol concentrations rose steadily and reached peak values just prior to parturition (Fig. 10/4). Immediately post-partum peripheral concentrations of progesterone and estradiol declined to basal levels during lactation.

Progesterone concentrations were not correlated with the number of *corpora lutea*, but tended to be of similar magnitude per pregnancy (stage of pregnancy in brackets, weeks post-conception):

| | | | |
|--------------|----------|-----------|-----------|
| Sow TH2 | 65,5 (8) | 53,5 (15) | |
| Sow TD3 | 43,5 (5) | 33,3 (8) | |
| Sow TD2 (I) | 27,6 (1) | 35,5 (11) | 23,7 (15) |
| Sow TD2 (II) | 66,2 (4) | 49,7 (11) | 68,2 (15) |

The finding that pregnancy progesterone concentrations were significantly lower in free-ranging bushpig females compared to those from captive individuals, is rather intriguing ($t = 2,99$, $df = 15$, $P < 0,01$). The average concentrations were 24,8 n Mol/l ($s = 9,227$; $n = 7$) and 43,9 nMol/l ($s = 14,847$; $n = 10$) for free-ranging and captive females respectively.

FIG.10/4: PERIPHERAL PROGESTERONE AND ESTRADIOL CONCENTRATIONS
IN PREGNANT BUSHPIGS



10.3.2.3 Gestation and survival of the conceptus

Sowls and Phelps (1968) recorded a probable gestation period of 17 weeks in the bushpig. This was crudely verified by observations in the study enclosure:

- (a) Female TD3 farrowed on 20.12.1981, but on 14.8.1981 ovulation had not taken place yet, judging from estradiol-17 β and progesterone

values of < 100 pMol/l and $< 1,0$ nMol/l respectively, on that date. The interval between these dates is 128 days. On the assumption that conception took place within a week after 14.8.1981, a 17-week gestation period may be derived.

- (b) Vulval swelling was observed in female TD2 on 31.7.1983. A single neonate was born 132 days later. On 16.8.1983 progesterone and estradiol- 17β values were 45,8 nMol/l and < 100 pMol/l respectively.

In the domestic pig a very high percentage of ova that were ovulated became fertilized and a major part of embryonic mortality could be accounted for by the degeneration of fertilized ova between day 9 and 16 of pregnancy (Perry and Rowlands 1962).

Analysis of the frequency distribution of deviations between numbered *corpora lutea* and number of concepti per animal revealed a regional difference ($G = 6,65$; $df = 1$; $P < 0,01$). In 10 of the 26 cases in the Southern Cape the difference between numbered *corpora lutea* and concepti exceeded 1 and ranging between 2 and 5. In the Eastern Cape only 1 of 17 cases deviated by more than 1. The lower percentage of ova developing into viable fetuses in the Southern Cape is also reflected in a lower prenatal litter size (10.3.3)

Size of litters born to females in the study enclosure was comparatively low ($\bar{X} = 1,7$ $s = 0,756$ $n = 7$). As a result of *ad lib* feeding, mother sows were very fat and it was suspected that the low litter size may be related to the "overfatness syndrome" known to reduce fertility in the domestic pig (Duncan and Lodge 1960, Scofield 1972, Hughes and Varley 1980). No correlation was found between indices of fatness (subcutaneous fat layer or intraperitoneal fat layer: 9.3.3) and prenatal litter size or number of ova failing to develop into viable fetuses. However, the degree of fat at ovulation and initial pregnancy is crucial in this regard. The available data is from animals shot after variable and extended periods of gestational anabolism (9.3.2). The condition parameters do not individually reflect "fatness" at conception. The average intraperitoneal fat layer thickness of pregnant bushpig sows in the Southern Cape was 18,0 mm ($n = 13$), which was significantly higher than the average of 9,7 mm for 10 Eastern Cape sows

($U = 102$, $P < 0,05$). This suggests that the overall level of fatness of Southern Cape sows at conception often was higher than for Eastern Cape sows and there may be an inverse relationship between "fatness" and prenatal litter size.

No trend was evident in maternal age and the percentage of successful implantations. Post-implantation conceptus mortality was insignificant but no data is available on the incidence of abortion of entire litters. The latter, to the extent that it may be presumed to occur, may well be related to maternal age, aggressive social interaction or condition.

10.3.3 Prenatal litter statistics and foetal development

The overall average prenatal litter size was 3,2. The difference in average prenatal litter size between the Southern Cape ($\bar{X} = 3,0$ $s = 1,30$ $n = 36$) and the Eastern Cape ($\bar{x} = 3,6$ $s = 1,06$ $n = 15$) was not statistically significant ($t = 1,50$; NS). The foetal sex ratio of 0,93 males to females did not depart significantly from unity.

There is wide intra- and interuterine variation in the sizes of apparently normal foetuses at equivalent stages of pregnancy and at birth (cf Warwick 1928). In multiparous mammals, the foetal mass at any stage of pregnancy tends to vary according the number of foetuses in the litter. Foetuses of smaller litters tend to be heavier (Cameron 1973, Smith and Sowls 1975, Graves and Graves 1977, Maynard *et al.* 1979, Van der Merwe and Skinner 1982). Maternal condition may strongly influence size at birth and foetal age determination by means of meristic data may yield highly questionable results (cf Verme 1977).

In an effort to overcome these problems, bushpig foetal litters were classified into age classes according to their stage of development, derived from material of known age for *Sus scrofa* (adapted from Henry 1968b, Diong 1973, Briedermann 1986). This was deemed appropriate since the two species have similar gestation lengths. Foetuses at corresponding stages showed close similarity in outward appearance. The adapted foetal age classes are shown in Table 10/6 (also Plate 13).

| TABLE 10/6: FOETAL AGE CLASSES (cf Henry 1968b) | | |
|---|---------|--|
| AGE | (days) | MORPHOLOGICAL CHARACTERISTICS |
| I | 20-30 | Body wall translucent, exposing internal organs; fore and hind limb and olfactory bud visible; cephalic flexure pronounced. |
| II | 30-40 | Appendages present; digits just visible; mouth and eye apparent; abdomen still convexed; small underdeveloped ear present with opening. |
| III | 40-50 | Body wall no longer translucent; nostrils open, embryonic appearance lost; hoove digits not upturned; ear still small and underdeveloped. |
| IV | 50-60 | Hooves present; 1st and 2nd digits of front feet upturned; external genitalia well developed; hair follicles discernable around snout, eyebrows and chin. |
| V | 60-70 | Ears proportional to body; hooves long and with all 4 digits of front feet upturned; hair follicles apparent around snout, eyebrows and chin. |
| VI | 70-80 | Hair on chin or eyebrows less than 3 mm long; hoof digits 3 and 4 of hind feet now also clearly recurved; canine and 3rd incisor present and just about to erupt |
| VII | 80-90 | Appearance of erupted upper and lower canini and incisors 3; hair on chin, snout and eyebrows less than 6 mm long. |
| VIII | 90-100 | Hair follicles visible over entire body; hair on snout and eyebrows 6-10 mm long. |
| IX | 100-110 | Scantily haired over entire body; longitudinal body stripe-spot patterns visible. |
| X | 110+ | Fully haired over entire body; body stripe-spot patterns fully apparent. |

Meristic data on 51 prenatal bushpig litters is summarized in Table 10/7.

Hugget and Widdas (1951) have demonstrated a direct relationship between the cube root of foetal mass ($W^{1/3}$) and gestational age (tg), as given by the equation

$$(W^{1/3}) = a(tg - t_0)$$

where a = foetal growth velocity and t_0 = intercept on the t - axis. The latter may be approximated with $0,2 \times tg$ for mammals with a gestation length between 100 and 400 days (Huggett and Widdas 1951).

PLATE 13

Bushpig foetuses of various age classes (post-conception age in days).

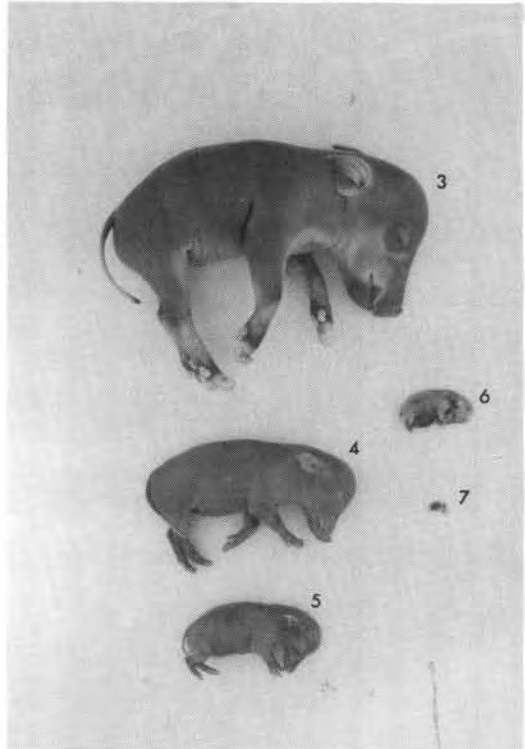
- | | | | |
|----|---|---------------------|--------------------|
| a. | 1 | X: 110 - 115 days | (0,29 x full size) |
| | 2 | VIII: 90 - 100 days | (0,29 x full size) |
| b. | 3 | VII: 80 - 90 days | (0,29 x full size) |
| | 4 | V: 60 - 70 days | (0,29 x full size) |
| | 5 | III: 40 - 50 days | (0,29 x full size) |
| | 6 | II: 30 - 40 days | (0,29 x full size) |
| | 7 | I: 20 - 30 days | (0,29 x full size) |
| c. | 1 | III: 40 - 50 days | (full size) |
| | 2 | II: 30 - 40 days | (full size) |
| | 3 | I: 20 - 30 days | (full size) |

PLATE 13

a



b



c

A 3-day old bushpig neonate weighed 1 200 g and a birth weight of 800 g was determined for a neonate recovered from the field. The birth masses of European wild boar neonates range between 700 and 1 000 g (Briedermann 1970, Hennig 1981). Sows and Phelp (1968) recorded bushpig neonate weights of between 679 and 880 g (n = 5). 920 g was taken as an average representative birth weight in this study. This is the average between 960 and 878 g, which each represented the average foetal mass from two near-term prenatal litters (1 010, 980, 900 g and 980, 800, 850, 880 g). For calculating the foetal growth velocity "a", a gestation period of 120 days (10.3.2.3) and a t-axis intercept of 20 days (derived from Warwick 1928, Table 10/7) were taken.

$$a = \frac{\sqrt[3]{920}}{120-20} = 0,0973$$

The corresponding a-value for the domestic pig was 0,12 (ex Frazer and Huggett 1974). Bushpig foetal litter ages could now be determined according to the following formula:

$$t = \frac{W^{1/3}}{0,0973} + 20$$

where t = foetal litter age from conception in days and W = average foetus mass/litter in grams.

Application of this formula in determining the ages of 51 prenatal litters resulted in 45 being allocated to the same 10-day age class as that determined from their morphological characteristics. Of the 6 cases (12%) allocated to adjacent developmental classes by the formula, 4 were age overestimates. All 4 cases were either singletons (n = 2) or doublettes (n = 2) and presumably the result of a disproportionately faster growth in the absence of crowding and competition for maternal resources.

TABLE 10/7: AGE CLASS-SPECIFIC MASS AND DIMENSIONS OF BUSHPIG FOETUSES

| | FOETAL AGE CLASS (DAYS) | NO. OF FOETAL LITTERS | MEAN, RANGE n | BODY MASS (g) | SH or CR (mm) | DCL (mm) | Head Length (mm) | Hind Foot Length (mm) | Ear Length (mm) | Tail Length (mm) |
|------|-------------------------|-----------------------|-----------------------|----------------------------|-------------------------|-------------------------|-------------------------|------------------------|------------------------|------------------------|
| I | 20-30 (25) | 1 | \bar{X} R } n | 0,5 0,5 0,5 3 | 13,0 11 14 3 | | | | | |
| II | 30-40 (35) | 5 | \bar{X} R } n | 4,8 2,2 7,1 17 | 35,8 26 42 17 | | | | | |
| III | 40-50 (45) | 5 | \bar{X} R } n | 20,7 11,9 27,0 21 | 65,1 54 73 21 | 101 86 114 21 | 26,4 23 30 21 | 14,1 11 16 21 | 6,7 5 8 21 | 19,9 15 24 21 |
| IV | 50-60 (55) | 6 | \bar{X} R } n | 43,1 19 57 22 | 84,1 65 94 21 | 123 106 140 21 | 34,8 30 38 21 | 19,5 16 23 21 | 10,2 8 12 21 | 26,7 17 31 21 |
| V | 60-70 (65) | 6 | \bar{X} R } n | 77,5 57 95 21 | 103 89 111 21 | 150 141 166 17 | 42,5 38 46 21 | 24,5 22 27 18 | 12,6 9 14 21 | 35,6 30 40 21 |
| VI | 70-80 (75) | 6 | \bar{X} R } n | 156 98 297 18 | 128 115 148 18 | 185 166 226 18 | 54,1 49 65 18 | 33,4 29 40 18 | 19,3 17 28 18 | 46,4 40 59 18 |
| VII | 80-90 (85) | 4 | \bar{X} R } n | 293 176 338 12 | 154 139 170 12 | 223 196 238 12 | 64,3 57 69 12 | 44,7 38 49 12 | 23,3 21 26 12 | 55,3 47 60 12 |
| VIII | 90-100 (95) | 8 | \bar{X} R } n | 404 260 634 23 | 170 151 202 23 | 259 231 305 23 | 75,7 65 96 23 | 53,8 46 65 23 | 28,7 24 33 23 | 66,0 52 77 23 |
| IX | 100-110 (105) | 6 | \bar{X} R } n | 610 356 960 11 | 198 190 205 2 | 313 291 340 11 | 95,3 83 104 11 | 69,3 60 78 11 | 34,5 30 37 11 | 79,4 71 90 11 |
| X | 110+ (115) | 4 | \bar{X} R } n | 735 528 996 15 | 208 195 225 9 | 316 260 340 15 | 101 90 110 15 | 73,5 67 83 15 | 39,7 34 47 15 | 84,7 72 95 15 |

Wide variation in mass was observed between individuals of the same litter, as also recorded for the European wild boar (Briedermann 1986) and other species. When individual foetus mass is expressed as a percentage of the largest foetus per litter, the distribution of intralitter size deviation is as follows:

| Percentage mass deviation | Percentage of foetuses compared |
|---------------------------|---------------------------------|
| 90 - 100 | 45 |
| 80 - 90 | 33 |
| 70 - 80 | 14 |
| 50 - 70 | 5 |

Only 45% of the foetuses compared weighed within 10% of the largest foetus in any particular litter and as many as 8% deviated by more than 30% from the heaviest foetus of the litter.

In 30 litters, foetuses of both sexes occurred. In 15 cases the average male foetal mass exceeded that of the females in the same litter. The situation was reversed in the remaining 15 cases and there is thus no evidence for sex differences in foetal growth rates.

10.3.4 Lactation

Prelactation secretion was observed in pregnant bushpig females as early as 12 - 14 days pre-partum (n = 4). In the warthog, small amounts of a viscous secretion could be expressed from teats of some pregnant females as early as 20 days pre-partum, when their udders showed a visible increase in size. The same is recorded in the European wild boar 9 days pre-partum (Martys 1982). While this secretion could usually be expressed from all six teats in the bushpig, the number of productive teats at any stage after parturition was usually equal to the number of surviving piglets.

Lactation of captive bushpig lasted about 5,5 months in 3 cases which were closely monitored (with litter sizes of 1, 3 and 4). There is some evidence that lactation does not last as long in free-ranging females. Female CW5 lactated for about 4 months (litter size: 4). Females O61 and CZ1, with 2 and 3 juveniles each, were post-lactational at 4,0 and 4,6 months post-partum respectively. The available data on bushpig milk composition is presented below (Table 10/8).

| TABLE 10/8: BUSHPIG MILK COMPOSITION | | | | | | | | | |
|---|---------|-----------------|-------------|-------------------|------------------------|---------|-------|---------|------|
| Sample Source | Age yrs | Collection Date | Litter Size | Weeks Post-partum | PERCENTAGE COMPOSITION | | | | |
| | | | | | Total Solids | Protein | Fat | Lactose | Ash |
| From free-ranging sows * | | | | | | | | | |
| OKC12 | 3,5 | 16.12.82 | 2 | ? | 14,71 | 6,41 | 2,66 | 4,38 | 1,26 |
| OKW48 | 5,0 | 30.10.82 | 3 | 2 | 14,74 | 5,54 | 6,13 | 2,38 | 0,69 |
| T24 | 2,9 | 16.12.83 | 2 | ? | 19,87 | 8,83 | 6,90 | 2,84 | 1,30 |
| CL2 | 2,3 | 16.01.83 | 2 | 8 | 24,01 | 7,87 | 9,94 | - | - |
| CZ1 | 7,4 | 12.10.82 | 2 | 13 | 32,54 | 11,99 | 16,82 | 2,16 | 1,57 |
| From sows in captivity | | | | | | | | | |
| TD3 | 12,5 | 06.01.82 | 2 | 3,0 | 40,99 | 11,33 | 24,16 | 3,98 | 1,52 |
| TD2.1 | 3,2 | 17.03.83 | 1 | 2,0 | 35,01 | 14,81 | 17,55 | 0,74 | 1,91 |
| TD2.2 | | 20.04.83 | 1 | 6,9 | 24,72 | 8,67 | 11,58 | 3,23 | 1,24 |
| TD2.3 | | 08.05.83 | 1 | 9,4 | 23,95 | 8,95 | 9,91 | 4,00 | 1,09 |
| TD2.4 | | 15.06.83 | 1 | 14,9 | 21,79 | 9,28 | 9,97 | 1,14 | 1,40 |
| TF5.1 | | 06.02.83 | 4 | 2,6 | 20,64 | 6,70 | 8,69 | 4,27 | 0,98 |
| TF5.2 | 2,4 | 16.02.83 | 4 | 4,0 | 23,50 | 6,71 | 10,70 | 4,84 | 1,25 |
| TF5.3 | | 04.03.83 | 4 | 6,3 | 23,00 | 7,95 | 9,58 | 4,28 | 1,19 |
| TF5.4 | | 25.03.83 | 4 | 9,3 | 21,37 | 8,03 | 7,70 | 4,30 | 1,33 |
| TF5.5 | | 10.04.83 | 4 | 11,6 | 22,07 | 9,42 | 9,33 | 1,73 | 1,60 |
| TF5.6 | | 22.04.83 | 4 | 13,3 | 24,28 | 9,82 | 9,22 | 3,64 | 1,50 |
| TF5.7 | | 06.05.83 | 4 | 15,3 | 23,36 | 11,16 | 8,44 | 1,63 | 2,14 |
| TF5.8 | | 04.06.83 | 4 | 19,4 | 25,93 | 15,25 | 7,77 | 0,98 | 1,93 |
| \bar{X} = | | | | | 24,25 | 9,37 | 10,39 | 2,97 | 1,41 |
| s = | | | | | 6,43 | 2,69 | 4,84 | 1,37 | 0,36 |
| n = | | | | | 18 | 18 | 18 | 17 | 17 |
| Percentage of total solids = | | | | | 100 | 39 | 43 | 12 | 6 |
| * OKC 12, OKW 48: Eastern Cape; others: Southern Cape | | | | | | | | | |

The cost of lactation to mother sows was strikingly demonstrated by CL2. This female had conceived at the age of 1,9 years, gave birth 4 months later and died 10,5 months post-partum during a cold and wet spell as a result of an acute negative energy balance. She then weighed only 46,0 kg (60,5 kg at age 2,3 years) and had a bone marrow fat percentage of zero. In this case poor post-lactational condition was prolonged and aggravated through territorial encroachment by neighbouring sows (4.3.2.1, Fig. 4/5). Further indications of the energy costs of lactation are evident from Table 10/9.

| TABLE 10/9: LACTATION AND CONDITION IN BUSHPIG SOWS | | | | | | |
|---|------------|------------------|----------------------|----------------|-----------------------|-------------------------------|
| Identifica- tion No. | Age yrs | Sampling Date | Maternal Mass(kg) | Litter Size | Months post-partum | Bone marrow fat percentage |
| B34 | 7,0 | 11.11.1981 | 79,5 | 1 | 0,5 | 85,0 |
| T24 | 2,9 | 16.12.1983 | 61,5 | 2 | ≤0,5* | 84,6 |
| OKW 48 | 5,0 | 30.10.1982 | 61,5 | 3 | 0,5 | 76,5 |
| OKC 58 | 5,1 | 01.09.1984 | 50,0 | 3 | 1,5 | 40,3 |
| OKC 12 | 3,5 | 16.12.1982 | 53,0 | 2 | ±2 | 40,5 |
| OKC 51 | 3,3 | 16.06.1984 | 55,5 | 2 | 2,4 | 82,1 |
| EC 22 | 6,0 | 18.01.1986 | 70,5 | 4 | 2,6 | 21,4 |
| OKC 16 | 6,0 | 26.03.1983 | 55,0 | 1 | 3,0 | 14,8 |
| O61 | 7,2 | 18.06.1981 | 67,0 | 2 | 3,5 | 62,1 |
| OKC 13 | 6,5 | 15.01.1983 | 57,0 | 3 | ±3 | 9,9 |

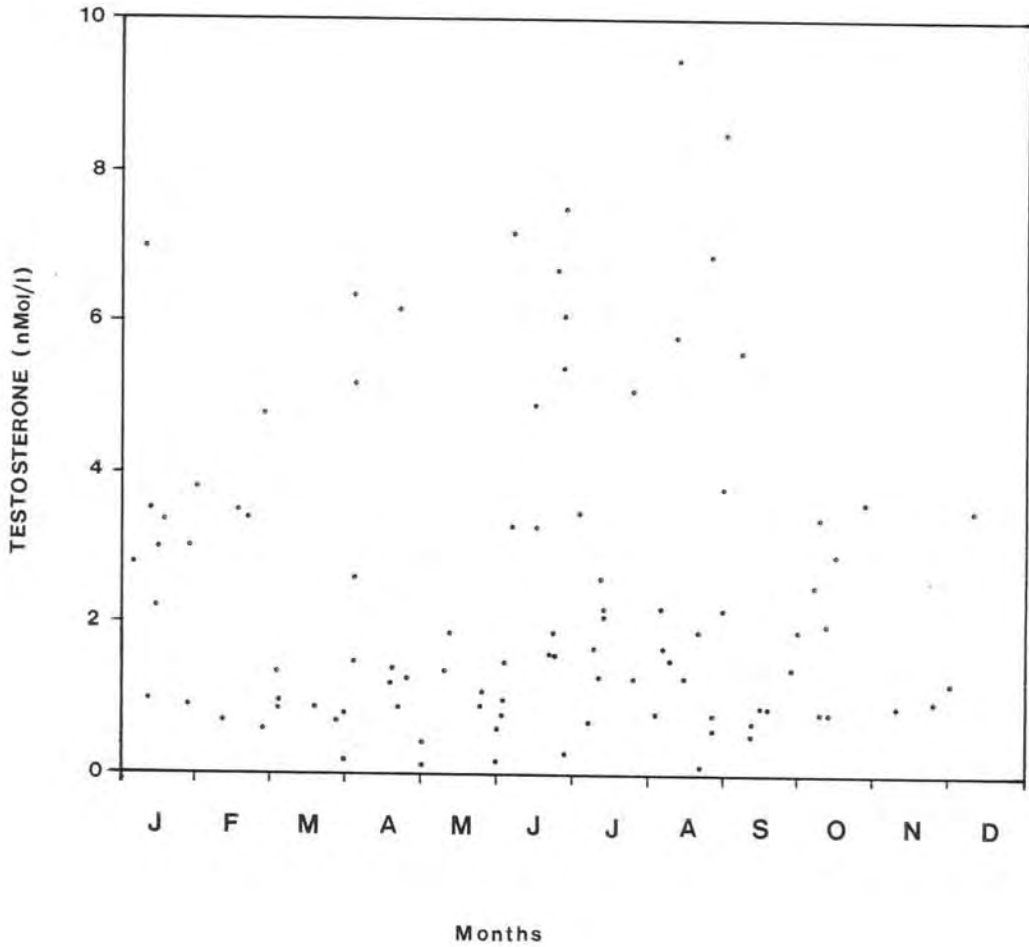
* *Corpora lutea* of pregnancy had not regressed yet

As expected, both duration of lactation and litter size affected maternal condition. The product of these two parameters exhibited an inverse relationship with maternal condition (Spearman rank correlation coefficient $r = -0,65$; $t = 2,42$; $df = 2$; $P < 0,05$). It is noteworthy that the two cases not fitting the pattern, namely those of OKC 51 and O61, also deviated from the normal farrowing season. In both cases, rebreeding after early loss of in-season litters is thought to have occurred.

10.3.5 Breeding seasonality

In the bushpig male no seasonal trend was found in testis mass, epididymis mass or seminiferous tubule diameter ($P > 0,05$). Neither did testosterone concentrations in the blood serum of males 2 years and older show any seasonal trend ($F = 0,970$ $df = 11$; 119 $P = 0,477$ NS; Fig. 10/5)

FIG. 10/5: PERIPHERAL TESTOSTERONE CONCENTRATIONS IN MALE BUSHPIGS
(2 YEARS AND OLDER)



In contrast female breeding showed a clear seasonal pattern (Table 10/10; Fig. 10/6). Cycling individuals were identified through the presence of *corpora lutea* of ovulation, developing or regressing *corpora lutea* or serum progesterone concentrations exceeding basal levels (10.3.2.2). This category may include a few undetected or undetectable cases of early pregnancy. Since inspection revealed no regional differences in the incidence of seasonality, the available data from the Southern and Eastern Cape was pooled (Table 10/10).

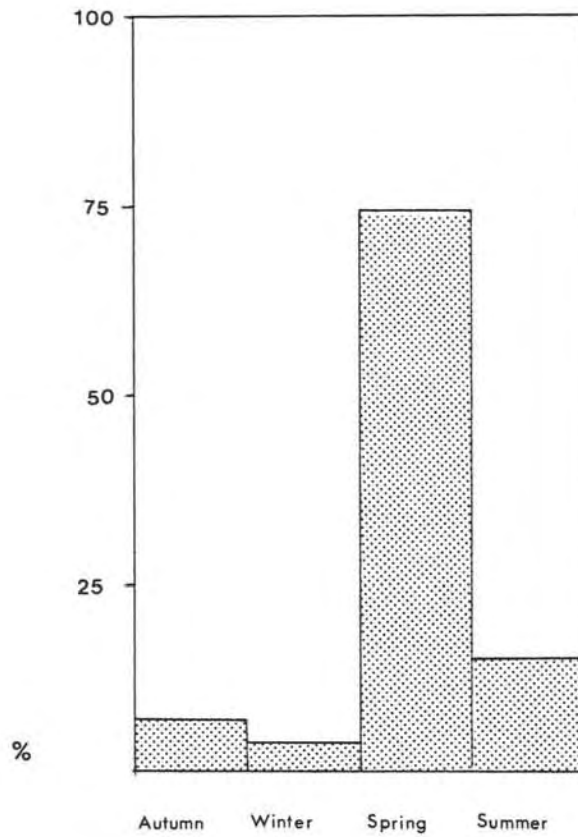
TABLE 10/10: MONTHLY FREQUENCY DISTRIBUTION OF REPRODUCTIVE STATES IN FEMALE BUSHPIGS (SOUTHERN AND EASTERN CAPE)

| MONTHS | Non-reproductive | Cycling | Pregnant | Lactating | n* |
|-----------|------------------|---------|----------|-----------|----|
| JANUARY | 6 | 3 | 0 | 3 | 12 |
| FEBRUARY | 2 | 0 | 0 | 2 | 4 |
| MARCH | 5 | 0 | 1 | 2 | 8 |
| APRIL | 6 | 1 | 0 | 1 | 8 |
| MAY | 5 | 2 | 0 | 0 | 7 |
| JUNE | 5 | 5 | 2 | 1 | 13 |
| JULY | 5 | 9 | 3 | 0 | 17 |
| AUGUST | 4 | 8 | 16 | 0 | 28 |
| SEPTEMBER | 5 | 4 | 7 | 1 | 17 |
| OCTOBER | 5 | 4 | 12 | 1 | 22 |
| NOVEMBER | 3 | 3 | 5 | 1 | 12 |
| DECEMBER | 4 | 0 | 3 | 3 | 10 |

* Includes only sexually mature females

The distribution of farrowing dates provides the clearest definition of breeding seasonality. They were estimated by extrapolating foetal litter ages to parturition and back-dating neonates. A pronounced spring farrowing peak emerged (Fig. 10/6; spring: September - November; summer: December - February; autumn: March - May; winter: June - August).

FIG. 10/6: SEASONAL FARROWING DISTRIBUTION
IN THE BUSHPIG : CAPE PROVINCE (n = 81)



10.3.6 Reproductive potential

10.3.6.1 Reproductive productivity

The reproductive productivity of a population may be estimated or defined by the product of litter size and proportion of females breeding per annum.

Litter size

The following estimates of litter size were obtained:

| | \bar{X} | s | n |
|---------------------------------|-----------|------|----|
| I Prenatal (Southern Cape) | 3,0 | 1,30 | 36 |
| II Prenatal (Eastern Cape) | 3,6 | 1,06 | 15 |
| III Pre-weaning (Southern Cape) | 2,1 | 0,88 | 10 |
| IV Pre-weaning (Eastern Cape) | 2,6 | 1,06 | 8 |
| V Post-weaning/juvenile (SC) | 2,0 | 1,00 | 9 |
| VI Post-weaning/juvenile (EC) | 1,6 | 0,89 | 5 |

The pre- and post-weaning litter size estimates from the Eastern Cape differed significantly (Mann-Whitney $U = 40$ $n_1 = 8$ $n_2 = 5$ $P < 0,005$). Combining all post-natal litter size estimates, i.e. of juveniles up to 12 months, resulted in an overall estimate of 2,1 ($s = 0,98$ $n = 32$).

There was no significant effect of maternal age on prenatal litter size.

| Maternal age | \bar{X} | s | n |
|-------------------|-----------|------|----|
| (I) <3 years | 3,00 | 0,93 | 8 |
| (II) 3 - 10 years | 3,26 | 1,29 | 27 |
| (III) 10+ years | 3,29 | 1,44 | 14 |

(Mann-Whitney U-test on averages I vs II: $U = 131,5$ NS)

Proportion of females breeding

The farrowing proportion (FP) is here defined as the proportion of sexually mature females of a population giving birth to young within a given year. Unless continuous surveillance of the entire female population is possible, the proportion of females breeding can only be conservatively approximated by calculating the reproductive proportion.

The reproductive proportion (RP) is defined as the proportion of sexually mature females either pregnant or lactating within a defined

monitoring period for a given year. This period is selected in order to optimize the post-mortem sample size, but also selected to span the period with the greatest likelihood of females being either pregnant or lactating. This parameter somewhat underestimates the true farrowing proportion and overestimates the proportion of females successfully weaning their litters. The underestimation results from undetected post-partum loss of entire litters within the monitoring period.

The incidence of reproduction in the Goudveld study enclosure is shown in Table 10/11. The death of the alpha boar on 8.12.1985 resulted in social disruption and the quality of the pair-bond between the alpha sow TD2 with her brother was uncertain. Therefore only the first 5 years were considered a reliable monitoring period. Over these 5 years a FP of 1,00 was maintained.

A simulated culling exercise was performed on a population with a reproductive schedule as in the enclosure (Table 10/11). Such simulated "shooting" of an alpha female once a week from August to December over the years 1981 to 1985 would result in a RP of 0,81. The deviation from 1,00 is brought about by late conception into August or later (1981) or as a result of weeks between pre-weaning litter loss and rebreeding (Table 10/11).

| MOTHER SOW | FARROWING DATE | LITTER SIZE | REMARKS |
|------------|----------------|-------------|---|
| TD3 | 16.12.1981 | 2 | First farrowing; neonates died 3 days later |
| TD2 | 19.09.1982 | 1 | |
| TD2 | 03.03.1983 | 1 | |
| TD2 | 10.12.1983 | 1 | |
| TD2 | 23.10.1984 | 3 | Neonates died between 1-3.11.1985 |
| TD2 | 01.10.1985 | 2 | |
| TD2 | 30.03.1986 | 2 | Neonates were not seen; died soon after birth |
| TD2 | ±1.09.1987 | ? | |
| Released | 05.01.1988 | | |

August to October were the peak months for late pregnancy and only a very small percentage of sows would have conceived later. Taking August to December as a monitoring period resulted in RP's of 0,64 and 0,75 for the Southern and Eastern Cape respectively (Table 10/12).

TABLE 10/12: INCIDENCE OF BUSHPIG REPRODUCTION FROM POST-MORTEM INSPECTION*

| MONTHS | SOUTHERN CAPE | | | | | EASTERN CAPE | | | | |
|--|---------------|----|----|---|-------|--------------|----|----|---|-------|
| | n | NR | P | L | Por L | n | NR | P | L | Por L |
| January | 7 | 6 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 |
| February | 3 | 2 | 0 | 1 | 1 | 2 | 1 | 0 | 1 | 1 |
| March | 5 | 4 | 0 | 1 | 1 | 2 | 0 | 1 | 1 | 2 |
| April | 8 | 7 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| May | 5 | 5 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 0 |
| June | 7 | 6 | 1 | 0 | 1 | 4 | 2 | 1 | 1 | 2 |
| July | 10 | 8 | 2 | 0 | 2 | 4 | 3 | 1 | 0 | 1 |
| August | 12 | 3 | 9 | 0 | 9 | 9 | 2 | 7 | 0 | 7 |
| September | 12 | 6 | 6 | 0 | 6 | 4 | 2 | 1 | 1 | 2 |
| October | 12 | 5 | 7 | 0 | 7 | 5 | 0 | 4 | 1 | 5 |
| November | 5 | 2 | 2 | 1 | 3 | 3 | 1 | 2 | 0 | 2 |
| December | 3 | 0 | 2 | 1 | 3 | 3 | 1 | 0 | 2 | 2 |
| AUG - DEC | 44 | 16 | 26 | 2 | 28 | 24 | 6 | 14 | 4 | 18 |
| *Collection periods: Southern Cape 1978 - 1985 Eastern Cape 1982 - 1985 | | | | | | | | | | |
| n : Total sample size; sexually mature females only NR: Non-reproductive; P: Pregnant; L: Lactating | | | | | | | | | | |

The sociospatial status of females of the Goudveld study population was known from capture-recapture monitoring (1981-1986). The reproductive success of 21 sexually mature sows was ascertained over 36 breeding seasons or breeding years in total. Of the 21 sows, 14 were pairbonded to males and territorial and 7 were non-territorial. Successful reproduction was verified in 18 of the 24 breeding years for territorial sows monitored. In two cases, individual sows could be monitored over 3 successive years and both farrowed in two of them. No successful farrowing was recorded for the 7 non-territorial sows monitored over altogether 12 breeding years. Thus a farrowing success rate of 75% was determined for territorial sows. This corresponded to 50% for the population of sexually mature females as a whole. The average age for territorial sows was 8,1 years (n = 14; 3,0 - 11,6 years), whereas for non-territorial sows it was 4,2 years (n = 7; 3,3 - 6,5 years). The difference between the two averages is highly significant (t = 2,862 df = 19 P < 0,01).

A variable and usually unknown proportion of females in a population is territorial. It is convenient to calculate population productivity from the percentage of females reproducing on total females potentially reproducing. A measure of population productivity (PP) may be obtained by multiplying litter size (ls) by the reproductive proportion (RP).

$$\text{Southern Cape: } PP = ls \times RP = 2,1 \times 0,64 = 1,34$$

$$\text{Eastern Cape : } PP = ls \times RP = 2,6 \times 0,75 = 1,95$$

These PP values provide estimates of the expected number of pre-weaning young per sexually mature female in the population. Immediate post-partum values obtained were 1,92 and 2,70 for the two regions respectively.

10.3.6.2 Determinants of reproductive turnover

(a) Regional differences in reproduction

Evidence strongly suggesting a higher reproductive turnover in Eastern Cape bushpigs relative to the Southern Cape is presented in Table 10/13.

| TABLE 10/13: REGIONAL DIFFERENCES IN REPRODUCTION OF MATURE BUSHPIG FEMALES: SOUTHERN VS EASTERN CAPE | | | |
|---|---------------|--------------|----------------------|
| | Southern Cape | Eastern Cape | Statistical Analysis |
| (I) FREQUENCIES OF REPRODUCTIVE vs NON-REPRODUCTIVE FEMALES (1) | | | |
| Reproductive | 36 | 28 | G = 4,84 |
| Non-reproductive | 52 | 18 | |
| % Reproductive | 41 | 61 | P < 0,05 |
| (II) FREQUENCIES OF LACTATING vs NONLACTATING FEMALES (2) | | | |
| Lactating | 4 | 5 | P = 0,103 |
| Non-lactating | 12 | 2 | |
| % Lactating | 25 | 71 | |
| (III) REPRODUCTIVE SUCCESS REFLECTED IN ADULT/YOUNG GROUP COMPOSITION | | | |
| No young | 21 | 5 | RXC test: |
| One generation of young | 28 | 22 | G = 9,82 |
| Two generations of young | 5 | 10 | P < 0,01 |
| % No young | 39 | 14 | |
| % 2 generations | 9 | 27 | |
| (1) Reproductive implies pregnancy or lactation (over full year) | | | |
| (2) Incidence of lactation over December-March period | | | |

(b) Female age and reproduction

In contrast to the situation in the Eastern Cape, reproductive success of sexually mature bushpig females is strongly influenced by age in the Southern Cape (Table 10/14). The ratio of reproductive to non-reproductive females in age classes below 6 years is only about one third of that for older females in the Southern Cape (0,49 vs 1,50). In the Eastern Cape these ratios are virtually equivalent for the two age groups (1,45 vs 1,40).

| TABLE 10/14: FEMALE AGE AND REPRODUCTION IN THE BUSHPIG (SOUTHERN AND EASTERN CAPE) | | | | | | |
|---|-------|--------------|------------------|-----------|-------|------|
| Age (years) | | Reproductive | Non-reproductive | | G* | P < |
| Southern Cape | | | | | | |
| I | 2 - 6 | 18 | 37 | I vs IV | 6,50 | 0,05 |
| II | 3 - 6 | 10 | 26 | II vs IV | 7,63 | 0,05 |
| III | 4 - 6 | 5 | 14 | III vs IV | 5,77 | 0,05 |
| IV | 6+ | 21 | 14 | | | |
| Eastern Cape | | | | | | |
| V | 2 - 6 | 16 | 11 | V vs VI | 0,002 | NS |
| VI | 6+ | 7 | 5 | | | |
| * G-test with Yates correction for continuity | | | | | | |

Further subdivision of age classes in the Eastern Cape was not attempted due to low sample sizes, but inspection revealed that the proportion of reproducing individuals of 2 - 4 year old females was lower than for those older than 4 years (2 - 4 year old females: 7 non-reproductive; 6 reproductive).

(c) Reproduction and food resources

Apart from these regional differences in reproduction (10.3.6.2a), which are presumably linked to differences in availability of food resource (8.3.4.3), the condition of non-pregnant, sexually mature females during April to October, was investigated. The measure of condition available was the subcutaneous fat layer index (9.3.3). The condition of non-gravid females early in this period (April to June) was contrasted with those culled later (July to October). Non-gravid females late in the potential period of conception had body conditions significantly lower ($\bar{X} = 7,57$, $n = 7$) than non-gravid females ($\bar{X} = 23,78$, $n = 9$) early in the period (Mann-Whitney $U = 55$; $P < 0,05$). Females from the first group either failed to ovulate, failed to conceive or ovulated late, in all cases apparently as a result of poor condition.

No differences in reproductive rate between years were found for the years with sufficient data for such an analysis (only Southern Cape for the years 1978, 1980, 1981, 1983, 1984; $G = 0,29$ NS). Good ironwood

(*Olea capensis* ssp. *macrocarpa*) fruiting was recorded in 1980, 1982 and 1984. However, any link between these events and reproductive rate could have been blurred by the fact that a variable number of samples originated from areas with agricultural food sources and little access to indigenous forests. Any possible interaction between reproductive output and mast fruiting therefore remains unresolved.

Within the Southern Cape, the condition of bushpigs from the foothill zone, as measured by the body mass to size index, was lower than that of animals from the plateau zone (9.3.3.1, Table 9/10). The fecundity of the latter was higher (11.2.2; Table 11/1).

10.4 Discussion

10.4.1 Aspects of reproductive biology

10.4.1.1 Sexual maturation

The attainment of sexual maturity in the male bushpig between 16 and 20 months closely corresponds to the age of maturity in the warthog (Clough 1969, Mason 1982). The male European wild boar is also generally taken to reach sexual maturity in the second year of life (Briedermann 1986). In contrast, according to Mauget (1980b), sexual maturity is already reached around 10 months of age, resembling the situation in the domestic pig. In the male domestic pig, testosterone concentrations tend to reach a peak at attainment of full sexual maturity at about 7 months, and decline thereafter with increasing age (Claus 1979). Testosterone concentrations in the bushpig appear to follow a similar trend with age, although markedly less pronounced and statistically not significant (10.3.1.1).

Free-ranging warthog females mature as yearlings (Bradley 1968, Boshe 1981). First conceptions or matings have been reported to occur between 17 and 19 months in the warthog (Child *et al.* 1968, Clough 1969, Mason 1982), giant forest hog (D'Huart 1978) and the bushpig (10.3.1.2). Under natural conditions of age class structure and food availability during average years, sexual maturity in European wild boar females is

attained between 15 and 20 months of age (Walker 1984 ex Santiapillai and Chambers 1980, Stubbe and Stubbe 1977, Briedermann 1986). However, a variable proportion already do so between 7 - 10 months, the difference being largely under the control of food availability (Briedermann 1986). Exceptional cases of captive warthog females reaching sexual maturity at 10 to 12 months have been reported and are attributed to accelerated growth due to a high plane of nutrition (Mason 1982).

Age and plane of nutrition, in conjunction with photoperiodism, seem to be the most influential environmental factors in the attainment of sexual maturity (Sadleir 1969, Briedermann 1986). For European wild boar males under controlled experimental conditions, Mauget and Pepin (1987) found that sexual maturity was reached at 10 and 16 months for animals fed *ad libitum* and on a restricted diet respectively. In females fed *ad libitum*, ovarian activity reflected by plasma progesterone levels was first observed at 22 months (\pm 53 kg). In the group of females on a restricted diet, puberty was delayed to the age of 33 months. The authors concluded that the onset of sexual maturity depended on a threshold level of body weight, seasonal constraints (since onset of puberty was never observed during summer) and social factors. The onset of sexual maturity in seasonally breeding species is apparently often determined by the synergistic effect of a critical body weight and photoperiod. Accordingly, should any particular animal fail to reach the critical weight during the photoperiodically sensitive period, sexual maturity is delayed for at least one year (Bauer 1987).

The critical body weight required for sexual maturity may differ between populations (cf Bauer 1987). This feature could then explain the fact that in domestic pigs, high planes of nutrition, although they result in greater weights at puberty, have little effect on the age of sexual maturity (McDonald *et al.* 1973). For the bushpig it is suggested that sexual maturity is invariably attained by yearlings of both sexes, but season, nutritional conditions and social status determine whether individuals participate in reproduction.

10.4.1.2 Breeding cycles in females

The pattern of ovulation in the bushpig is similar to that of other wild suid species. The female appears to be polyoestrus. Ovulation is apparently possible at any time of the year, but a seasonal peak in conception is evidenced by the seasonal distribution of farrowing (10.3.5). Corpora albicantia from successive pregnancies did not accumulate in the bushpig ovary, in contrast to the situation in the warthog (Mason 1982). As in other suids (e.g. Anderson and Melampy 1972) the bushpig sow exhibits lactational anoestrus. There was no evidence of reproductive senescence (10.3.2.1), which corresponds to the situation as in the European wild boar (Briedermann 1986) and warthog (Mason 1982).

D'Huart (1978) gives the gestation period of the giant forest hog as about 151 days. Scaled to size, this is similar to the gestation periods of bushpig, domestic pig and European wild boar. A figure of 17 weeks, i.e. about 4 months, was reported for the bushpig (Asdell 1964, Sowls and Phelps 1968) and verified in this study. Gestation may last between 112 and 126 days in feral and domestic *Sus scrofa* (Walker 1968, Henry 1968a, Briedermann 1971, Mauget 1982). In contrast, warthogs have a considerably longer gestation period of between 167 - 175 days (*op. cit.* Mason 1982).

Adult females of warthog, European wild boar and bushpig are of similar body size and the extended gestation in the warthog is therefore unexpected. Some mammals produce particularly precocial young after extended gestation periods (Eisenberg 1983) but warthog neonates are not larger at birth nor more precocial than those of the other two suid species (cf Mason 1982, Rodgers 1984). Reduced nutritional costs/litter during pregnancy may be achieved by a reduction in litter size and by prolonging gestation, thereby reducing the rate of foetal growth, i.e. nutrient demand per unit of time (cf Eisenberg 1983). Lengthening of the gestation period relative to the demands for protein or other nutrients can reduce their daily cost if maintenance is a relatively small proportion of that cost. The pregnant female can benefit by lengthening the gestation period if protein or minerals are limiting, but gains nothing by prolonging it if energy is limiting (Robbins 1983). Warthog pregnancy is timed to occur during winter (e.g. Mason 1982).

For the warthog as a non-ruminant in a grazing niche, the longer gestation is accordingly interpreted as a consequence of limited protein (and phosphorus?) availability during winter. The small litter size of the warthog, compared to that of the European wild boar, may be a consequence of the same set of constraints.

Henry (1968b) investigated whether foetal development in the European wild boar was comparable with that of the domestic pig in view of similar gestation lengths. Measurements of both species were similar in foetuses of the same age. His data also showed that it was possible to determine the age of foetuses to within 10 days by morphological differences. Analysis of foetal development in the bushpig indicated that both morphological, as well as meristic data, may also be used with success in determining the ages of foetuses with sufficient accuracy to permit determination of mating and farrowing seasons.

Progesterone and estradiol 17- β concentrations during ovulation and pregnancy in the bushpig are comparable to those in the European wild boar (cf Maugé 1980b), but lower than in the domestic pig (cf Catchpole 1977, Dziuk 1977). Circulating progesterone concentrations are variable in both pattern and level (Hughes and Varley 1980) and levels during the initial phases of pregnancy are similar to those during the luteal phase of the oestrus cycle (Shearer *et al.* 1972). Progesterone concentrations of pregnancy exceed those found during the cycle in many species (Catchpole 1977), so that pregnancy can be detected from progesterone levels. For example, during the latter two thirds of gestation, Ramsay and Sadleir (1979) found that blood progestin levels from a single sample provided a useful diagnostic tool to determine pregnancy rates in wild bighorn sheep populations. Variability in progesterone concentrations and wide overlap between ovulatory and pregnancy levels precluded their use to diagnose pregnancy in the bushpig.

From an early peak, progesterone levels in the domestic pig decline gradually towards the final stages of gestation, falling to low basal levels at parturition (Dziuk 1977). Estradiol levels increase in the latter half of gestation, reaching peak values shortly before parturition (Robertson and King 1974, Dziuk 1977, Hughes and Varley 1980). A comparable pattern was recorded in the European wild boar

(Mauget 1980b). In contrast, the progesterone levels during pregnancy in the bushpig did not vary predictably and estradiol levels started to rise at an earlier stage (Fig. 10/4).

Progesterone levels during pregnancy were significantly higher in captive than in free-ranging bushpig sows (10.3.2.2). Most determinations of free-ranging individuals were from shot animals, as opposed to those for the captive group, which were all taken from immobilized individuals. Wesson *et al.* (1979b) demonstrated that progesterone levels in wild deer fluctuated in relation to the method of capture, suggesting an extra-ovarian source of the hormone. Interpretation of serum progesterone levels from stressed animals may thus be misleading if the adrenal is a significant source (Plotka *et al.* 1983). However, unlike some other species, the domestic pig's only source of progesterone is the ovary and the maintenance of pregnancy depends entirely on luteal function (Hughes and Varley 1980). If the same applies in the bushpig, increased progesterone levels in stressed, immobilized captive animals cannot be explained, as suggested, by the effects of handling.

Progestin concentrations in white-tailed deer (*Odocoileus virginianus*) were found to be positively related to dietary protein and energy availability (*op. cit.* Franzmann 1985). The higher progesterone levels in captive pregnant females may thus be related to their higher nutritional status (cf 9.3). Minimum progesterone requirements for the maintenance of pregnancy in the domestic pig were determined as about 6 ng/ml (Ellicot and Dziuk 1973 *ex Dyck* 1982). Ovarian progesterone secretion is maintained at relatively normal levels in pigs subjected to extreme conditions of prolonged starvation during pregnancy. Abortions occur in starved dams only when serum progesterone concentrations drop to below 10 ng/ml (Anderson 1980). It is conceivable that in wild suids nutritional status is more critical in the maintenance of pregnancy. Abortions were recorded in warthog sows in poor condition (Mason 1982) and the mechanism of abortion was suggested to be the same as in the domestic pig, namely disruption of luteal function and a sharp fall in progesterone secretion (Wrathall 1975). Pregnant bushpig sows subject to declining food availability may abort, which may explain the discrepancy between the number of pregnant and lactating sows in the

Southern Cape (10.3.6.2). Alternatively, or additionally, abortions may also result from escalating conflicts between bushpig sows (cf Huck, Bracken and Lisk 1983).

10.4.1.3 Litter size

Litter size in polytocous animals is limited by ovulatory rate and fertilization rate of the ova and affected by prenatal mortality (Hagen and Kephart 1980, Hughes and Varley 1980). In domestic pigs, nearly all ova shed at oestrus are fertilized after mating (Scofield 1972), but prenatal losses are high. The causes of the high embryonic wastage, often approaching 40% (Duncan and Lodge 1960, Scofield 1972, Anderson 1980) are unclear. Intrauterine crowding, maternal nutrition and thermal effects are among the factors that have been studied (Hagen and Kephart 1980). The biggest single factor causing foetal loss appears to be available uterine space (Hughes and Varley 1980), but this view contrasts with that of Anderson (1980) who relates losses to placental insufficiency.

Prenatal litter sizes of between 4,8 to 7,4 and prenatal mortality percentages of 25 to 34,7% have been reported for a feral *Sus scrofa* population in the United States (Conley *et al.* 1972, Barrett 1978, Sweeney *et al.* 1979, Diong 1982, Baber and Coblenz 1986). Prenatal losses tend to be smaller in wild pigs than in domestic pigs (cf Scofield 1972). For example, European wild boar prenatal mortality percentages were of the order of 12,5% (France: Mauget 1982) and 14,8% (Germany: Stubbe and Stubbe 1977), with corresponding prenatal litter sizes of 4,6 and 5,3 fetuses per litter respectively. Hagen and Kephart (1980) recorded averages of 9,8 and 6,2 fetuses/litter in primiparous Yorkshire and feral gilts respectively and concluded that the smaller litter size in the feral line resulted from a lower ovulatory rate.

Prenatal litter size increased with maternal body mass from 2,5 (30 - 39 kg) to 4,3 (60 - 69 kg) to 5,6 (90 kg +) in the European wild boar (Mauget 1980b). Similarly, average prenatal litter sizes varied from 5,3 in juvenile female European wild boar to 6,5 in adults (Stubbe and Stubbe 1977). Maximum ovulation and implantation rates were not

reached until about age 5 years in peccaries. This coincided with the age at which the animal reached maximum size (Low 1970). Boshe (1981) recorded increasing average prenatal litter sizes with increasing age in the warthog.

Most prenatal losses occur in the embryonic period, around implantation (Scofield 1972, Den Hartog and Van Kempen 1980). On the basis of the discrepancy between ovulations and number of foetuses, Child *et al.* (1968) recorded a prenatal mortality of 16,9% for warthog in Zimbabwe, but there was no evidence of foetal resorption or abortion. In the same species, Clough (1969) gave a prenatal mortality of 17,9% and concluded that, in the absence of any indications of foetal resorption, most of the loss was through non-fertilization or failure to implant. The corresponding mortality percentage found by Mason (1982) was relatively low, namely 9,1%. It included indications of foetal resorption in 3 pregnancies. Mason (1982), in his study of the warthog, concluded that loss of ova through non-fertilization or failure to implant and develop were the predominant forms of prenatal mortality. The absence of foetal resorption observed by Baber and Coblentz (1986) in feral pigs was also taken to suggest that most prenatal mortality occurred in the first trimester of pregnancy. In this study a prenatal mortality of 28,5% was determined in the bushpig, which presumably also occurred in early pregnancy (10.3.2.3). A lower incidence of prenatal survival was evident in the bushpig population of the Southern compared to the Eastern Cape (10.3.2.3). This was also reflected in prenatal litter size differences between the regions, being 3,0 and 3,6 respectively (10.3.6).

Southern Cape bushpig sows exhibited greater "fatness" at ovulation (10.3.2.3; 10.3.6.2), as did *ad lib* fed captive individuals. The average litter size in captivity was low - 1,7 neonates/litter. Much evidence has accumulated on the effect of "overfatness" on various facets of reproduction, especially prenatal mortality in the domestic pig. A high energy intake by pregnant gilts has been found to have unfavourable effects such as increased embryonic mortality, more complications at farrowing, more cases of low milk production and a tendency for greater fertility problems (Den Hartog and Van Kempen 1980). These effects of prolonged "overfeeding" must however be

distinguished from underfeeding, which also reduces reproductive turnover, and are not be confused with the effect of short-term "overfeeding", namely flushing. Many studies have shown that for the domestic pig *ad libitum* feeding during rearing and high-level feeding after maturation increases embryonic losses and lowers litter size (*op. cit.* Duncan and Lodge 1960, Scofield 1972, English *et al.* 1977, Hughes and Varley 1980). This phenomenon was also observed in the European wild boar in Germany (Gottschlich 1975) and Russia (Sludskii 1956), where "overfatness" was found to be associated with lowered fertility, delayed farrowing and reduced litter sizes. In the case of the bushpig, it is proposed that the overfatness syndrome is also involved in prenatal mortality and influences litter size. "Overfatness" implies readily available food resources, at least as regards energy-rich items, and storage in the form of adipose tissue. That a resource surplus should mitigate against reproduction does not make sense according to the theory of reproductive fitness. The overfatness phenomenon is therefore viewed as only one part of a trade-off. It is suggested that what is lost in terms of litter size due to overfatness, is gained through better juvenile growth and survival. Different reproductive tactics appear to be involved in Southern and Eastern Cape bushpigs (Chapter 12).

The available data for the bushpig suggests a lower juvenile survival rate in the Eastern Cape. The preweaning litter size is 2,6 and the post-weaning juvenile litter size only 1,6. No such difference is evident in the Southern Cape (2,1 versus 2,0). Reported litter sizes in the bushpig range from 1 - 8, with 3 - 4 the most common and rarely exceeding 6, the number of mammae (Ansell 1960, Sows and Phelps 1968, Skinner, Breytenbach and Maberly 1976). Postnatal litter sizes in the warthog are similar to those in the bushpig (Mason 1982). Litter sizes in adult European wild boar are consistently higher than those of both the bushpig and warthog, averaging 5,3 young (Briedermann 1986). Primigravid warthog and European wild boar females, on average, have lower litter sizes (Clough 1969, Boshe 1981, Mason 1982, Briedermann 1986). This trend is not clearly evident in the bushpig (10.3.6.1). The higher litter sizes in the European wild boar are interpreted as a strategy to use food resource surpluses opportunistically in unstable and unpredictable environments. Eisenberg (1983) has proposed that

selection favours a high reproductive potential in forms that suffer the greatest loss of offspring during an average annual cycle as an adaptation to ecological niches that are to some extent unstable and show great fluctuations in carrying capacity.

A notably large within-litter variation in the size of fetuses was noted in the bushpig (10.3.3), as in other suid species. The associated "viability gradient" among the young may be of selective advantage in that the available resources may be unequally allocated according to the principle "them that has, gets" (cf Graves and Graves 1977). Under conditions of resource limitation, the available resources are thereby channeled to those which may be reared successfully, rather than to all with the risk of losing all. Under favourable conditions, productivity is optimized in that the weaker may also be reared successfully.

10.4.1.4 Lactation

The composition of bushpig milk is contrasted with that of other suid species in Table 10/15. It generally appears somewhat more concentrated, especially as regards fat and protein.

| Species | Mean Percentage composition | | | | | Source |
|--------------------|-----------------------------|---------|------|---------|-----|--|
| | Total Solids | Protein | Fat | Lactose | Ash | |
| Domestic pig | 19,9 | 5,8 | 8,2 | 4,8 | 0,9 | Braude <i>et al.</i> 1947 ex Rook and Witter (1968) |
| Domestic pig | 20,1 | 7,3 | 6,8 | 5,1 | 1,0 | Bowland (1966) ex Mount and Ingram (1971) |
| Domestic pig | 21,2 | 6,1 | 9,6 | 4,6 | 0,9 | Perrin (1954) |
| Domestic pig | 18,4 | 5,8 | 6,2 | 5,4 | 0,9 | Salmon-Legagneur (1965) |
| Domestic pig | 20,0 | 5,5 | 8,5 | 4,5 | 1,0 | English <i>et al.</i> (1977) |
| Domestic pig | 19,6 | 5,4 | 8,3 | 5,0 | 0,9 | Maynard <i>et al.</i> (1979) |
| Domestic pig (av) | 19,7 | 6,0 | 7,9 | 4,9 | 0,9 | |
| European wild boar | 16,0 | 9,0 | 4,0 | 2,0 | 1,0 | Haber (1969) ex Briedermann (1986) |
| Warthog | 18,9 | 7,0 | 7,3 | 3,6 | 1,0 | Roth (1967) |
| Bushpig | 24,2 | 9,4 | 10,4 | 3,0 | 1,4 | This study |

Juvenile requirements for protein to sustain growth are a particularly important factor influencing milk composition (Martin 1984). For interspecies comparison there appears to be an inverse relationship between milk protein percentage and days required to double birth weight (Johnson 1974, White and Luick 1984). Altricial mammals typically have milk with relatively high fat and protein contents (Jenness and Sloan 1970, Martin 1984). The relatively high milk protein and fat content of suid milk fits this pattern.

Intraspecific differences in milk composition in suids and other species (Table 10/15) are mainly the effects of variable concentration. Once the changes from colostrum to milk have taken place, there is a small but steady decline in percentage protein, fat and lactose, i.e. total solids, until the peak of lactation (Cowie and Buttle 1980). There is a general inverse relationship between milk yield and composition (McDonald *et al.* 1969, Johnson 1974, Maynard *et al.* 1979, Cowie and Buttle 1980). Thus, any influences leading to reduced yield, like the decline in yield as lactation progresses, sickness or off-feed, result in increased protein and particularly fat percentages (Johnson 1974, Maynard *et al.* 1979). Illness, associated with zero food intake, may accordingly be taken to explain the high total solid and fat percentages of sow TD3 (Table 10/8).

Milk yield is dependent on the plane of energy nutrition during lactation. The decline in yield following low energy intake is associated with a decrease in lactose and an increase in fat, ash and protein content (Rook and Witter 1968, White and Luick 1984). However, when energy is available in excess, milk yield may be lower. Maynard *et al.* (1979) reported that cattle grown on high energy intakes produced less milk and overfattened heifers exhibited poor lactational performance later in life. In the domestic pig, plane of feeding significantly affected only milk protein percentage. The average values for all sows and lactations were 5,54% on the high and 6,10% on the low plane (Duncan and Lodge 1960). It is suggested that the relative availability of dietary protein and energy may be responsible for these patterns. A relative excess of energy in relation to dietary protein or body protein reserves is expected to lead to a decline in milk yield and an increase in milk constituents. Excess dietary energy is tentatively

proposed as the reason for the relatively high milk total solids, protein and fat percentages of captive and free-ranging Southern Cape bushpig compared to those of free-ranging bushpig in the Eastern Cape (Table 10/8).

Long periods between suckling events and the conservation of body water are reasons for the evolution of concentrated milk in mammals (cf Trillmich and Lechner 1986). For example, the concentrated milk of cervids is interpreted as an adaptation to permit infrequent suckling and hence reduce the risk of predation (Loudon and Kay 1984). The ability to concentrate milk should be advantageous if relatively large amounts of nutrients have to be transferred during a suckling bout and conservation of body water is a constraint. This is to be expected in altricial, multiparous mammals with long intervals between suckling bouts due to foraging requirements. The relatively concentrated milks of non-domestic suid species fits this hypothesis.

The energetics of lactation apparently play a central role in reproductive success. A particular feature of mammalian lactation is that body stores may contribute precursors for milk secretion (Pond 1984). Lactation therefore enables mammals to reproduce successfully in impoverished or disturbed habitats where food is scarce or available only in a form suitable for adults and subadults.

Much evidence exists for a substantial increase in food requirements during lactation for a variety of mammals and of an increase in milk production following an improved food supply (Duncan and Lodge 1960, Sadleir 1969, English *et al.* 1977, Pond 1977, Maynard *et al.* 1979, Hartmann *et al.* 1984). For the domestic sow it was found that milk yield could be increased by improving nutrition both during the preceding pregnancy or during lactation itself (English *et al.* 1977). For sows in good condition it was found that the distribution of feed between pregnancy and lactation was less important than the total intake during the reproductive cycle (De Geeter *et al.* 1972, *op. cit.* Hartmann *et al.* 1984).

Lenkeit and his colleagues (1955, 1956 ex Duncan and Lodge 1960) found that in sows which had been well-fed during pregnancy and had stored

excess nitrogen, nitrogen balance was negative in the early stages of lactation. However, sows with good stores of nitrogen gave a better lactation performance than those poorly fed during pregnancy and with little or no surplus nitrogen. Also the importance of an adequate dry period to build up nutrient reserves is well established (Maynard *et al.* 1979).

Mahan and Mangan (1975) demonstrated a nutritional carry-over from pregnancy to lactation in that litter gains increased as gestation protein level increased from 9 - 17% when the sows had been fed an inadequate low protein diet (12%) during lactation. This is in agreement with the suggestion that maternal tissue reserves accumulate during pregnancy and are used to provide nutrients during lactation (Mahan and Grifo 1975). Acceptable lactational performance in the sow, as judged by a prolonged adequacy of milk yield for optimal juvenile growth and high mass at weaning, required dietary crude protein levels of 14-16% (Duncan and Lodge 1960, Baker *et al.* 1970, English *et al.* 1977, Maynard *et al.* 1979). The precise mechanism of metabolic effects appears to be complex. Hassan and Roussel (1975) found that the increase in milk yield with increasing protein level in the diet was associated with an increase in total food intake rather than of crude protein *per se*. This also suggests that the balance between energy and protein content of the diet is important in some way. The influence of protein body reserves and dietary levels on the seasonality and frequency of breeding in the bushpig is discussed below (10.4.2; 10.4.3).

The length of the lactation period varies substantially in various suid species (Table 10/16). These variable records may have resulted partly from the difficulty of determining age at weaning under free-ranging conditions and may also be partly due to real variation linked to food resources.

| TABLE 10/16: LACTATIONAL PERIODS IN SUID SPECIES | | |
|--|-----------------|-----------------------------|
| Species | Period (Months) | Source |
| Malayan wild pig | ± 4 | Diong (1973) |
| Feral pig | 1,3 - 5,5 | Giffin (1974) |
| Feral pig | 2,5 - 5,0 | Barrett (1978) |
| Feral pig | 3,5 - 4,2 | Jensen and Recen (1985) |
| Feral pig | 3 - 4 | Baber and Coblentz (1986) |
| European wild boar | 2,5 - 3,5 | Sludskii (1956) |
| European wild boar | 2 - 3 | Frädrich (1968) |
| European wild boar | 2,5 - 3,5 | Myrcha and Jezierski (1972) |
| European wild boar | 3 - 4 | Schnorrenberg (1979) |
| European wild boar | ± 3 | Hennig (1981) |
| European wild boar | 3 - 4 | Briedermann (1986) |
| Giant forest hog | 2,0 - 2,5 | D'Huart (1978) |
| Warthog | 5,0 - 5,3 | Bradley (1968) |
| Warthog | 2,5 + | Child et al. (1968) |
| Warthog | ± 3 | Clough (1969) |
| Warthog | 5,3 | Cumming (1975) |
| Warthog | ± 5 | Mason (1982) |
| Bushpig | <4 - 5,5 | This study (10.3.4) |

Although lactation may last 5 months, milk probably becomes much less important to the survival of juveniles after 3 months of age and Cumming (1975) reported a litter surviving after being orphaned at nearly 13 weeks. A feral pig litter that was weaned at just over one month turned out to be scrawny, indicating that mother's milk is necessary for a longer period to ensure healthy development (Giffin 1974). In contrast, a litter weaned at 5,5 months produced animals larger than normal animals. The importance of extended lactation is also borne out by the findings of Sadleir (1984) in black-tailed deer, *Odocoileus hemionus columbianus*. Although fawns were receiving less than 20% of their total energy intake from milk at 100 days of age, many were still suckling small quantities at 200 days.

The available evidence indicates that weaning usually occurs earlier in free-ranging than in captive bushpigs (10.3.4). Gosling (1980) found the same in the coypu, *Myocastor coypus*. The average lactation period of captive female coypus was 42% longer than that of their feral counterparts. This was attributed to lower levels of food availability in the feral population, i.e. lactation of wild females was constrained by a reduced food supply. Earlier weaning has been reported for nutritionally stressed females in vervet monkeys *Cercopithecus aethiops* (Lee 1984), reindeer *Rangifer tarandus* (White and Luick 1984) and the

feral pig (Baber and Coblenz 1986). Lactation has also been shown to be energetically demanding in the bushpig (10.3.4) and the difference in age at weaning under free-ranging and captive conditions may be similarly explained.

The young are not normally weaned until they are able to gather, masticate and digest the adult diet (Pond 1977). Nursing by mothers in poor condition becomes a limiting factor earlier than by those in good condition (as indicated above). This is presumably because the cost of a given amount of milk is considerably higher when the mother is in poor condition, while the benefit to the offspring remains more or less unchanged (Trivers 1974). The capacity of female mammals to invest nutrients in their offspring depends on their body reserves at parturition, their own requirements and the nutrients they can obtain by feeding during lactation. The potentially beneficial role of "baby sitting" by male bushpigs was outlined above (4.4.3.4). If resources are scarce for prolonged periods throughout the breeding season, the only way to meet the high cost of lactation would be by supplementation from stored energy (cf Mattingly and McClure 1982). Females maximize the utilization of low resource levels by accumulating the required body reserves during pregnancy (9.3.2; 9.4.5) in order to meet the relatively high demands of lactation.

Lactation is probably that characteristic of mammals with the greatest influence on their life history strategies (Sadleir 1984). In wild mammals, natural selection has moulded lactation so as to maximize the reproductive success of the female. The quantity of milk produced by red deer females *Cervus elaphus*, for example, represents a compromise between maximum growth of the young and maintenance of maternal condition, leading to successful ovulation towards the end of lactation (Loudon and Kay 1984). At the ultimate level females are thus faced with a trade-off between maternal cost in terms of reproductive effort during a given year and benefit in terms of "inclusive fitness" effects, in that or subsequent years (cf Berger 1979).

10.4.2 Breeding seasonality

Natural selection is expected to favour seasonal timing of reproduction such that the combined effects of food availability for the mother, food for the offspring before and after weaning, predation risk and weather conditions result in the greatest number of surviving offspring (Sadleir 1969). In seasonal environments one would therefore expect the peak of lactation to coincide with, or follow soon after, the food peak and hence there should be a birth peak some time before (Van Schaik and Van Noordwijk 1985). In most African ungulates which breed seasonally, parturition occurs during the period of active vegetation growth, which is mainly during spring in subtropical (Spinage 1973) and temperate regions (Gwinner 1981a). Growth of the offspring coincides with the period when environmental conditions are most favourable (Gwinner 1981a). For most of the African continent, parturition peaks are accordingly timed to take advantage of increased rainfall (Eltringham 1979).

The environmental factors known to influence reproduction in mammals include food availability, aspects of the physical environment such as photoperiod, temperature and rainfall, and a variety of social cues (Bronson 1985). Those environmental variables that, in the course of evolution, have exerted selection pressure to restrict an activity to a particular time of the year, are called ultimate factors (Gwinner 1981a). The ultimate factors controlling seasonal breeding are climate and energy availability or nutrient quality, or both. Specific nutrients which may vary seasonally and are potentially critical in controlling seasonality in breeding include the essential amino acids, certain polyunsaturated fatty acids, a variety of minerals and some vitamins (Bronson 1985).

Most seasonal activities cannot be initiated instantaneously when the ultimate factors reach optimal values. To guarantee that the young are born in the optimal season, the preceding processes (e.g. gestation) must be initiated long in advance (Gwinner 1981a). Many organisms make use of reliable forewarning stimuli, which vary in close relation to the ultimate factors, to prepare themselves in advance for seasonal events. Seasonal forewarning stimuli or predictors are for example, temperature or photoperiod (Gwinner 1981a). Photoperiod is the most "noise-free"

predictor of seasonal change (Bronson 1985) and is commonly employed. Cues of this kind are termed "proximate factors", as opposed to the ultimate factors, which exert their effects during evolution by changing gene frequencies (Gwinner 1981a). The proximate cue initiates physiological preparation, either directly or by entraining circannual physiological rhythms. The actual occurrence of events, such as mating, is furthermore often influenced by condition thresholds (i.e. nutritional status) or social circumstances to which individual animals are subjected.

Apart from some cases of deviation in response to local habitat conditions, the prevailing time of farrowing slightly precedes or coincides with the beginning of the wet season, when fresh grass shoots become available (Mason 1982). On the equator warthogs breed all the year round or show two farrowing peaks coinciding with the beginning of the two wet seasons (cf Clough 1969), as is the case for many other ungulates in these regions with a bimodal rainfall pattern (*op. cit.* Mason 1982). Giant forest hog piglets in Zaire were observed in most months of the year, but two pronounced birth peaks were evident (D'Huart 1978). The timing of these birth peaks was such that the piglets benefitted at weaning from the tender new growth of annual grasses with a higher protein content than that of perennial grasses (D'Huart 1978).

In contrast to domestic pigs (Hafez and Signoret 1969), autumn/early winter mating and spring farrowing prevails in the European wild boar, although some breeding may occur out of season (Briedermann 1971, 1986; Iff 1976, Stubbe and Stubbe 1977, Santiapillai and Chambers 1980, Mauget 1980b, 1982; Hennig 1981). Most late farrowings result from sows farrowing a second time after the early loss of the first litter (Iff 1976). Late out of season birth may lead to a smaller size at the onset of the winter and this retardation effect is then usually sustained through the yearling phase into adulthood (Cabon 1958b, Hennig 1981). Out of season juveniles have a lower survival rate (Kozlo 1970).

Photoperiod is apparently involved as proximate cue in the reproductive seasonality of the European wild boar. This is suggested by the cessation of breeding in summer independently of the plane of nutrition, even under stable feeding conditions (Mauget 1982, Pepin *et al.* 1987).

Whereas photoperiod regulates the cycle of physiological preparation, the actual timing of conception is apparently also dependent upon diets of sufficient nutritional quality to attain some threshold of body condition (cf Baber and Coblenz 1987). Thus, depending on nutritional condition, especially in respect of energy, the anoestrus-oestrus transition in autumn may be relatively early or late (Mauget 1980b). An earlier onset of oestrus when food is readily available is common (Mauget 1982, Briedermann 1986, Pepin *et al.* 1987). This may also be the reason why older sows farrow first (Briedermann 1971b). They presumably attain the necessary condition threshold earlier.

The two preconditions for conceptions to occur are thus a photoperiodically cued physiological readiness and an adequate plane of nutrition. The condition threshold provides adaptability to prevailing conditions and allows the "monitoring" of whether and when feeding conditions are suitable to enter pregnancy and its associated energy storage metabolism. Early conception allows an extended period of juvenile growth before the onset of winter and full recovery of maternal reserves after the drain of lactation (cf Maynard *et al.* 1979). When early onset of breeding is followed by sustained favourable conditions, a second farrowing in the same year is apparently possible in European wild boar (Mauget 1982). For the European wild boar in the Chize forest, France, Mauget (1982) found two types of farrowing distributions: a unimodal distribution peaking in April/May and a bimodal distribution with its two peaks in January/February and August/September, respectively. From spring to summer, the frequency of anoestrus increased progressively. From summer to early autumn, the whole population was in anoestrus. From October (autumn), the onset of the mating season was regulated by the availability of food. Depending on food availability in autumn, cyclic activity occurred early (October) or was delayed (December). Subsequently, there were either one or two litters per year (Mauget 1982).

This bimodal distribution of farrowing should not be confused with the double farrowing peak of the giant forest hog in tropical Africa. In the former case, two litters may apparently be produced per female in a given year, whereas in the giant forest hog, different females of the

multifemale group give birth during the two peak periods of the same year (D'Huart 1978).

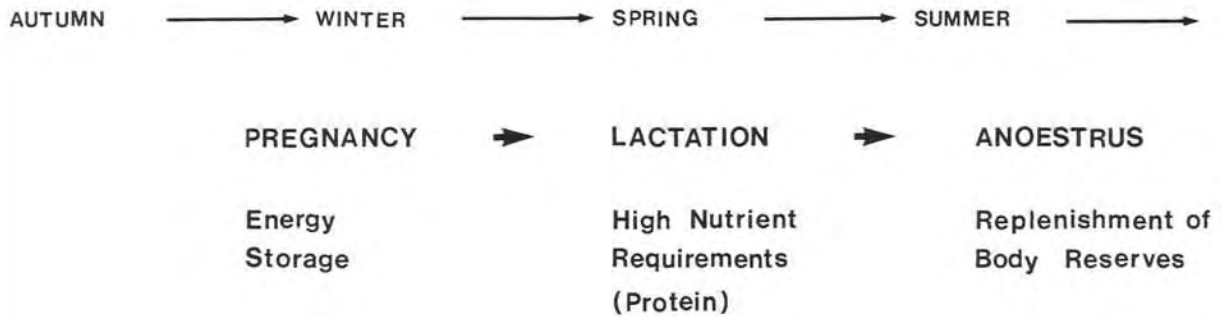
Bushpig farrowing has been reported from spring to early autumn, i.e. October to March, but mainly from October to January (Thomas and Kolbe 1942, Ansell 1960, Sowls and Phelps 1968, Milstein 1971, Smithers 1971, Tinley 1977). These records are in agreement with the findings of the present study (10.3.5).

In the bushpig only one litter is raised successfully per annum. With a 4-month gestation period it would theoretically be possible to farrow and raise two litters. This suggests that resources for reproduction are limiting, requiring optimal spacing of the various phases of the cycle according to seasonal constraints, in order to maximize reproductive success. Even slight seasonal changes, which improve conditions for a particular species, may constitute sufficient selection pressure in favour of seasonal breeding (Millar 1972). Over a period of 7 years the bushpigs in the study enclosure, provided with a balanced, *ad libitum* food supply, maintained the same reproductive regime as their free-ranging counterparts in that the breeding season remained constant and no more than one litter a year was raised successfully. Maintenance of the seasonal pattern suggests that a proximate cue, presumably photoperiod is involved in entraining a circannual reproductive rhythm. The reproductive sequence (10.3.5) is illustrated in Fig. 10/7.

There are several possible advantages to this seasonal sequence:

- (I) Vegetative growth in spring results in increased availability of digestible protein and phosphorus to meet lactational demands.
- (II) Increasing ambient temperatures reduce energy costs of suckling and growing juveniles.
- (III) Large fat deposits laid down during pregnancy aid sows to thermoregulate during winter and their loss before the onset of summer reduces heat stress.
- (IV) The relatively low protein/energy ratio in the winter diet favours energy storage during pregnancy.

FIG.10/7: REPRODUCTIVE PHASES AND SEASON IN BUSHPIGS



The present study has produced some evidence in support of these advantages. Additional indirect evidence comes from the results of numerous authors.

- (I) The sow's requirements for protein and phosphorus increase during lactation as do those of juveniles for the initial phase of rapid growth (8.3.4.1). The link between protein availability and milk yield was discussed in section 10.4.1.4 (also Clutton-Brock *et al.* 1982). Bushpigs obtain most protein from herbage and animal matter (8.3.3.2). The herbage fraction in the diet of Southern Cape animals is highest during spring and autumn while it is at a minimum in autumn in those from the Eastern Cape (8.1.2.1). The crude protein level appears to be somewhat higher in Southern Cape spring diets. The lowest values were found in autumn in both regions (8.3.3.2), coinciding with the periods of anoestrus. The diets of lactating females had higher percentages of ash (8.3.3.2) and phosphorus (8.3.3.3).

Protein and phosphorus contents of the herbage of a diversity of vegetation types in the Southern Cape were found to be substantially higher in spring than in winter (Joubert *et al.* 1969). The digestibility of protein of fast growing tissues, such as are found during spring, is expected to be comparatively high (8.2.3; 8.3.4.3).

Bissonette's (1976) study of the collared peccary shows some similarities. The highest primary production of forbs occurred with the onset of spring and early summer rains and coincided with the farrowing peak. The high protein content of forbs and their palatability when actively growing, made them an ideal resource for lactating females.

- (II) The spring/summer period is the most advantageous for juvenile growth both nutritionally and energetically. Bushpig neonates are comparatively small (5.3.2). This has thermoregulatory implications (7.4.4) and it is noteworthy that altricial mammals typically have milk which is particularly rich in protein and fat (10.4.1.4). Juveniles under thermal stress or in negative energy balance will oxidize protein for the maintenance of thermal homeostasis, leading to growth impedence and lowered survival (9.4.2; 9.4.3). Thermally stressed suckling juveniles may also be a greater drain on maternal resources. If sows are overtaxed, an earlier cessation of lactation may possibly result (10.3.4; 10.4.1.4). Thus, both juvenile growth and maternal energetics may be involved, with possible implications for the survival of both, and for the chances of the sow rebreeding in the next season (10.4.1.4).
- (III) During pregnancy, increased amounts of energy are stored as subdermal fat (9.4.5). This has insulating value in winter, but may interfere with effective heat dissipation during periods of high ambient temperatures (7.3.2; 7.4.2.1). Accumulating subdermal fat in winter and losing it during lactation in spring thus has thermoregulatory advantages.
- (IV) Females should select a diet with a high energy/protein ratio during pregnancy, since it favours energy storage (9.4.3; 9.4.5). During lactation a high protein/energy ratio would best meet the

protein/phosphorus needs. Such a pattern is in accordance with plant phenology and food availability. A low dietary P/E ratio was found in autumn and winter (8.3.3.2). During this period pregnant females would be expected to take quantities of the carbohydrate-rich food items which are available. Such a foraging tactic could be facilitated by the greater efficiency in feed utilization during pregnancy (Den Hartog and Van Kempen 1980, Cole 1982) and may explain the greater crude fibre content of the diets of pregnant bushpig females (8.3.3.2). Conversely, a low dietary TPR associated with winter diets favours a low metabolic turnover rate which is not conducive to the efficient mobilization of stored energy reserves (8.3.4.3). This may be the reason for the relatively high energy retention of lactating sows in winter (10.3.4: Table 10/9).

It is not only the general matching of season and reproductive phase which is important, but also the fact that parturition occurs early in the optimal farrowing season. This ensures that sows have access to superior plant nutrient resources for lactation. In addition, there is sufficient time for full-length lactation and for reserve replenishment during the post-lactational anoestrus. Juveniles have a long period in which to grow before the onset of winter (cf Bunnell 1982, Clutton-Brock *et al.* 1982, Thomson and Turner 1982, Skogland 1983).

The relative importance of the various factors favouring seasonal breeding is uncertain. It appears that in larger, more homeostatic organisms, there is a premium on producing young at times when the food supply is near maximum for the year, rather than when physical environmental conditions are suitable (Giesel 1976). However, trophic maxima normally coincide with near optimal physical factors. Overall, selection pressures seem to have acted to fix all the phases of reproduction temporally in a way which is most advantageous to the survival of the species (Millar 1972).

In seasonally breeding mammals there seem to be three major patterns (Millar 1972):

- (I) In some species the male is capable of reproduction all year and the seasonal sexual activity in the female largely determines the mating season.
- (II) In the majority of species both male and female are sexually active during a fixed season and their sexual rhythms overlap to a greater or lesser degree.
- (III) In a few species the females are sexually active throughout the year and the males become sexually active only during the mating season (e.g. *Camelus*).

Seasonality or the absence thereof, in testis weight, spermatogenesis or steroid concentrations in male warthogs and European wild boar seems to parallel female reproductive seasonality. Where warthogs exhibit seasonal breeding, fluctuations in testis weight were recorded (Child *et al.* 1968, Mason 1982, 1986, Rodgers 1984). In marked contrast, Clough (1969) found no indication of a regular annual cycle among warthogs of either sex at the equator. Kozlo (1975) recorded seasonal changes in testis weight of European wild boar in Russia. Mauget (1980) recorded the highest testosterone levels in European wild boar in France during late autumn and winter, but the exocrine testis function persisted throughout the year. Whereas sows ovulate and may farrow at any time of the year, even outside the peak farrowing period, the boar is sexually potent all year round (Hennig 1981). In the domestic pig, which is reproductively non-seasonal, the maximum production of testicular steroids coincides with the natural mating season, i.e. autumn and early winter (Schopper *et al.* 1984). No evidence of any form of sexual seasonality was found in the male bushpig in contrast to the situation in females (10.3.5). Maintenance of the ability to breed outside the mating season may be related to maintenance of the dominance hierarchy and territorial behaviour (cf Millar 1972).

10.4.3 Reproductive turnover: an interspecific comparison

Mean litter sizes in various warthog populations ranged between 2,5 to 3,3 and the percentages of females farrowing in a given year between 72% and 98% (Child et al. 1968, Bosche 1981, Mason 1982, Rodgers 1984). Litter size was reported to be linked to nutritional condition (Mason 1982). Bushpig litter sizes were similar to those of warthog (10.4.1.3), but fertility rates tended to be lower (10.3.6.1). In the giant forest hog, D'Huart (1978) established a mean litter size of 2,5 with 46% of the females farrowing. He never observed more than one lactating female per group, although many groups contained more than one sexually mature female.

In the European wild boar, litter sizes are markedly influenced by maternal age and condition (Briedermann 1986):

European wild boar prenatal litter sizes

| | Mast years | Non-mast years |
|-----------|------------|----------------|
| Juveniles | 4,6 | 3,2 |
| Yearlings | 6,7 | 5,4 |
| Adults | <u>6,8</u> | <u>6,2</u> |
| Average | <u>5,6</u> | <u>5,0</u> |

Under fully natural conditions, i.e. no agriculture and little hunting, juvenile sows are virtually never pregnant and litter sizes are somewhat lower (Kozlo 1975 ex Briedermann 1986). The average litter size decreases from west to east with increasingly difficult ecological conditions. Reproductive rates decline most markedly in the younger females, whereas older sows are less affected (Briedermann 1986). Average litter sizes for selected populations ranged between 4,6 and 7,5 (De Vos and Sassani 1977, Stubbe and Stubbe 1977, Mauget 1980, Briedermann 1986).

The reproductive output of a population is largely determined by the proportion of females breeding. In Germany, the proportions of wild boar females breeding usually range between 30% - 60% in juveniles, 80% - 100% in yearlings and 90% - 100% in adults. Guideline estimates for the three age classes are taken as 35%, 80% and 90% respectively

(Briedermann 1986). Where supplementary feeding is practised 50% of the juvenile females and all yearling and adult sows may breed (Meynhardt 1980). Under natural and harsher conditions, juvenile sows do not normally breed while 31% of the yearling and 78% of the adult sows were reported to do so by Kozlo (1975 ex Briedermann 1986). In the same area the percentage of females breeding may fluctuate widely from year to year, e.g. 17% in one year and 90% in another, depending on food availability, (De Vos and Sassani 1977).

An index of the potential reproductive turnover may be calculated from the product of neonatal litter size and proportion of females farrowing, i.e. the number of young per annum and sexually mature female (Table 10/17).

| TABLE 10/17: REPRODUCTIVE POTENTIAL OF SELECTED SUID SPECIES (Neonatal litter size x farrowing proportion) | | | | |
|---|----------------------------------|----------------------|-------------------------------------|---|
| Species | Locality (Conditions) | Age class | Young born per female* | Authors |
| BUSHPIG | Southern Cape Eastern Cape | | 1,92 2,70 | (10.3.6.1) |
| WARTHOG | Tanzania Zululand Tanzania | | 2,26 3,17 2,59 | Bosche (1981) Mason (1982) Rodgers (1984) |
| GIANT FOREST HOG | Zaire | | 1,14 | D'Huart (1978) |
| EUROPEAN WILD BOAR | France | | 4,14 | Mauget (1980b) Briedermann (1986) |
| | <u>Germany:</u> | | | |
| | Unfavourable | Juvenile | 0,85 | |
| | | Yearling | 2,90 | |
| | | Adult | 4,80 | |
| | Average | Juvenile | 1,30 | |
| Yearling | | 4,00 | | |
| Adult | | 5,20 | | |
| Favourable | Juvenile | 1,90 | | |
| | Yearling | 5,30 | | |
| | Adult | 6,10 | | |
| Russia | Juvenile Yearling Adult | 0,01 1,00 4,00 | Kozlo (1975 ex Briedermann 1986) | |
| *All sexually mature females, unless age class is given | | | | |

The favourability of ecological conditions (Table 10/17) is largely a function of food availability, notably the occurrence or absence of mast fruiting. Reproductive rates in the European wild boar deviates above or below mean values by approximately 40% in juveniles, 25% in yearlings and 10% in adults (Briedermann 1986). They are about twice as high as in the bushpig (Table 10/17).

10.4.4 Determinants of reproductive success

10.4.4.1 Reproduction and food availability in suids

Many studies of ungulates have shown that reproductive performance is related to the mother's condition or to factors which affect this (Sadleir 1969, Caughley 1977). Field studies of collared peccaries, *Tayassu tajacu*, have shown substantial decreases in herd recruitment during periods of below-average rainfall, presumably as a result of decreased food quantity and quality (Low 1970, Bissonette 1976, Bissonette 1982 ex Lochmiller et al. 1986). Under experimental conditions in captivity, behavioural oestrus, ovarian morphology and incidence of pregnancy in collared peccaries reflected a general cessation of reproductive activity in response to poor nutrition (Lochmiller et al. 1986). Reproductive rate was similarly related to food availability in the warthog (Cumming 1975, Mason 1982).

A higher reproductive output when food is abundant (e.g. after oak or beech masts) in free-ranging *Sus scrofa* has been reported by numerous authors: Kozlo (1970), Henry and Conley (1972), Pine and Gerdes (1973), De Vos and Sassani (1977), Graves and Graves (1977), Hennig (1981) and Briedermann (1986). Much of the relatively high reproductive rate of European wild boar in Western Germany, or Western Europe generally, is based on access to agricultural crops (Hasselbach 1970, Briedermann 1986). The role of food in determining the reproductive output in the domestic pig, has been studied exhaustively (e.g. Duncan and Lodge 1960, Anderson and Melampy 1972, Lodge 1972, English et al. 1977). O'Grady et al. (1973) and Rattray (1977), among others, emphasised the importance of dietary energy for reproductive success.

Apart from nutritional effects generally, the important role of proteins in pig production has been discussed by many authors (*inter alia*: Duncan and Lodge 1960, McDonald *et al.* 1973, Baker *et al.* 1970, Elsley and McPherson 1972, Svajgr *et al.* 1972, Mahan and Grifo 1975, Mahan and Mangan 1975, Hammell *et al.* 1976, English *et al.* 1977, Mahan 1977, Anderson 1980). Some of their more important findings are listed below:

- (I) Continued protein deficiency in the diet for longer than one reproductive cycle markedly impaired the subsequent reproductive efficiency of sows, as measured by incidence of oestrus, interval from weaning to oestrus and ovulation rate.
- (II) The restriction of dietary protein during gestation can impede not only initial milk secretion, which can affect neonatal survival, but also subsequent milk production and weight gains of the progeny.
- (III) Adequate milk yield is dependent on the protein level in the diet during lactation. Litter gains and weights at weaning were enhanced by high protein levels.
- (IV) Differences in milk production following low protein levels during pregnancy only became apparent towards the end of lactation, reflecting gradual catabolism of maternal protein reserves.
- (V) Adequate intakes of protein are required during lactation in order to ensure the rapid onset of oestrus and ovulation after weaning. Dietary protein during lactation is thus critical in determining the rebreeding interval.

Protein quality is also involved. Fowler and Robertson (1954 *ex* Hughes 1982) reported that gilts fed protein of animal origin reached puberty significantly earlier than counterparts fed plant protein. This suggests that amino acid balance plays a role. A ration of equal parts of ground oats and barley with 1% each of salt and limestone was given to sows for 5 breeding seasons by McElroy and Draper (1950 *ex* Duncan and Lodge 1960). On the average such sows produced 2,7 fewer live pigs per litter than controls given a ration containing protein partly of animal origin.

Bushpig reproduction and food resources will be examined in the next section (10.4.4.2).

10.4.4.2 Food resources and regional differences in reproduction

Populations of Columbian ground squirrels (*Spermophilus columbianus*) at high altitudes, known to have lower levels of food availability than low altitude populations, had smaller litter sizes, fewer lactating females, females maturing later, but juveniles and adults surviving better (Dobson 1985). The causal link between these reproductive and life history features and the availability of food resources was verified experimentally. Protein supplementation resulted in increased litter sizes, greater proportions of lactating females, earlier sexual maturation and improved juvenile and adult survival (Dobson 1985). Strikingly similar trends were found in the reproductive parameters of Eastern and Southern Cape bushpig populations (10.3.3; 10.3.6.2).

- (I) Southern Cape prenatal litter sizes tended to be smaller than those in Eastern Cape populations (3,0 versus 3,6 but statistically non-significant).
- (II) The percentage of reproductive females was lower in the Southern Cape (41% versus 61%).
- (III) The percentage of lactating females was lower in the Southern Cape (25% versus 71%).
- (IV) The percentage of cases with two generations of young per group was also lower in the Southern Cape (9% versus 27%).
- (V) The likelihood of breeding clearly increased with age in the Southern Cape, but this trend was only poorly developed in Eastern Cape bushpig females.
- (VI) Survival of both juveniles (10.4.1.3) and adults (11.2.4) appeared to be higher in the Southern Cape.

It is suggested that these differences in reproductive parameters are related to differences between the regions in the availability of dietary protein and possibly also phosphorus (8.3.4.3).

Differences in reproduction of red grouse (*Lagopus lagopus scoticus*) on poor and rich Scottish moors (Miller *et al.* 1966, Moss *et al.* 1975) provide another striking analogy to the regional reproductive differences in the bushpig.

Rich moors were found to overly base-rich rocks such as limestone, diorite and epidiorite and poor moors were over acidic rocks, such as granite. The heather (*Calluna vulgaris*) on the rich moors contained more nitrogen and phosphorus. Rich moors sustained high mean grouse densities which fluctuated relatively little from year to year. On average, the grouse on the rich moors bred better and their breeding success varied less than on poor moors. Average breeding densities were correlated with the quality and age of the heather on poor and intermediate moors and were exceptionally high in relation to the amount and age of the heather on rich moors. A long period of growth in nitrogen content favoured good breeding in grouse and fluctuations in breeding success from one spring to the next were correlated with heather growth (Miller *et al.* 1966, Moss *et al.* 1975). In an experiment Miller *et al.* (1970) showed that fertilization of a heather moor with calcium ammonium nitrate increased the productivity and nitrogen content of heather and the red grouse living there bred better.

It is suggested that superior reproductive performance on base-rich substrates (grouse on rich moors, bushpigs in the Eastern Cape), is primarily the result of higher protein availability in these environments. This may be related to one or more of the following: higher protein content of the vegetation; higher protein digestibility since plants grow faster and are less defended chemically where mineral levels are high; higher populations of vertebrates and invertebrates serving as supplementary sources of protein to herbivores (8.2.3; 8.2.4; 8.3.4.2; 8.3.4.3). The lack of sufficient phosphorus may be an additional problem in nutrient poor environments. As noted by Maynard *et al.* (1979), deficiencies of vitamin A, protein or trace elements are also involved in some of the reproductive problems in phosphorus-deficient areas.

10.4.4.3 Body condition, social status and reproductive success

Intensive studies of red deer, *Cervus elaphus*, have revealed interactions between condition, social factors, fecundity and survival (Clutton-Brock *et al.* 1982). The possibility of similar interactions in other mammals and the bushpig is discussed in this section.

Fecundity in red deer hinds was closely correlated with measures of body condition, which depended on the quantity and quality of resources in the maternal home range. Lower Kilmory red deer hinds, with a relative abundance of good grazing, showed high fertility, in contrast to Shamhnan Insir hinds. Hinds at Shamhnan Insir which calved as 3-year olds and succeeded in raising their calves into the winter never calved again the following year, whereas they commonly did so at Kilmory. The fecundity in hinds of 5 years old or older did not differ significantly between the two areas (Clutton-Brock *et al.* 1982). Mitchell *et al.* (1976) also found that red deer hinds in nutritionally poor environments bred in alternate years. Munding (1981) considered alternate-year breeding typical for nutritionally stressed populations. The costs of reproduction were also reflected in the consistently higher age-specific mortality rate of milk hinds compared with yeld hinds. These differences in survival were most pronounced among young and old animals (Clutton-Brock *et al.* 1983). Reduced maternal body condition, survival and fecundity as a consequence of successful reproduction was also shown for several other iteroparous vertebrates studied (Clutton-Brock *et al.* 1983).

The findings of the present study show that bushpig reproduction has many parallels. Sows in poor physical condition had lower conception rates (10.3.6.2). The costs of reproduction were reflected in loss of maternal body condition (10.3.4). The failure to breed in successive years is more pronounced in nutritionally less favourable areas, as reflected by the significantly lower percentage of two generations of young per group in Southern Cape bushpigs (10.3.6.2). However, social dominance interacts with food availability in determining reproductive success. Only territorial, pair-bonded bushpig sows participate in successful breeding. In the Southern Cape, the chances of attaining this status is age-dependent (10.3.6.1; 10.3.6.2).

The mean reproductive success of red deer hinds in larger female groups was lower than in smaller groups (Clutton-Brock *et al.* 1982). The lower reproductive success of members of large groups was partly a consequence of an increase in their age at first breeding, but differences in calf mortality were also involved (Clutton-Brock *et al.* 1983). The breeding of juvenile and to some extent even yearling European wild boar females is considered to be the result of an artificial age structure and largely atypical of natural populations (Stubbe 1971, Stubbe and Stubbe 1977). According to these authors, shooting of older individuals disrupts the age structure to such an extent that sows of all age classes start to breed. It is postulated here that the shooting of older, more dominant individuals leads to a breakdown of the age-graded dominance hierarchies, which would otherwise have prevented the younger, subdominant females from participating in successful reproduction. These younger age classes are usually numerically dominant and if their members breed, this has far-reaching effects on the reproductive turnover. Both food availability (body condition) and social status appear to exert an interdependent effect. Social factors are apparently more stringent under nutritionally unfavourable circumstances.

Many bushbuck hunters maintain that the shooting of old rams causes an increase in reproduction, which they attribute to the removal of senile males. Rather, this effect may be related to the phenomenon discussed above. Removal of old, dominant rams may result in smaller groups in which the effect of age-graded female dominance in regulating reproduction in subordinate females is reduced.

The chances of becoming involved in reproduction increases with age of the surviving bushpig females (10.3.6.1; 10.3.6.2). This is evidently linked to increasing chances of establishing a territory, ensuring pair-bonding with a male and acquiring adequate food resources for reproduction. The positive relationship between age and reproduction is prominent in the Southern Cape but virtually absent in the Eastern Cape. This is attributed to homogeneity of habitat quality in the Eastern Cape, resulting in territorial saturation. Under such circumstances most surviving females are territorial and pair-bonded. In the Southern Cape we have a wider gradient of habitat quality. The less competitive,

younger females survive in the non-territorial poorer habitat, territorial interstices or as "floaters" (4.3.2).

Whereas in the Eastern Cape the percentages of pregnant and lactating females were of a similar order of magnitude, in the Southern Cape the proportion of lactating females was considerably lower (10.3.6.2). This suggests that reproductive success was lower in relation to the number of pregnant females. Females in good enough condition during the mating season presumably ovulate and conceive, even though they may not yet have attained a secure territorial status. If they cannot sustain body condition (10.4.1.2), because food resources are inadequate, or if they cannot maintain a stable pair bond or are defeated during aggressive encounters, such females abort. Neonates may be deserted following mate desertion. This was observed when a near-term bushpig sow, together with the boar to which she was pair-bonded, was released from enclosure B into foreign terrain. Both had been radio-collared for some time. Shortly after release the male deserted the sow and she in turn deserted the neonates (5.3.2.3).

Even after giving birth the female who bears altricial young has the option of killing and eating her young in response to adverse environmental circumstances. In the latter phases of gestation she can abort and devour the litter, thus recycling the nutritional resources (Eisenberg 1983). The mechanisms and interactions resulting in either abortion or desertion are not well understood.

When food resources are limited, there appears to be increasing segregation of bushpig individuals (4.3.1.3). Pair bonds are probably unlikely to be established or sustained. In the absence of a functional pair-bond, abortion or litter desertion may occur.

In the red fox, *Vulpes vulpes*, studied by Von Schantz (1981), most adult females, dominants as well as subordinates, become pregnant, but beta females do not raise their cubs. Studies on captive foxes indicated that abortion or desertion by beta females might be caused by social interactions with the alpha female (Macdonald 1979).

Removal of older, dominant individuals in the European wild boar results in younger, subdominant females starting to breed earlier, given adequate body condition (cf Stubbe and Stubbe 1977). Such interference may lead to population growth. In the bushpig, removal of alpha females merely results in their replacement by non-territorial individuals, but not in the successful reproduction of non-territorial females.

In conclusion, physical condition apparently determines the physiological readiness for reproduction in bushpig females, but socio-spatial status is central to rearing success. A corollary is that productivity indices based on pregnancy rates under the conditions prevailing in the Southern Cape may be overestimates.

10.5 Synopsis

- (I) Sexual maturity in the bushpig male is attained at 16 - 20 months of age. Most females reach sexual maturity between 17 and 22 months. Due to factors of social position and condition, successful breeding may only occur much later. There was no evidence of reproductive senescence (10.3.1).
- (II) Survival of concepti was lower in Southern Cape than in Eastern Cape bushpig females (10.3.2.3). This was also reflected in the lower prenatal litter size. The overall mean prenatal litter size was 3,2 (Southern Cape: 3,0; Eastern Cape: 3,6). Prenatal development closely resembled that in the European wild boar and foetal age classes were defined accordingly. Foetal mass was highly variable within litters (10.3.3).
- (III) The duration of lactation in captivity was 5,5 months, but it appeared to be shorter under free-ranging conditions and vary according to food availability. Bushpig milk was found comparatively rich in protein and fat (10.4.1.4). The nutrient/energy costs of lactation were significantly related to its duration and to litter size (10.3.4).
- (IV) Males exhibited no seasonality in sexual activity but a clear farrowing peak was evident in spring, with seventy-four percent of all births occurring during September, October and November

(10.3.5). The seasonal cycle apparently serves to correlate the nutritional and energetic requirements of mother and young during gestation and lactation with seasonal pulses of nutrient availability and energetic demands (10.4.2).

- (V) During August to December 64% of females from the Southern Cape and 75% of those from the Eastern Cape were pregnant or lactating. Only pair-bonded, territorial sows reared young successfully (10.3.6.1). Reproductive rates were higher in the Eastern than in the Southern Cape and in older compared to younger sexually mature females in the Southern Cape. Females in poor body condition showed a lower incidence of breeding (10.3.6.2).
- (VI) The reproductive potential of the bushpig was found to be approximately half that of the European wild boar and was of the order of 2 - 3 young born/sexually mature female and year (10.4.3). It is suggested that regional differences in fertility and reproductive success are a consequence of the limited availability of digestible protein and possibly also of phosphorus in the Southern Cape. These in turn were related to the effects of plant life history tactics and the generally lower carrying capacity of nutrient poor environments for vertebrates (10.4.4). Interesting inter-relationships between maternal body condition, age, sociospatial status, home range quality gradients and reproductive success were pointed out (10.4.4.3).
- (VII) Breeding bushpig females in the Southern Cape were fatter (10.3.2.3; 10.4.1.3), while Eastern Cape females were smaller (9.3.3.1) and leaner (10.3.2.3), but exhibited higher fecundity. These seemingly paradoxical reproductive tactics are interpreted in the context of life history strategies in Chapter 12.

11. POPULATION DYNAMICS

11.1 Introduction and methods

The dynamics of bushpig populations are influenced by most of the factors dealt with in previous chapters (social organization: 4, habitat use: 6, energetics: 7, 8, 9 and reproduction: 10) and are an integral part of the species' life history tactics (12). Knowledge of population dynamics is also of direct relevance to management (13).

Population dynamics involve the numerical response of populations to environmental factors over space and time. It was difficult to obtain enough data to differentiate between spatial and temporal components. The low densities at which bushpigs occurred and the difficulties of observing them in thick cover and at night limited the extent of data which could be obtained. When pooled over time (years), sufficient data were available for regional comparison, but pooling over space did not provide meaningful and sufficient data to describe population changes over time.

The capture programme (1.3.1) allowed population densities in two areas (Goudveld and Diepwalle) to be reconstructed. The value of fecal pellet group counts as indices of population density was investigated. The capture programme, as well as various other opportunistic observations, provided some information on mortality patterns. Data on population structure (age and sex classes) became available from capture (1.3.1) and post-mortem sampling (1.3.2).

The extent of the data over time was limited, but by pooling it, information on regional differences in population dynamics became available. Data on density and mortality factors, as well as on fecundity (10.3.6), provided a crude measure of population turnover adequate for management and other purposes. The population features and regional differences which were identified raised issues concerning patterns of population regulation and life history tactics which are discussed below.

11.2 Results

11.2.1 Abundance

Intensive capture/recapture operations over 8 600 ha on Goudveld and 5 200 ha on Diepwalle (1.3.1.1) made it possible to reconstruct the bushpig populations of these areas. That of Goudveld, as on 1.1.1981, is shown below. The area was traversed by capture operations within the course of 12 months. It is assumed that no substantial, population increases or decreases had occurred within this period (sex and age indication in years; M: male, F: female, J: juvenile, Y: yearling).

- CAI (M:9,3)
- * CBI (M:3,6) CB2 (F:±5) CB3 (?Y) CB4 (?Y)
- * TD4 (F:10,7) TD5 (M:7,7) TD6 (M:J) TD7 (M:J) CD1 (F:Y)
CD2 (M:Y) CD3 (M:Y)
- * CC1 (F:J) CC2 (F:10,5) CC3 (M:7,3)
- * CE1 (F:2,5) CE2 (M:12,0)
- * CF1 (F:Y) CF2 (M:Y) CH1 (M:7,0)
- * CG1(M:10,8) CG2 (F:Y) + CK2 (F:± 10) CII (M:Y)
G13 (M:10,7)
CJ1 (F:±4)
CK1 (F:11,5)
M7 (F:14,5)
- * CL1 (F:10,0) CL2 (F:J) CL3 (F:J) CL4 (M:J) CL5 (M:9,5)
CM1 (M:7,3)
CN1 (M:1,9)
- * CO1 (F:J) CO2 (F:10,4)
- * CP2 (M:±3) CS1 (M:2,7) M10 (F:10,8)
- * CU1 (M:14,8) CU6 (F:±10)

Asterisks indicate groups associated with family territories. If the 10 family territories, with an average size of 720 ha each (6.2.1.1), are assumed to be fully contiguous, the 44 bushpigs inhabited approximately 7 200 ha, resulting in a density estimate of 0,51/km². The pre-farrowing estimate (1.10.1980) is $44 - 5 \div 72 = 0,45$ bushpigs/km². However, territories were not contiguous (4.3.2). The capture area of 8 600 ha was bounded to the north by the Outeniqua mountain crest and on the eastern and western sides by the Knysna and Homtini river gorges.

Radio-tracking studies indicated that these topographical obstructions, although they did not constitute total barriers to movement, tended to coincide with territory boundaries (4.3.2). On the southern boundary of the capture area, edge effect had to be accommodated. The mean width of a 720 ha territory, taken as a square, is 2,7 km. Edge effect was accounted for by adding an area the size of half a territory along the length of the southern boundary of the capture area, i.e. $0,5 \times 2,7 \times 8,2 \text{ km} = 1\ 100 \text{ ha}$. Accordingly, the 44 bushpigs, occupied an area of $8\ 600 + 1\ 100 = 9\ 700 \text{ ha}$, giving $0,45 \text{ bushpigs/km}^2$ and a pre-farrowing density of $0,40/\text{km}^2$.

The Goudveld population was again reconstructed three years later, to the date 1.1.1984, when the density was $0,35 \text{ animals/km}^2$ (pre-farrowing density: $0,31/\text{km}^2$). These estimates were similar to those obtained for Diepwalle State forest. The Diepwalle population, as on 1.1.1983, consisted of the following groups and individuals:

- * DA1 (F:11,8)
D13 (M:3,4)
- * DC1 (M:8,3) and yearlings DM2, DM3, DM4
- * DB1 (F:12,0) DB2 (adult M)
- * DD1 (M:6,2) DD3 (adult F)
- * DG1 (F:3,1)
- * DE1 (M:3,0) DE3 (F:7,5)
DF1 (M:3,0)
- * DI1 (F:11,7) DJ1 (M:4,1) and juveniles DJ2, DJ3
DK1 (M:±3)

Asterisks again indicate territory-holders. On the basis of 7 non-overlapping home ranges (territories) of 722 ha (6.2.1.1), density estimates of $0,38$ (overall) and $0,34$ (pre-farrowing) bushpigs/ km^2 resulted.

Faecal pellet groups are the only signs of bushpig presence of sufficient visibility and abundance to be considered as potential indices of population density. The distribution of pellet groups is however not random. In the study area they were concentrated on slippaths running through the indigenous forests. The results of pellet

group counts exhibited large annual variability in spite of using relatively long sample strip distances.

| | | Pellet groups/km | Distances sampled (km) |
|------|-----------|------------------|---------------------------|
| 1978 | Goudveld | 35,8 | 15,0 |
| | Diepwalle | 30,6 | 8,6 |
| 1980 | Goudveld | 13,9 | 11,9 |
| 1982 | Goudveld | 19,0 | 21,3 |
| | Diepwalle | 21,9 | 15,2 |
| 1983 | Goudveld | 18,3 | 13,7 |
| | Diepwalle | 6,5 | 15,2 |
| 1984 | Goudveld | 28,1 | 20,0 |
| 1985 | Goudveld | 18,4 | 11,6 |

During 1979 about 50 bushpigs were shot south of Goudveld but this declined to only 8 in 1980 and 6 and 1981. This coincides with a population peak prior to and including 1979 reported by local hunters. The subsequent decline thereafter is crudely reflected by the pellet group densities shown above.

Pellet group density indices were variable and rather problematic as indices of population density for a number of reasons:

- (I) Pellet groups were found to have a distinctly non-random distribution. Concentrations occurred in open patches (5.1.2.1), notably slippaths, canopy gaps with little ground vegetation and roads. This creates problems for representative sampling, particularly when comparing different vegetation types.
- (II) Rates of pellet decay varied over sites with different microclimates and over time according to weather pattern. Pellet groups disappeared within a month or lasted longer than six months. Moisture greatly accelerated rates of decay.
- (III) The disappearance of pellet groups was variably influenced by invertebrate activity, which differed over sites.

Population density estimates for Eastern Cape bushpigs did not become available during this study. In one instance, 16 animals from at least 4 family groups were shot within two months in an area of 600 ha of Valley Bushveld. Take-offs of this magnitude were not recorded in the Southern Cape, suggesting higher population densities in the Eastern Cape.

11.2.2 Fecundity

The fecundity rate of a female is measured as the number of live births she produces over an interval of time, generally one year (Caughley 1977). Litter size appeared to be independent of female age in the bushpig, but the proportion of females breeding was higher in older females (10.3.6.2). The mean fecundity parameters, pooled over age classes, were as follows (10.3.6.1):

| | Proportion of females breeding | Litter size |
|-------------------------|--------------------------------------|-------------|
| Southern Cape | 0,64 | 3,0 |
| Southern Cape foothills | 0,53 | 3,0 |
| Eastern Cape | 0,75 | 3,6 |

In a fecundity table, fecundity rates are given per age class. The litter sizes used in Table 11/1 represent the mean foetal litter sizes during pregnancy, i.e. the pre-natal litter size at mid-pregnancy. This should be a realistic estimate of live births, since there was little evidence of intra-uterine mortality during the latter half of pregnancy (10.3.2.3).

The fecundity rate (m_x) is the age-specific birth rate and is most often expressed as the average number of female offspring (assuming 50% females) born to each female of each age class (Caughley 1977). For the fecundity rates defined in this way, the m_x -values of Table 11/1 must be divided by two. Age class, as well as regional, differences in fecundity rates were evident (Table 11/1).

| TABLE 11/1: FECUNDITY TABLE FOR BUSHPIG FEMALES IN THE SOUTHERN AND EASTERN CAPE | | | | | | | | |
|--|-----------------------|-----------------------------|------|-----------------------------|------|--------------|-----------------------------|------|
| AGE CLASSES (Years) | SOUTHERN CAPE | | | | | EASTERN CAPE | | |
| | Plateau and foothills | | | Foothills | | Litter size | Proportion females breeding | mx |
| | Litter size | Proportion females breeding | mx | Proportion females breeding | mx | | | |
| 0 - 1 | - | 0 | 0 | 0 | 0 | - | 0 | 0 |
| 1 - 2 | - | 0 | 0 | 0 | 0 | - | 0 | 0 |
| 2 - 3 | 3,0 | 0,49 | 1,47 | 0,35 | 1,05 | 3,6 | 0,53 | 1,91 |
| 3 - 4 | 3,0 | 0,49 | 1,47 | 0,35 | 1,05 | 3,6 | 0,53 | 1,91 |
| 4 - 5 | 3,0 | 0,49 | 1,47 | 0,35 | 1,05 | 3,6 | 0,86 | 3,10 |
| 5 - 6 | 3,0 | 0,49 | 1,47 | 0,35 | 1,05 | 3,6 | 0,86 | 3,10 |
| 6+ | 3,0 | 0,88 | 2,64 | 0,70 | 2,10 | 3,6 | 0,86 | 3,10 |

mx: mean live births per female per annum

11.2.3 Mortality

Starvation, inclement weather and predation were responsible for juvenile and yearling mortality. Pre-weaning juvenile mortality in the study enclosure was associated with thermoregulatory stressful periods in most cases (5.3.2.4). Bushpig bones have been collected below Crowned Eagle (*Stephanoqetus coronatus*) nests in the Southern (Boshoff 1982; unpublished data) and Eastern Cape (Jarvis, Currie and Palmer 1980). The mandibles from the Southern Cape nests belonged to individuals 2 to 3 months old. A verified case of leopard predation on a bushpig yearling is on record for the Southern Cape study area. Of the 12 cases of verified adult mortality in the intensive study area, specifically Goudveld, starvation (n = 5), intraspecific strife (n = 4) and control measures by farmers (n = 3) were the causes. All 4 recorded cases of mortality due to intraspecific strife were of females (CF1, CI2, CO2, CW5).

Links between external parasite loads and mortality were not specifically investigated nor noticed. From bushpig skin samples, ticks (*Rhipicephalus simus* and *Ixodes pilosus*) and lice, *Haemotopinus latus*, were identified at the Regional Veterinary Laboratory, Stellenbosch.

The intensive capture programme (11.1) on Goudveld State forest was used to estimate mortality rates. The recorded number of deaths or disappearances is divided by the total exposure time, i.e. the total time that individuals were both under observation and alive (cf Bart and Robson 1982). It is not always known whether individuals that disappeared actually died or dispersed, nor is the exact time of death known of those who did not survive. The amount of time that they were exposed to the risk of death can not thus be determined precisely. Twenty-five bushpigs older than 2 years were under observation during the capture programme for altogether 417 months, i.e. the sum of their first to last capture intervals. Of these, 10 were known to have died, 6 disappeared, i.e. either died or dispersed, and 9 definitely survived the entire exposure period. The minimum adult mortality rate may thus be estimated as $10 \text{ deaths} \div 34,75 \text{ animal years of exposure time} = 29\%$. A maximum adult mortality rate may be estimated on the assumption that all 6 individuals which disappeared actually died. The capture area was covered once a year, and if each of the 6 individuals was taken to have died, on average, six months after the last capture, the total exposure period would amount to $34,75 + 3,00 = 37,75 \text{ animal years}$. The maximum mortality rate estimate then is $16 \div 37,75 = 42\%$.

Of 17 recruits to the yearling age class, 4 died before the age of 2 years. This corresponds to a yearling mortality rate of 24%.

Litter size at birth was only known in a few cases and it was therefore not deemed possible to determine the juvenile mortality rate reliably by contrasting juvenile disappearance with the "observation" period. Most litters were recorded at variable time periods after parturition. Observations therefore did not cover the period when the highest juvenile mortality is expected. Total litter losses also remained undetected.

The age class frequency distributions for bushpig populations in the study area are presented in Table 11/2. In no case did they differ between the sexes (Southern Cape foothills: $G = 7,42 \text{ df} = 10 \text{ NS}$; Southern Cape plateau: $G = 6,52 \text{ df} = 12 \text{ NS}$; Southern Cape: $G = 12,36 \text{ df} = 13 \text{ NS}$; Eastern Cape: $G = 5,68 \text{ df} = 10 \text{ NS}$).

relatively high proportion of animals in these upper age classes in the Southern Cape population (Table 11/2).

Valid life tables can only be compiled from the age distribution of populations when they are stationary. Stationary age distributions result when the populations do not change in size and where their age structures are constant over time (Caughley 1966, 1977). These conditions or assumptions are seldom completely fulfilled in wildlife studies. Even so, the life tables constructed from the data presented in Table 11/2 (standing age distributions) are believed to be of some value in obtaining a crude idea of overall mortality patterns and possible differences in survivorship between populations.

Following Caughley (1977), the following statistics and symbols were used in compiling the life tables (Tables 11/3 and 11/4).

| | |
|--|-------|
| Age | x |
| Number surviving at each age x | f_x |
| Probability at birth of surviving to age x | l_x |
| Probability of dying in each age interval x, x + 1 | dx |
| Mortality rate (dx/l_x) | q_x |
| Survival rate ($1 - q_x$) | p_x |

The age class frequencies of Table 11/2 for the Southern and Eastern Cape were graphically smoothed for the frequencies of animals one year and older. The number surviving at each age were read off from the smoothed curves, whereas the observed frequencies in Table 11/2 represent the survival probabilities at the age class midpoints. The number surviving at age 0 years, i.e. the number of live births, was calculated from fecundity rates (Table 11/1) and the number of females in the sampled populations (Table 11/2). The juvenile litter size (10.3.6.1) representing survival at age 0,5 years, was included as a data point for the smoothed curve.

TABLE 11/3: LIFE TABLE FOR SOUTHERN CAPE BUSHPIGS (1978 - 1986)

| Age (years) x | Adjusted frequency f | Survival l_x | Mortality dx | Mortality rate qx | Survival rate px |
|---------------------|----------------------------|-------------------|-----------------|-------------------------|------------------------|
| 0 | 194 | 1,000 | 0,485 | 0,485 | 0,515 |
| 1 | 100 | 0,515 | 0,211 | 0,410 | 0,590 |
| 2 | 59 | 0,304 | 0,113 | 0,372 | 0,628 |
| 3 | 37 | 0,191 | 0,062 | 0,325 | 0,675 |
| 4 | 25 | 0,129 | 0,036 | 0,279 | 0,721 |
| 5 | 18 | 0,093 | 0,011 | 0,118 | 0,882 |
| 6 | 16 | 0,082 | 0,005 | 0,061 | 0,939 |
| 7 | 15 | 0,077 | 0,010 | 0,130 | 0,870 |
| 8 | 13 | 0,067 | 0,005 | 0,075 | 0,925 |
| 9 | 12 | 0,062 | 0,010 | 0,161 | 0,839 |
| 10 | 10 | 0,052 | 0,006 | 0,115 | 0,885 |
| 11 | 9 | 0,046 | 0,010 | 0,217 | 0,783 |
| 12 | 7 | 0,036 | 0,010 | 0,278 | 0,722 |
| 13 | 6 | 0,031 | 0,005 | 0,161 | 0,839 |
| 14 | 4 | 0,021 | 0,010 | 0,476 | 0,524 |
| 15 | 3 | 0,015 | 0,005 | 0,333 | 0,667 |
| 16 | 2 | 0,010 | 0,005 | 0,500 | 0,500 |
| 17 | 1 | 0,005 | | | |
| 18 | 1 | 0,005 | | | |

TABLE 11/4: LIFE TABLE FOR EASTERN CAPE BUSHPIGS (1982 - 1984)

| Age (years) x | Adjusted frequency f | Survival lx | Mortality dx | Mortality rate qx | Survival rate px |
|------------------|-------------------------|----------------|-----------------|----------------------|---------------------|
| 0 | 110 | 1,000 | 0,555 | 0,555 | 0,445 |
| 1 | 49 | 0,445 | 0,218 | 0,490 | 0,510 |
| 2 | 25 | 0,227 | 0,091 | 0,401 | 0,599 |
| 3 | 15 | 0,136 | 0,036 | 0,265 | 0,735 |
| 4 | 11 | 0,100 | 0,027 | 0,270 | 0,730 |
| 5 | 8 | 0,073 | 0,009 | 0,123 | 0,877 |
| 6 | 7 | 0,064 | 0,009 | 0,141 | 0,859 |
| 7 | 6 | 0,055 | 0,010 | 0,182 | 0,818 |
| 8 | 5 | 0,045 | 0,009 | 0,200 | 0,800 |
| 9 | 4 | 0,036 | 0,000 | 0,000 | 1,000 |
| 10 | 4 | 0,036 | 0,009 | 0,250 | 0,750 |
| 11 | 3 | 0,027 | 0,009 | 0,333 | 0,667 |
| 12 | 2 | 0,018 | 0,009 | 0,500 | 0,500 |
| 13 | 1 | 0,009 | | | |

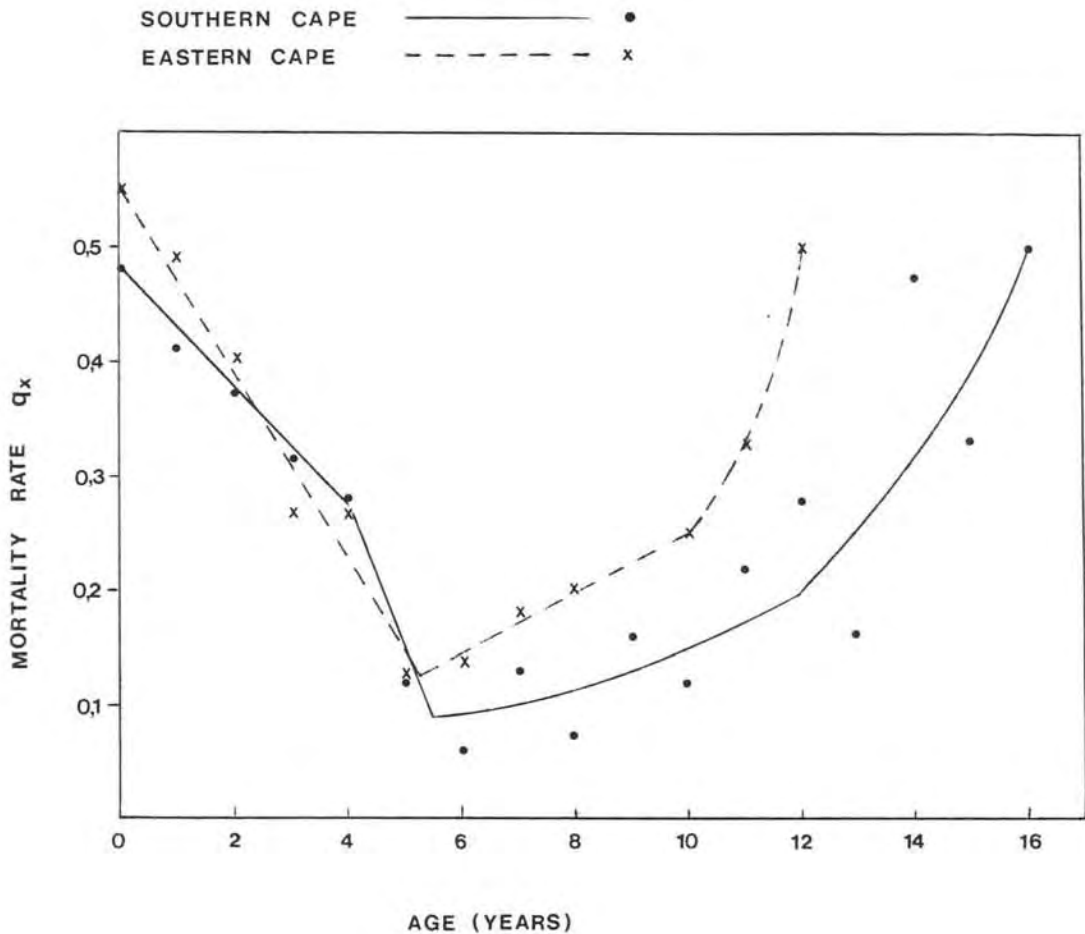
The mean mortality rates of individuals older than 2 years were 19% for the Southern Cape foothills population, 24% for the Southern Cape overall and 27% for the Eastern Cape. The patterns of age-specific mortality reflected by the data differ substantially between the Southern and Eastern Cape (Fig. 11/1).

The mortality rates determined for the Southern Cape foothills population according to the age structure of live individuals in the population (life table analysis) and from capture data (the Goudveld study population being part of the foothills population) differ substantially.

Mortality rates (%)

| Age classes in years: | 0 - 1 | 1 - 2 | 2+ |
|-----------------------|-------|-------|----|
| Life table analysis | 47 | 45 | 19 |
| Capture data analysis | ? | 24 | 35 |

FIG.11/1: MORTALITY PATTERNS IN BUSHPIGS
 (plotted against the start of the age interval)



These discrepancies are explained as follows: the capture data values are taken to reflect the situation during the actual period of sampling, at which time a population decline occurred (0,45 to 0,35 animals/km²: 11.2.1). The life table analysis, on the other hand, is a product of the age structure of the sampled population. The age structure is however the result of the dynamics of the population over some period prior to sampling.

11.2.4 Comparative population parameters

The data indicate that bushpig from the three regions studied may be clearly differentiated on the basis of population characteristics. Their population parameters are compared in Table 11/5.

| table 11/5: bushpig population parameters summarized | | | |
|--|-------------------------------|-----------------------------|-----------------|
| parameters | southern cape foothills | southern cape overall | eastern cape |
| sex ratio (2 years +) : males/females | 1,13 | 1,07 | 0,78 |
| mean fecundity (2 years+) : mx | 1,59 | 1,92 | 2,70 |
| proportion females breeding (2 years+) | 0,53 | 0,64 | 0,75 |
| life expectancy at birth | 2,6 | 2,8 | 1,8 |
| generation length t* | 8,1 | 6,6 | 5,4 |
| juvenile mortality rate | 0,47 | 0,48 | 0,55 |
| yearling mortality rate | 0,45 | 0,41 | 0,49 |
| mean mortality rate (2 years+) | 0,19 | 0,24 | 0,27 |
| *t: mean lapse of time between a females date of birth and the mean date of birth of her offspring (caughley 1966) | | | |

The three populations exhibit divergent trends in respect of fecundity and survival parameters and sex ratios. These will be referred to below in the context of life history tactics (11.3.4,12).

11.3 Discussion

11.3.1 Population density estimation

Most wild suid species are difficult to count because of their habitat preferences and low densities. Consequently, few actual censuses of wild pigs over large areas have been successfully carried out (Barrett 1982).

The mark-recapture method is decidedly useful where live trapping is feasible (Barrett 1982) and also accurate if sufficient data can be obtained. This is a function of trapping input and population density. Unless virtually the entire population can be recorded in this way, as in this study, mark-recapture estimates usually incorporate closed population models. The major problem then involves a compromise between

sample size and the assumption of a closed population. The time interval during which there are no births or deaths requires that the entire sampling procedure be accomplished within a few months at the longest. Unless densities are high, the sample sizes associated with tagging of low density species are accordingly usually too small (cf De Master *et al.* 1980).

Giffin (1974) found the strip count method, using dogs to flush the pigs, accurate and practical in the rain forests of Hawaii, but feral pig densities there exceeded 25 animals/km². Indices of abundance based on the extent of signs left by the animals, like tracks and faeces, have been used, but were mostly poorly correlated with actual densities determined independently (Barrett 1982). However, wild boar track counts in snow were usefully correlated with drive count estimates by Pucek *et al.* (1975) and Dzieciolowski (1976).

Koster and Hart (1988) investigated the potential of pellet group counts, drive counts and track counts to estimate the abundance of *Cephalophus* spp in tropical forests (Zaire). Useful results were obtained, but the species involved had densities of the order of 20 times those of bushpigs in the study area. The radio-active faeces marking technique, where the population estimate is based on the ratio of marked to unmarked faeces, was used for population density estimation of river otters, *Lutra canadensis* (Shirley *et al.* 1988) and coyotes, *Canis latrans* (Knowlton *et al.* 1986). This technique may also have potential for the bushpig.

Pellet group count indices may provide crude indicators of changes in population density of bushpigs over time. Sufficient permanent sample strips would have to be monitored according to standardized counting procedures in order to achieve useful results. Strip lengths of twenty kilometers or more (11.2.1) suitable for pellet group counting may not be readily available in smaller areas. In the entire study area, suitable sample strips are probably only formed by slippaths in the indigenous forests. In other habitat types, faeces deposition may be rather diffuse (e.g. pine plantations) or localities where faeces are concentrated are difficult to detect and poorly accessible (e.g. Valley Bushveld).

Thus circumstances limit the census techniques of potential use, but low densities render even these impractical. The manpower input required would be prohibitive under most circumstances.

11.3.2 Comparisons of population density

Among mammals, density is closely related to the average adult body mass and the trophic level occupied by the species (*op. cit.* Robinson and Redford 1986). After these two factors are accounted for, population densities also appear to vary with habitat (Robinson and Redford 1986).

Highly digestible plant parts (fruits, seeds, shoots, flowers) account for only a small fraction of the plant biomass and hence support only a small biomass of herbivores. Thus, those species concentrating on small packages of highly digestible food have a relatively low biomass density (cf Geist 1978a). As predicted, at a given body mass, population densities of grazing or browsing herbivores are greatest. The ranking of other dietary categories in descending order is frugivore-herbivores, frugivore-granivores, frugivore-omnivores, insectivores-omnivores, myrmecophages and carnivores (Robinson and Redford 1986). In accordance with these trends, warthogs as grazing herbivores generally have higher population densities than omnivorous European wild boars. Warthog densities for average quality habitats range between 2 to 5 animals/km² (Cumming 1975, Rodgers 1984) but values exceeding 15 animals/km² have been recorded (Bradley 1968, Cumming 1975). In comparison, European wild boar densities, although variable, are generally lower (Table 11/6).

The higher densities are undoubtedly the result of access to agricultural crops or supplementary feeding. Jezierski and Myrcha (1975) mention that the densities approaching 10 wild boar/km² reported by Andrzejewski and Jezierski (1978), are the product of yearlong supplementary feeding. They calculated the food carrying capacity of forest ecosystems at 1,7 wild boar/km² during autumn/winter and 0,8 animals/km² in spring and summer.

| TABLE 11/6: EUROPEAN WILD BOAR DENSITIES | | |
|--|----------------|---|
| Density (per km ²) | Locality | Source |
| 0,46 | India | Schaller (1967) ex Santiapillai and Chambers (1980) |
| 0,5 - 2,0 | Germany | Briedermann (1970b) |
| 1,23 - 2,46 | Germany | Hasselbach (1970) |
| 1,8 - 2,0 | Russia | Kozlo (1970) |
| 1,2 - 1,8 | Poland | Mackin (1970) |
| 0,3 | Sri Lanka | Eisenberg and Lockhart (1972) |
| 1,5 | Germany | Beuerle (1975) |
| 0,44 - 3,08 | Eastern Europe | <i>op. cit.</i> Beuerle (1975) |
| 2,7 | Eastern Europe | <i>op. cit.</i> Beuerle (1975) |
| 0,4 - 0,8 | Eastern Europe | <i>op. cit.</i> Beuerle (1975) |
| 1,2 - 10,0 | Poland | Andrzejewski and Jezierski (1978) |
| 4,2 | Nepal | Dinerstein (1980) |
| 0,68 | Sri Lanka | Santiapillai and Chambers (1980) |
| 0,25 - 1,0 | Germany | Hennig (1981) |

From questionnaires, Rand (1955 *op. cit.* Milstein 1971) estimated that there were approximately 9 700 bushpigs in the Cape Province. Expressed in relation to the area of potential bushpig habitat, this figure results in an overall density estimate of 0,32 animals/km². Mentis (1970) reported 0,22 bushpigs/km² in the Umfolozi Game Reserve, Natal. These earlier estimates are of the same order of magnitude as those determined during this study (0,3 - 0,5 bushpigs/km², 11.2.1) and correspond well with European wild boar densities in similar habitats (cf Eisenberg and Lockhart 1972, Santiapillai and Chambers 1980: Table 11/6).

Although there is circumstantial evidence suggesting higher bushpig densities in the Eastern Cape in comparison to the Southern Cape (11.2.1), the situation is by no means clear. It was argued elsewhere that the habitat quality (8.2.4; 8.3.4.2; 8.3.4.3) as well as the reproductive rate (10.4.4.2) is higher in the Eastern Cape. There are many records of a positive relationship between habitat quality and population density. Cumming (1975) found that high density warthog habitats had alluvial soils carrying a good cover of palatable grasses while low density habitats were mostly characterized by sandy soils. In Denmark a direct correlation was found between soil quality of the various regions and the number of roe deer (*Pelea capreolus*) killed annually by hunters (Klein and Strandgaard 1972). In contrast, Von

Schantz (1981) found similar numbers of red fox (*Vulpes vulpes*) in mineral and peat soil habitats. He was however able to identify the mineral soil habitat as being of higher quality despite the similarity in density, as it contained a higher proportion of reproducing adults. The same may be the case with regional differences between bushpig population densities which may not necessarily be evident from the available data.

Van Horne (1983) investigated the assumed relationship between density and habitat quality and found that the correlation may be blurred under certain circumstances. Social interactions may prevent sub-dominants from entering high quality habitat. For territorial species and when favourable habitat is limited, a surplus of adults of breeding age may accumulate in poor habitat where successful breeding does not take place. The surplus individuals may then collect in these habitat sinks, where densities may fluctuate widely. In regions where the habitat is heterogenous in space and time, sink populations may reach high densities when the environment becomes temporarily favourable. Overflow from zones of high quality habitat into those where quality is lower may then occur during periods of high reproduction and high overall density. Densities may thus reflect conditions in the recent past or temporary present, rather than long-term habitat quality (Van Horne 1983).

The circumstances in the Southern Cape appear to be similar. There was some evidence for regional, as well as smaller scale, fluctuations in bushpig densities (11.2.1). In contrast to the Eastern Cape, the heterogenous quality of the habitat (e.g. foothills versus plateau zone, home ranges dominated by pine plantations versus indigenous forest) allowed the survival of non-breeding subdominants (10.3.6). Only by environmental variation of some sort, coupled with regular episodes of dispersal can non-dominant competitors survive (Levin 1976). After an extended favourable period before 1979 it appears that bushpigs overflowed from the agricultural plateau into the foothill zone (11.2.1). The subsequent population decline in the foothill zone was particularly marked. It was characterized by lower reproductive rates (11.2.2), poor body condition of individuals (9.3.3) and emigration (4.3.5.2).

It thus appears that Southern Cape bushpig population densities may equal those in the Eastern Cape during certain phases, but probably not in terms of long-term averages.

11.3.3 Survivorship

Caughley (1966) concluded that many published life tables were invalid due to inadequate sample size, failure to meet the assumption of a steady state age distribution, strong sampling bias of the zero age class and confusion as to whether the sample represented animals living or having died. The schedules, rather than being typical or normal for a species, most likely represent a population response to a given set of environmental circumstances. Since environments vary over space and time, a given life table represents only one of almost an infinite number of states (Caughley 1966). Only when a population's exponential rate of increase is zero and when it had been zero for some time, and when the survival and fecundity schedules have remained constant for some time, is the standing age distribution the same as the temporal age distribution of the cohorts that collectively constitute the population (Caughley 1977). These conditions are seldom completely met (cf McCullough 1979). Anderson *et al.* (1981) pointed out additional serious limitations of the life table methods for estimating survival parameters.

Life table parameters are accordingly often misinterpreted or misused, especially in connection with estimating rates of population increase (Caughley and Birch 1971). The same l_x schedule can generate very different mortality rates depending on whether the population is growing or not (Murray 1979). In the light of these complexities, the survival statistics (11.2.3) are presented with reservations and should only be taken as crude indicators.

High juvenile mortality rates have been reported in most wild pig populations, e.g. Frädrieh (1968), Hennig (1981). According to Briedermann (1986), juvenile mortality is associated with chilling, starvation, disease or predation. Cold stress reduced the acquisition of colostrum immunoglobins in piglets (Blecha and Kelley 1981) and may result in states of critical negative energy budgets. In litters

farrowed during cold weather, chilling is reported to have caused about a quarter of the piglet deaths during the first post-natal day (Curtis 1970). Litter losses often occur in the European wild boar when births occur early in the season and stressful weather is experienced (Briedermann 1973).

Chilling was also reported to be the main cause of mortality in European wild boar juveniles by Meynhardt (1981 ex Dietrich 1984). Nearly 37% died within the first 8 months of life. The mortality rates reported for juveniles vary widely (Briedermann 1986). Lebedeva (1956 ex Jezierski 1977) found that in the Bialowieza primeval forest, on average about 40% die during the first year of life. In a year with abundant food, mortality may be only about 10%, while in years with difficult weather conditions and poor food supply as many as 80 - 90% of the young may die. Up to 50% of the newborn piglets may be lost within the first month of life (Eisenberg and Lockhart 1972). Mortality rates for the first year of life generally vary between 25 and 75 % (Martys 1982, Sludskii 1956, Briedermann 1986). The crude overall average juvenile mortality rate of 50% in European wild boar is thus similar to that found for the bushpig in this study (11.2.3). Juvenile mortality rates in the warthog are just as variable (Child *et al.* 1968, Clough 1969, Rodgers 1984). The value of comparing mortality rates is doubtful since they are probably only meaningful in the context of the prevailing conditions and population dynamics.

Calculated life expectancies at birth were in the order of 1,8 - 2,8 years in bushpigs (11.2.4). The equivalent values for the European wild boar were considerably lower: 1,1 - 1,5 years (Briedermann 1986). Life expectancy is a composite parameter involving reproductive turnover, mortality rate and ecological longevity. The difference in life expectancy is a consequence of many species-typical factors in the bushpig. These may be lower reproductive rate, higher ecological longevity and possibly more juvenile and yearling mortality due to predation (11.2.3). Adults of both species are relatively invulnerable to attack from predators (Ryan 1965, Eisenberg and Lockhart 1972; 11.2.3). Also, in both species, the presence of ectoparasites did not seem to affect the health of the host, even when heavy infestations occurred (Henry and Conley 1970, Barrett 1978; 11.2.3).

11.3.4 Comparative population dynamics

The data in Table 11/5 (11.2.4) indicates differences between bushpig populations in the Southern Cape foothills and the Southern Cape region as a whole and between the Southern and the Eastern Cape. These involve trends in

- the preponderance of males
- lower fecundity
- higher adult survival

They may merely characterize populations at different stages of long-term fluctuations. For example, Jezierski and Myrcha (1975) found that during a period of rapid growth in a European wild boar population and during the initial phase of its decline, there was a predominance of females in the older age classes. Subsequently the sex structure of the population started to change markedly in favour of males. However, especially in species with food resource territoriality, the spatial distribution of areas with divergent habitat quality appears to be involved in determining the nature and degree of population fluctuations (cf 11.3.2). In the Great tit (*Parus major*), a territorial species, Klomp (1980) found that the amplitude of the population fluctuations in densely populated deciduous woodland was smaller than in thinly populated habitats. This phenomenon was explained by the occupancy of the deciduous woods to saturation and an overflow of the surplus birds to less favourable habitats. It was most clearly expressed in areas where the habitats were adjacent. Evidence for a parallel situation in the bushpig was presented in section (11.3.2).

Regional differences seem not to be merely the outcome of populations being at different stages of fluctuation. Heterogeneity in habitat quality and in the availability of food seem to be involved as well. Southern Cape bushpig populations also differ from those in the Eastern Cape in having:

- relatively more solitary, non-territorial females
- relatively few young females breeding successfully (10.3.6)
- lower average availability of high quality food (8.3.4.3).

Greater population fluctuations in poorer quality areas are taken to be the result of the low reproductive rate not being able to sustain continuous territorial saturation. This would favour the survival of adults and particularly of non-breeding, non-territorial individuals. The Eastern Cape populations, with higher reproductive and lower adult survival rates, also differed from those in the Southern Cape in respect of:

- smaller female skeletal size (9.3.3.1)
- lower female to male body mass (9.3.1).

It has been fairly well established that increased reproductive effort at any age is associated with reduced postreproductive growth and survivorship (Stearns 1976, 1977).

Under conditions of higher average availability of food it is adaptive to breed early and frequently at the cost of reducing adult size and survival (12). This interpretation agrees with the findings of Dobson and Murie (1987) regarding Columbian ground squirrels. Natural populations at higher food availabilities showed lower survival, but higher reproductive rates (10.4.4.2).

Hunting may also have affected bushpig populations. Intensities were variable, but on average hunting pressure was higher in the Eastern Cape. Through increasing adult mortality exploitation may open up breeding opportunities in territorial species leading to earlier breeding and smaller adult size.

In summary, the population features described in this study may be explained by (a) phase of population fluctuation, (b) gradients in the food resource availability or (c) exploitation effects. In an attempt to seek further clarification, population data from species with a social organisation similar to the bushpig were reviewed.

The coyote, *Canis latrans*, population studied by Gese *et al.* (1989) exhibited a preponderance of males, a low proportion of juveniles, low reproductive output (none of the yearlings reproduced, low mean litter size) and a low mean population density. In contrast more intensely

exploited populations had a preponderance of females and a higher proportion of juveniles. In exploited beaver, *Castor canadensis*, populations in the Chena River area adult mortality was higher, age at first reproduction lower, adult female body size smaller and adult males were larger than females. These features were in contrast to another Alaskan beaver population in the Birch Creek area which was not exploited (Boyce 1981). In both cases the differences were attributed to the effects of exploitation. The characteristics of the exploited populations resemble those of the Eastern Cape, rather than those of the Southern Cape.

Moore and Millar (1984) compared coyote populations from Eastern New Brunswick/Nova Scotia with those from Western New Brunswick/New Hampshire. In the first there was a preponderance of males, lower proportions of juveniles in certain years and poor female reproductive performance, as evidenced by a lower proportion of adult females breeding. The differences were attributed to the Eastern New Brunswick population having been in a phase of recolonization, whereas the Western population was resident. The equivalent dichotomy between Southern and Eastern Cape bushpigs can also be interpreted in this way (option a).

Regional differences between bushpig populations were explained in terms of food resource availability gradients (option b), related to differences in the geological parent materials prevalent in each region (8.3.4.3). Applying this argument to the areas studied by Boyce (1981) and Moore and Millar (1984) leads to the predictions that nutrient-rich geological substrates should be present in the Chena River and Western New Brunswick/New Hampshire regions. This was found to be the case. The geology of the Chena River area consists of phyllites, schists and slate, whereas sandstone conglomerates predominate in the Birch Creek area (Bennison, undated). Western New Brunswick is characterized by agriculture on soils overlying granites whereas conifer forests predominate in Eastern New Brunswick, growing on soils derived from sandstone and shale conglomerates (personal observation, 1986).

In conclusion, food (as explained in section 8.3.4.3) is proposed as the major factor responsible for the differences observed in the dynamics of the study populations, as well as of those cited above. Higher

exploitation levels appear to be merely a concomitant feature of populations with a higher reproductive turnover.

11.3.5 Population regulation

11.3.5.1 Introduction

Population regulation is here defined as the continual adjustment of population density to an equilibrium level determined by critical resources. Population density will increase until the birth rate and the death rate are equal. For this to happen either the birth rate must fall or the death rate must increase as density rises. Populations do not stop increasing unless either the birth rate or death rate is density dependent (Keith 1974).

Enright (1976) demonstrated that a factor like the local average weather, acting in a purely density-independent manner, could in principle be a major determinant of the equilibrium abundance of a species, acting in the same way as it does to determine distributional limits. Thus, the equilibrium abundance of a species can usually be altered by any environmental factor which has a consistent effect on either birth rate or mortality rate, regardless of whether that action itself depends upon density of the species (Enright 1976). Although density independent factors can affect the mean density level of populations, and can contribute to differences in this value between populations, they cannot regulate population density, i.e. they cannot account for the restricted fluctuations around a constant mean level. For regulation, the action of density related factors is necessary (Klomp 1962).

The differentiation of density independent and density dependent factors is confusing. Any critical extrinsic factor influencing birth and death rates ultimately involved in the determination of equilibrium density (over space) is also proximately involved in the regulation of population density (over time). The interaction between equilibrium density and mode of population regulation is furthermore sometimes altered by intrinsic (social) factors which determine at what stage of the density build-up relative to the limiting resources regulation takes effect and which population segments are primarily affected (11.3.5.2).

The special role of territoriality in this context is discussed in relation to the bushpig in section 11.3.5.3.

Populations are regulated intrinsically when the animals lower their rate of increase behaviourally or physiologically as a reaction to rising density. They are regulated extrinsically if the equilibrium is a direct consequence of interaction between the population and the organism providing its food (Caughley and Krebs 1983). Intrinsic regulation is achieved more by the things the animals do than by direct interaction of the animals with critical resources or predators. Intrinsic regulation is not an alternative to extrinsic regulation, but an addition to it that comes into play at population levels below which extrinsic mechanisms would otherwise wind rate of increase down to zero (Caughley and Krebs 1983). Intrinsic regulation appears to be more prevalent in smaller, extrinsic regulation among larger animal species. These authors provide a hypothetical explanation for this dichotomy in the mode of population regulation.

Although it is commonly agreed that food is the ultimate factor determining the optimal ceiling density to be maintained, the relationship between food availability and population density is not clear-cut and direct. Undernourishment in populations at optimum density is rather atypical. Starvation, when it occurs, is a sporadic and accidental cause of mortality rather than a regular one. Large scale starvation is virtually confined to unstable transitory (suboptimal) habitats, due to their short term critical resource fluctuations where mechanisms of population homeostasis cannot operate effectively. Wynne-Edwards (1962) listed a few regulating mechanisms which link available food resources to population density: varying the quota of breeders, resorption of embryos, survival of the new born, acceleration or retardation of growth rate and maturity, and ejection of surplus members of the population. Many of these mechanisms involve sociospatial behaviour, but social behaviour is usually not regarded to be the ultimate population regulating factor.

11.3.5.2 Modes of population regulation: a model

The aim of this section is to present a general hypothesis accommodating the various modes of population regulation. Although only limited data is available for the bushpig, the model presented below will serve to place it and population regulation generally into perspective, and to indicate future research needs.

Modes of population regulation can be divided into two main categories, representing the extremes of a continuum determined by the nature of the food resources (*vide* 8.2.3).

- * Food resources are concentrated (ubiquitous) but of relatively low quality (low nutrient density):
 - Food resources cannot be monopolised by dominants (scramble competition).
 - Fluctuations in the availability of food resources act directly on populations (extrinsic regulation).
 - All members of a population are affected (absence of a food access gradient according to social position).
 - Societies are gregarious, i.e. have large social units (herds) and social stress as a result of crowding is unlikely to be prevalent.

- * Food resources are dispersed, but of relatively high nutrient density:
 - Food resources are commonly monopolised by dominants (interference competition)
 - Access to food resources is mediated by social rank and sociospatial interaction (intrinsic regulation)
 - Subdominants are commonly affected by food shortages (steep food resource access rank gradient)

- Psychosocial stress in relation to population density is a central feature. Even dominants are negatively affected under conditions of prolonged crowding.

This framework helps to clarify the interaction between body size and intrinsic versus extrinsic population regulation expounded by Caughley and Krebs (1983). The nature of the food resources which result in extrinsic regulation also favour large body size (relatively low food quality) and vice versa.

Extrinsic regulatory mechanisms in large mammals were listed by Laws (1981) as: reproductive rate of adult females, age of first reproduction, immature mortality rates and adult mortality rates, in that order of importance with increasing population density. Other authors tend to place more emphasis on mortality than reproduction (Hanks and Mackintosh 1973 ex Laws 1981). Buffalo populations in the Serengeti were regulated by adult mortality caused by undernutrition (Sinclair 1974). These divergent interpretations may be resolved as follows:

- * Plant prey populations are characterized by a high turnover, short-life and high ratio of tissue expansion to consolidation (the C_4 -photosynthetic pathway predominates). Food quantity for maintenance is critically limiting under conditions of food shortage. Reproduction of the associated herbivores is relatively invariant, with greater emphasis on mortality as regulating mechanism (e.g. buffalo cf Sinclair 1974).
- * Plant prey populations are characterized by a lower turnover; long-life, and low ratio of tissue expansion to tissue consolidation (the C_3 -photosynthetic pathway predominates). Food quality for reproduction precedes quantitative food shortages as a factor in the mechanism of population regulation. The reproductive output is more variable over time depending on availability of food, while mortality is relatively invariant and less important as a regulatory factor (e.g. elephant cf Laws 1981).

These interactions between food resources and population regulatory mechanisms will not be elaborated further since they follow logically from the findings in section 8.3.4.3.

Mechanisms for intrinsic regulation of animal numbers are thought to be a consequence of selection, under conditions of mutual interference, in favour of genotypes that have a worse effect on their neighbours than *vice versa* (Chitty 1967 ex Krebs 1978). According to the self-regulation hypothesis, indefinite increases in population density are prevented by changes in the quality of the population (Krebs 1978). These changes in quality may be physiological or behavioural, genotypic or phenotypic. Three different mechanisms of self regulation have been proposed (Krebs 1978):

- (I) the Stress Hypothesis suggests that mutual interactions lead to physiological changes, phenotypic in origin, that reduce births and increase deaths.
- (II) the Behaviour Hypothesis suggests that mutual interactions involving spacing behaviour prevent unlimited increase and that spacing behaviour is not an inherited trait.
- (III) the Chitty Hypothesis postulates that spacing behaviour limits population density and that individual differences in spacing behaviour have a genetic basis and respond rapidly to natural selection.

However, it is proposed here that the mechanism of change in population quality with increasing density involves three elements, the first two being central to the hypotheses above:

- endocrine adaptive responses
- spacing behaviour at least to some degree
- non-genetical inheritance of sociopsychologic predisposition (maternal effects?)

Evidence consistent with the third element is reported by Thomson 1957, Denenberg *et al.* 1962, Christian and Davis 1964, Denenberg and Rosenberg 1967 and Moore 1968 *ex Geist* 1978a. According to these authors psychologic disturbance/stress may *inter alia* raise the level of adrenocortical hormones and affect the unborn young and also their offspring in various ways, for example, greater emotionality or lower body mass. The effects are transmitted across generations and, given sufficient social pressure, also affect the socially dominant segments of the populations.

There is good evidence that, in populations where intrinsic regulation is operative, social factors will limit population growth despite an abundance of all environmental requirements. As social pressure increases, it acts as a progressively stronger stimulus to the endocrine adaptive response mechanism, resulting in stimulation of pituitary-adrenocortical activity, inhibition of reproduction and increased mortality. Diminished reproductive function in the female may be expressed by inhibition of oestrus, increased intra-uterine mortality, reduced numbers of implanted ova, increased postparturient mortality due to suppression of lactation and diminished maternal behaviour (Christian 1963, Christian and Davis 1964).

The decline in body mass in certain European wild boar populations under conditions of prolonged high levels of food availability (10 years) but high and increasing population densities reported by Briedermann (1986), is amenable to interpretation according to the endocrine adaptive response mechanism. Whether this mechanism operates in bushpigs awaits further detailed investigation. Preliminary investigation of white blood cell characteristics of Southern Cape bushpigs suggests relatively raised neutrophil levels and eosinopenia in free-ranging as against captive bushpigs (Table 11/7). Should the difference be real, rather than the result of raised captive eosinophil values due to endoparasitism, it could imply increased pituitary-adrenocortical activity in free-ranging bushpigs (*cf* Christian 1963). Alternatively, the differences could result from nutritional constraints.

The apparent paradox of a sparse population exhibiting reproductive inhibition and growth following a decline results from the prolonged

effect of high population densities (Christian 1963). This may be transmitted through non-genetical inheritance (*vide* Denenberg and Rosenberg 1967). The possibility cannot be excluded that the bushpig population low in the Southern Cape (11.2.1) is part of an endocrine feedback mediated response. This is suggested by: the white blood cell characteristics of free-ranging bushpigs (Table 11/7), low progesterone levels during pregnancy (10.3.2.2); relatively few parturient females which raise their young (10.4.4.3); high aggressivity among females (5.2.2.3) and particularly large territory sizes (6.2.1.1).

| TABLE 11/7: WHITE BLOOD CELL PARAMETER LEVELS IN SOUTHERN CAPE FREE-RANGING VERSUS CAPTIVE BUSHPIGS | | | |
|---|----------------------|---------------------------|---------------------------------------|
| | Captive Bushpigs (a) | Free-ranging Bushpigs (b) | Statistical Significance (a versus b) |
| <u>Lymphocytes (%)</u> | | | |
| n | 50 | 54 | t = 0,54 (NS) |
| \bar{x} | 21,8 | 20,8 | |
| s | 8,43 | 10,34 | |
| <u>Neutrophils (%)</u> | | | |
| n | 50 | 54 | t = 5,25 P < 0,001 |
| \bar{x} | 60,5 | 71,3 | |
| s | 10,39 | 10,56 | |
| <u>Eosinophils (%)</u> | | | |
| \bar{x} | 9,39 | 0,91 | G = 69,94 P < 0,001 |
| Frequencies: | | | |
| ≤ 1% | 7 | 46 | |
| ≥ 2% | 54 | 8 | |

11.3.5.3 Territoriality and population regulation

Territorial behaviour has evolved as a result of the net advantages accruing to individual competitors (Begon *et al.* 1986). Brown (1964 ex Krebs 1978) already pointed out that territorial behaviour can be selected for in situations where its only selective advantage is relative, i.e. the exclusion of other individuals from breeding opportunities. As an independent consequence of territorial behaviour, population regulatory effects may result (Begon *et al.* 1986).

Territorial behaviour limits recruitment by limiting the number of individuals that can establish territories and participate in breeding (Klomp 1972, Keith 1974, Murray 1979). Territoriality thereby acts in a density-independent fashion, even though territory size and the population's crude birth rate vary with density (Murray 1979)

Population density is determined by territoriality in that the latter prevents the recruitment rate from increasing with increasing population density due to territory size being largely unresponsive to changes in population density. Territory size rather varies and is a function of the interactions between the quality of the environment, the condition and number of competing individuals and the behaviour of the species (Murray 1979).

There is circumstantial evidence that the mode of population regulation in the bushpig differs between the Southern and the Eastern Cape. These possible differences are discussed below in terms of the nature of the food resources, sociospatial tactics and their consequences for population regulation.

The nutrient status of an environment appears to determine the ratio between nutrients suitable for production and for storage (maintenance) in plants, as well as the concentration of digestibility-interfering substances, for the associated herbivores (8.3.4). In the Southern Cape, a nutrient-poor environment, food resources for reproduction are relatively more limiting than those for mere survival. The opposite applies in the Eastern Cape, a nutrient-rich environment. In the Eastern Cape, bushpig life history is characterized by a fast turnover: high rates of both reproduction (R) and mortality (M) and relatively short life spans. In the nutrient-poor environments, slower population turnover rates with relatively low reproductive rates and long life spans are adaptive (Chapter 12). In the nutrient-rich environments populations would thus tend to be close to their current carrying capacities: high, invariant R and high variable M. Circumstances in the nutrient-poor environments would be expected to favour less precise (delayed) responses to changes in carrying capacity: low variable R and longevity, i.e. low, relatively invariant M. For extrinsic regulation this dichotomy is exemplified by the buffalo and elephant (11.3.5.2).

From the above it follows that territories in the nutrient-rich environment (Eastern Cape) which are large enough for survival (S) are also large enough for reproduction (food for S relatively more limiting than for R). Together with the relatively high R, this is expected to result in closely packed minimum-sized territories (territorial saturation). In the Southern Cape, where food resources for R are relatively more limiting than for S, areas unsuitable for territories are expected to exist, and to allow the survival of animals (dispersal sinks due to heterogeneity of habitat quality). Heterogeneity of habitat quality in the Eastern Cape would merely result in variable territory sizes. Bushpig survival in the Eastern Cape is accordingly dependent on territory ownership, but all territories have sufficient resources for reproduction, unlike the Southern Cape situation.

This hypothesis would explain the higher proportion of reproductive to non-reproductive bushpigs in the Eastern Cape compared to the Southern Cape. The findings of Von Schantz (1981) for the fox, *Vulpes vulpes*, where a lower proportion of alpha individuals (breeders) was found in peat than in mineral soil habitats (11.3.2) form an interesting parallel.

Population build-ups or eruptions can only occur as a result of phases of relatively high recruitment or high adult survival or both. These should be possible where non-territory owners can survive, and become old enough to become competitors. In the Southern Cape this appears to be possible in the dispersal sinks, while in the Eastern Cape it is precluded by territorial saturation. Thus, in the Eastern Cape all surviving females breed, whereas in the Southern Cape only the more dominant are territorial and reproduce, hence the positive correlation between age and reproduction there (10.3.6).

It is also postulated that the availability of nutrients required for reproduction would tend to fluctuate more over time than those required for mere survival (production nutrients versus energy-providing nutrients). This trend would be of far greater consequence in a nutrient-poor environment like the Southern Cape where nutrients for reproduction are relatively more limiting. In addition, sociospatial conditions there provide more opportunities for populations to

accumulate (survival of non-breeders). Against this background a two-phase scenario is developed for Southern Cape bushpig populations.

Increasing phase:

- food for reproduction readily availability
- high recruitment
- low aggressivity levels/relatively small territories

Population density peak:

- high frequency of social strife
- young born during this phase inherit a predisposition for social intolerance (11.3.5.2)

Decreasing phase:

- relatively low reproductive rates
- high aggressivity levels/large territories

The lowest level of aggressivity is physiologically (endocrinologically) most compatible with high fecundity (cf Christian 1970), but high aggressivity is believed to be adaptive when food resources for reproduction are relatively scarce (Marquiss 1977 ex Krebs 1978). Under the circumstances prevailing in the Southern Cape, a density-responsive endocrine feedback system, oscillating between reproductive inhibition/social intolerance and high reproductive output/social tolerance, would be adaptive and may be operating in the scenario outlined above. The characteristics of the Southern Cape study populations indicated them to be in the decreasing phase (11.2.1; 11.2.4).

The postulated model for Southern Cape bushpigs corresponds well with findings on red grouse (*Lagopus lagopus scoticus*). In some years the birds were very aggressive, took up large territories and had low breeding densities. In others they were relatively docile, took up small territories and had high breeding densities (Krebs 1978). Marquiss (1977 ex Krebs 1978) found no association between the measures of dominance (related to territorial ownership) and aggressiveness (related to territory size) in grouse on a high nutritive plane, but a close correlation in those on a low nutritive plane. Both dominance and aggressiveness were inherited traits, but presumably via non-genetic

maternal effects (Krebs 1978). Inheritance of aggressiveness appears to be proximately induced by "crowding", since spacing behaviour changed with numbers also in the absence of corresponding changes in food supply (Krebs 1978).

The model of differences in population regulation between regions of divergent nutrient status, developed here for the bushpig, appears to have wider applicability. Christian (1970) noted that rodent species adapted to discontinuous habitat (brushland, forest edge) were subject to conspicuous changes in adrenocortical and reproductive function with changes in population density, involving density-dependent feedback operating through social intolerance and aggressivity. According to the model, this resembles the situation in bushpig populations in the Southern Cape. Rodent species inhabiting continuous and extensive areas of similar habitat (deciduous forest, prairie) seldom irrupt, are not responsive to density-dependent adrenocortical feedback and are generally more socially tolerant (Christian 1970). This situation parallels that of Eastern Cape bushpigs (small territories, little scope for population accumulation). However, the model developed here extends beyond that of Christian (1970) and links the regional differences in mode of population regulation not only to habitat variability, but ultimately to differences in the nature of the food resources.

11.4 Synopsis

- (I) Population density estimates in the Southern Cape range between 0,35 to 0,45 bushpigs/km².
- (II) Mean fecundity levels of females 2 years and older (mean live births/female/annum) were 1,59; 1,92 and 2,70 for the Southern Cape foothills, Southern Cape and Eastern Cape populations respectively. Fecundity varied with age, especially in the Southern Cape.
- (III) Mortality was often due to starvation in all age classes. Inclement weather and predation were prominent mortality factors for immature bushpigs, whereas intraspecific strife played a significant part in adult mortality, especially in females. Mortality estimates for 1 and 2 year old bushpigs varied between

41% and 45%, and were similar in both year classes. Adult mortality rates varied between 19% and 27%.

- (IV) Generation length and life expectancy at birth were 6,6 and 2,8 years in the Southern Cape and 5,4 and 1,8 years in the Eastern Cape respectively.
- (V) Population dynamics and regulation in the two regions were contrasted and found to conform to a proposed, and apparently more universally applicable, dichotomy in life history tactics (Chapter 12), ultimately linked to regional differences in the nature of the food resources (Chapter 8).

12. LIFE HISTORY TACTICS

12.1 Life history parameters

Following Dunbar (1982), "adaptation" may be defined as an attribute that permits the possessor to accomplish those immediate objectives that it must achieve in order to survive and reproduce successfully and "fitness" as a measure of the rate of spread of a given gene. Evolutionary explanations of observed patterns according to the Darwinian formula involve four elements (Dunbar 1982):

- individual variation in particular characters.
- at least partial genetic inheritance thereof.
- some variants are better adapted (adaptation).
- disproportionate contribution of the better adapted variants to the species' gene pool in future generations (fitness).

Accordingly, natural selection favours those individuals with the greatest fitness, i.e. those that make the greatest proportionate contribution to the future of the population to which they belong. The life history components affect this contribution through the media of fecundity and survival (Begon *et al.* 1986). The various components include size, rates of growth and development, reproductive traits (length of pre-reproductive period, litter size, interval between litters, investment per offspring) and maintenance allocation (energy storage, longevity). A given combination of these in terms of their means and variance is a life history tactic (Stearns 1976).

In the context of the ecological significance of life histories we are dealing with the products of the evolutionary process and ways in which these products interact with the immediate environment (Begon *et al.* 1986), i.e. with the genotypic outcome of the selective process and the phenotypic response to environmental constraints. The interaction between the evolutionary product and the present environment may in itself have evolved. Law (1979) views a life history as a point of

balance between the conflicting requirements of different activities of an organism. As such, a life history basically constitutes a trade-off between the requirements of reproduction and survival. Different environments push the point of balance in different directions, depending on the relative importance of reproduction, maintenance and growth.

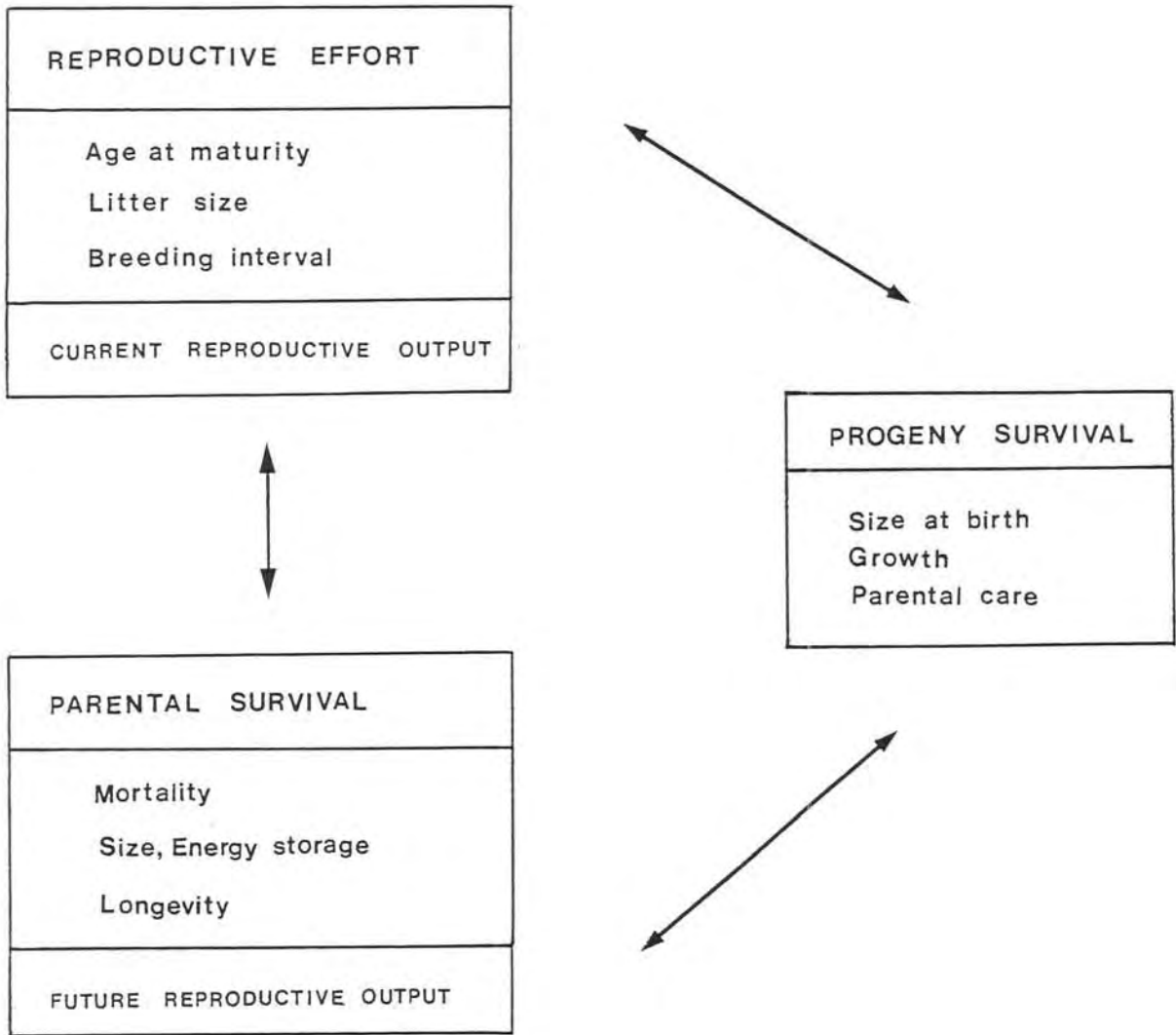
12.2 Life history patterns

12.2.1 Trade-off in life history

The inverse relationship between fecundity and longevity, suggesting a trade-off between reproduction and maintenance (survival), is a widespread phenomenon (Murphy 1968, Giesel 1976, Pianka 1976, Stearns 1976, Calow 1977, Horn 1978, Murray 1979, Wittenberger 1979, Bell 1980, Parry 1981, Clutton-Brock 1984). This implies that an increase in fecundity results in decreased adult survival (Stearns 1976). If reproduction is not costly, then fitness is maximized by maximizing reproduction up to the physiologically attainable limit. If reproduction is costly, then at some point the cost may exceed the benefit (Bell 1980). Whether it is advantageous to exchange some adult survival for increased fecundity depends both on how much fecundity is gained per unit of adult survival lost and on the direction of natural selection (Green 1980). Since parental fitness is a product of the number of young and their survival to maturity (cf Lloyd 1987), the investment/offspring can be considered the third component of a triumvirate of life history trade-off (Figure 12/1).

Life history tactics thus involve a trade-off between offspring number and quality, and current offspring number and future reproductive output. An optimum litter size is a direct consequence of an optimum current reproductive effort coupled with an optimum expenditure/progeny (Pianka 1976). In terms of age at first breeding, organisms that devote a large proportion of available resources to reproduction at an early age are less likely to survive to later ages of reproduction than those that place less emphasis on early reproduction (Giesel 1976, Calow 1977, Wittenberger 1979).

FIG.12/1: LIFE HISTORY TRADE-OFFS



12.2.2 Hypothetical causal systems

The r-and K-selection hypothesis was originally formulated as a model of density-dependent natural selection (Boyce 1984). Closer perusal and comparisons reveal widespread misinterpretation and complications (Boyce 1984), but the theory of the model is taken by many to predict the association of the biological traits constituting life history tactics into two groups (Stearns 1976):

- (I) r-selection: early age at first reproduction; large litter size, semelparity, little or no parental care, large reproductive effort; small, numerous offspring; low assimilation efficiency and a short generation time.

(II) K-selection: delayed reproduction, iteroparity, small litters, parental care, smaller reproductive effort; fewer, large offspring; high assimilation efficiency and long life life-spans.

Deterministic models (r-and K-selection) predict that organisms exposed to high levels of density-independent mortality, wide fluctuations in population density or repeated episodes of colonization (unpredictable, ephemeral environments) will evolve towards a combination of early maturity, larger litters, higher reproductive effort and shorter life-spans than will organisms exposed to density-dependent mortality or constant population density (Stearns 1977, Begon *et al.* 1986). r-selected organisms are taken to experience their environment as unstable and unpredictable, with selection favouring a high reproductive effort in order to exploit the transient good times. However, in an environment that is unpredictable, natural selection may just as likely favour those genotypes that sacrifice a high reproductive input in favour of resource allocations which enhance survival through the unpredictable bad times (Horn 1978, Boyce 1979). This paradox disappears when the models distinguish the opposite effects of juvenile versus parental mortality (Horn 1978). Stochastic models (bet-hedging) predict the evolution of the same combinations of life history traits, but for different reasons: when fluctuations in the environment result in highly variable juvenile mortality, a syndrome of delayed maturity, smaller reproductive effort and greater longevity should evolve (Murphy 1968, Stearns 1977). On the other hand, environmental variability that increases adult mortality favours increased reproductive effort, larger litter sizes and short-lived organisms (Stearns 1976).

Thus, juvenile and parental mortality have opposite effects on the prediction of adaptive tactics. Juvenile mortality biases toward K-selection traits, but adult mortality biases toward r-selection traits (Horn 1978). Furthermore, the effect of increased variation in mortality is analogous to lowering the respective average survivals. Horn (1978) found fully concordant results from an analysis of either average mortality or unpredictable variations in mortality.

Environmental variability may shape the evolution of life histories through its impact on demography (i.e. through r-and K-selection), but also independently thereof by imposing selective mortality (Boyce 1984).

These complex life history interactions are summarized in Figure 12/2 (ex Horn 1978).

The models described place much emphasis on environmental and associated demographic variability as the causes underlying life history optima. However, apart from variability over time, adaptation to mean long-term resource availability can also influence life history patterns.

12.2.3 Is resource level or its variability the salient life history factor?

Eastern and Southern Cape bushpig populations exhibit differences in life history traits which agree with those predicted by the r/K selection model (Table 12/1).

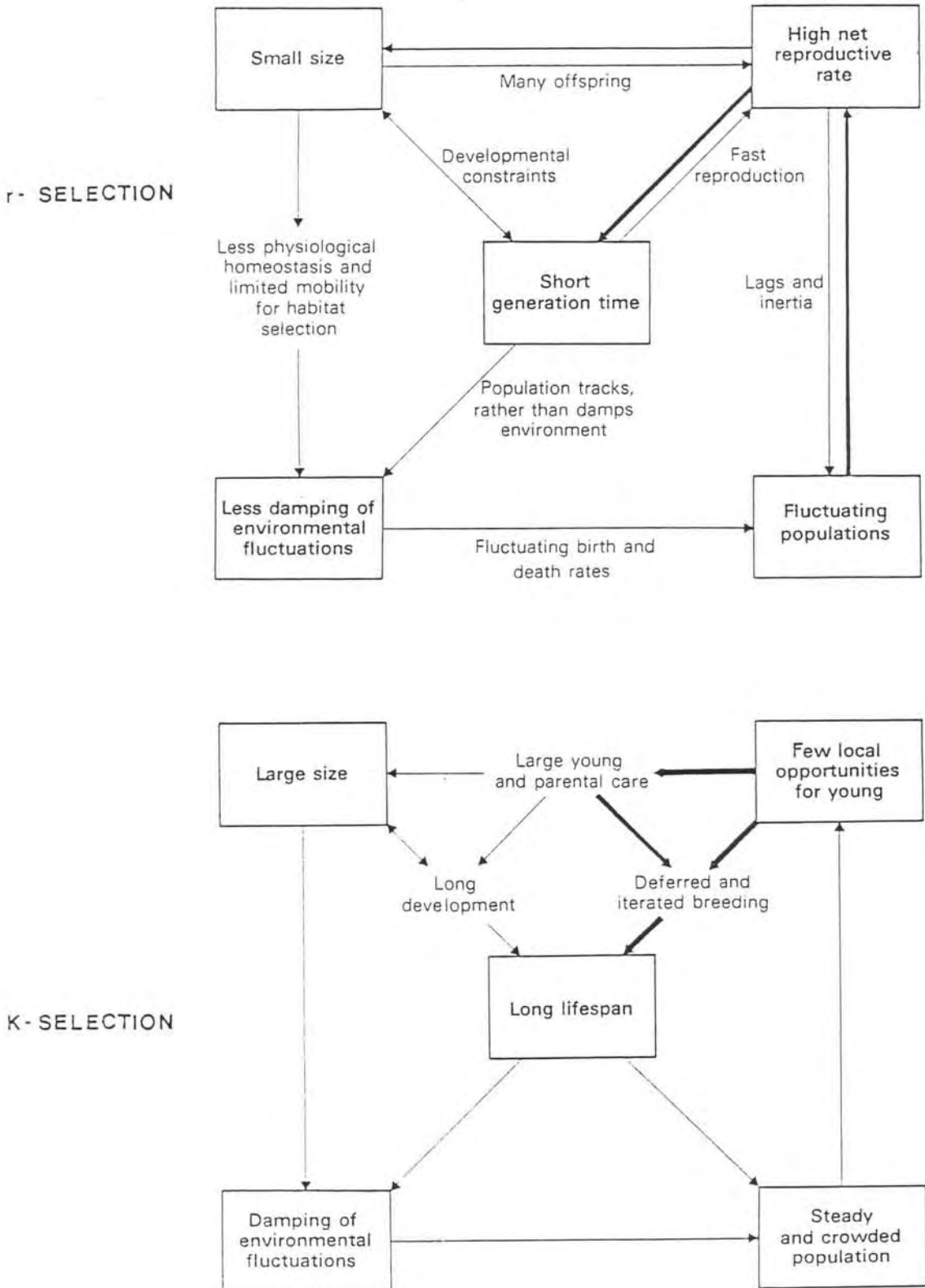
| Trait | Eastern Cape | Southern Cape | Text reference |
|-----------------------|--------------|---------------|------------------|
| Female body size | Small | Large | 9.3.3.1 |
| Age at first breeding | Early | Late | 10.3.6.2.b |
| Litter size | Large | Small | 10.3.2.3; 10.3.3 |
| Breeding interval | Short | Long | 10.3.6.2 |
| Longevity/Survival | Low | High | 11.2.4 |
| Energy storage level | Low | High | 9.3.2; 10.3.2.3 |

However, causally the situation does not seem to fit the models based on environmental or demographic variability/predictability over time as described in the previous section. There is no evidence of lower population density in the Eastern Cape, indeed the opposite seems more likely (11.2.1). Neither can the Southern Cape populations be considered more stable (11.2.1; 11.3.1) and if anything, the available data indicate covariation of juvenile and adult mortality in both regions (11.2.4). Thus, neither the r/K selection nor the bet-hedging hypothesis seems to apply.

As pointed out by Stearns (1976), many investigators try to give evolutionary explanations for phenomena which may merely represent phenotypic responses to factors such as differences in the prevailing

FIG.12/2: POSITIVE FEEDBACK LOOPS IN r- AND K-SELECTION

ex HORN (1978)



level of food availability. Also Calow (1979) noted that if resources are adequate to ensure all maintenance requirements, increased reproductive allocation need not entail survival costs.

The reproduction versus survival trade-off is based on the premise that total lifetime reproduction is to be maximized, i.e. parents should either have many offspring over a shorter life-span or fewer offspring over a longer life-span. However, is maximum total lifetime reproduction of a particular organism really the critical issue? The time factor may not be disregarded. The compound interest law demands that, all other things being equal, the fittest individual is the one which breeds first (Giesel 1976). The genetic pressure, even in a stable situation, will tend to favour early maturity and high birth rates, possibly involving short life (Murphy 1968). Natural selection favours genotypes with a high reproductive rate when resources are abundant, but genotypes with low resource demands have a selective advantage when resources are scarce (Boyce 1979, 1984). Accordingly it is argued here that the optimum life history tactic is the one coinciding with maximum genetic representation in the gene pool. This requires the maximum number of viable offspring to be produced per unit of time which is attainable under the prevailing resource conditions, and a plastic response to these conditions.

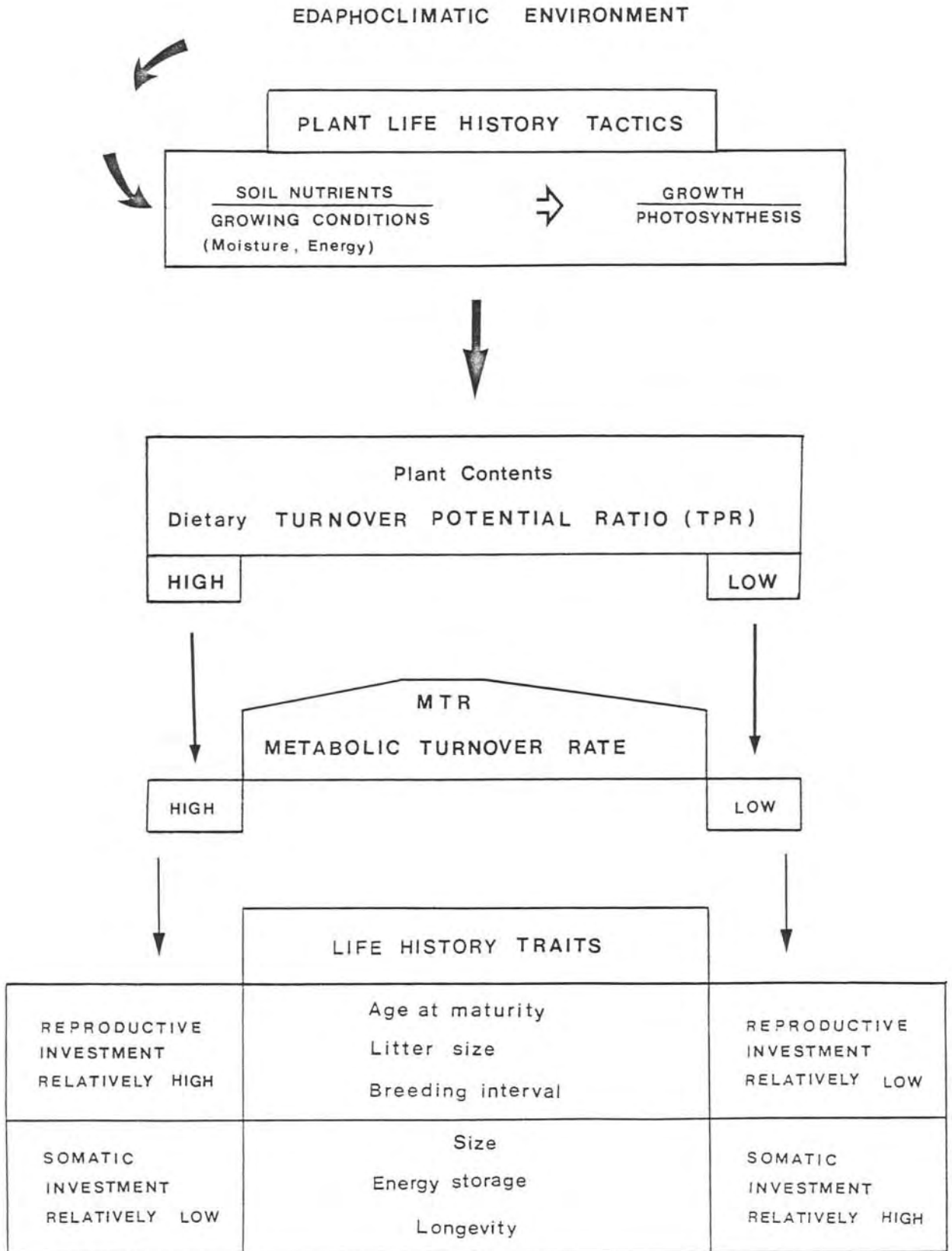
Whereas the r- and K-selection and bet-hedging models invoke differences in the variability or predictability of environmental factors in different habitats, Robson and Murie (1987) suggest that the mean conditions of environmental factors, or the magnitude of the one or other extreme, might be just as strong a selective influence as the variation or predictability of a factor (the resource limitation hypothesis). In the following section a model is developed to explain bushpig life history features which is in line with the resource limitation hypothesis.

12.3 Life history tactics: a model

12.3.1 The model: metabolic turnover limitation

The metabolic turnover limitation model is summarized in Figure 12/3. The main postulates are as follows:

FIG.12/3: POSTULATED LIFE HISTORY INTERACTIONS



- (I) In accordance with the particular niche occupied by the species, plants are adapted to their edaphoclimatic environment (8.2.4). Their response to the habitat is manifested in the life history tactics and in particular in the relative investment in tissue expansion (growth rate) versus tissue consolidation during the growing period (8.3.4.3).
- (II) Plant life history tactics thus affect the relative proportions of plant constituents on a continuum, indicated by the turnover potential ratio (TPR: 8.3.4.3). This index reflects the ratio of production (largely NPK) to maintenance nutrients (E: energy) and the rate at which both may be assimilated by herbivores (structural CHO content) (8.3.4.3).
- (III) It is proposed that, given sufficient maintenance nutrients, the level of available production nutrients assimilable per unit of time determines the optimal level of metabolic turnover of the consumer. The nutrient assimilation rate is strongly affected by the occurrence in the diet of diluting structural constituents or secondary compounds which reduce digestibility (8.3.4.2).
- (IV) The compound interest effect (12.2.3) requires an individual to breed as much and as early as possible for the greatest fitness, with due regard to viability of the offspring. The level of reproductive investment is dependent on the metabolic turnover rate, which in turn reflects the availability of highly assimilable production nutrients in the diet (high TPR).
- (V) Thus, genetic pressure results in the full use of available production nutrients, traded off against survival. Maximum reproductive investment as a result of high dietary TPR involves a higher survival risk since maintenance nutrients are then more easily limiting. Also, the higher metabolic turnover rates result in reduced longevity (12.3.4).
- (VI) If all available nutrients are to be used optimally for the maximum production of viable offspring per unit of time, two requirements must be met. Production nutrients must be fully utilised to realise the reproductive potential (offspring quantity) and excess maintenance nutrients (i.e. stored energy

arising as a result of restricted reproduction and low TPR) must be channelled into high quality offspring and enhanced parental survival.

Additional supportive evidence for the model is discussed in sections 12.3.2 - 12.3.4.

According to the model bushpigs in the Eastern Cape invest relatively more in reproduction and less in maintenance than those in the Southern Cape (Table 12/1). This agrees with the edaphoclimatic differences between the regions, as well as the nature of the diets (8.3.4.3). The difference in reproductive output also appears to be much greater than indicated by pregnancy rates, since there is a much higher proportion of lactating females in the Eastern Cape (10.3.6.2). Regional dietary differences also favour higher metabolic turnover rates in the Eastern Cape. These are particularly crucial during lactation, whereas lower metabolic turnover rates during gestation favour energy storage.

The later age of first breeding in Southern Cape bushpig females is believed to be the result of three factors: the longevity of territory owners; better survival of pre-reproductives (non-saturation of territories); and the prevention of successful breeding by subdominants through social aggression (territorial ownership as a prerequisite for breeding).

Sex ratio patterns (11.2.4: Table 11/5, 12.3.5) and modes of population regulation (11.3.5.2; 11.3.5.3) also fit the model neatly. Studies of a variety of species have revealed dichotomies similar to those reported here for the bushpig, although the authors concerned have not necessarily recognised or interpreted them as such (12.3.5).

12.3.2 Herbivore food resources, soils and climate

Plant growth form is a result of the niches available, i.e. of functional space (e.g. soil depth, cf Tinley 1982) and functional time (e.g. length of growing season). Tissue turnover (e.g. deciduousity versus evergreenness) is reflected by potential growth rate, which is

influenced by the availability of soil nutrients (8.2.4). The two salient features determining plant life history tactics are:

- Soil nutrient availability (→ growth rate)
- Conditions favourable to photosynthesis

The annual photosynthetic output depends on the proportion of the year with a favourable moisture balance and adequate energy. This is determined by the climate, but also by effective soil depth, through its direct effect on the availability of moisture and in providing the space for adequate absorption systems (roots).

A full discussion of interactions between edaphoclimatic factors and plant life history tactics is beyond the scope of this study. Trends relevant to it are those occurring across a gradient from savanna (C_4) through Valley Bushveld (CAM) to Knysna Forest (C_3) (prominent photosynthetic pathways in parentheses):

- Decreasing soil nutrient availability.
- Increasingly favourable conditions for photosynthesis.
- Increasing investment in maintenance relative to reproduction (tissue longevity, size, energy content, secondary compounds).
- Increasing growth in absolute quantity (somatic investment) in comparison to high growth rates and reproductive investment (extended versus fast growth).

The reasons for these trends were discussed in sections 8.2.4 and 8.3.4.3. Their implications for herbivores as they affect the availability and digestibility of nutrients were pointed out in section 8.3.4.3. These trends, as discussed in the various sections, also provide the link between plant prey and predator life history tactics and explain the plant/herbivore life history analogy. The turnover potential ratio (TPR: 8.3.4.3) partially resembles the M/C ratio of Bell (1982). It reflects the inherent growth capacities of the plants making up the herbivore diet relative to their photosynthetic output, and depends on the prevailing edaphoclimatic conditions.

A corollary is of interest. The likelihood and degree of fat storage is inversely related to the protein/energy (P/E) ratio of the diet (9.4.5). This in turn is directly related to the dietary TPR (8.3.4.3). It helps to explain why C₄ savanna grazers typically lay down very little fat, whereas herbivores feeding primarily or exclusively on C₃ plants (browsers) may carry larger fat deposits whilst still experiencing deficiencies in production nutrients for reproduction.

12.3.3 Metabolic relationships and life history traits

Fig. 12/4 illustrates four inverse relationships commonly recorded in the literature: body size/food; body size/reproduction; reproduction/longevity; longevity/food. They are applicable to the life history traits of the bushpig, as influenced by diet (12.2.3: Table 12/1). The two diagonals in Fig. 12/4 represent the reproductive and somatic investment axes. Whereas the four inverse relationships are probably not directly causally linked, the metabolic turnover rate (MTR) is central to the two axes. The MTR is defined and its role discussed in the next section (12.3.4).

(a) Food and body size

Inverse relationships between food quality and body size have been demonstrated for ungulates and primates, among others (*op. cit.* Clutton-Brock and Harvey 1983). On account of their higher metabolic rates, small species must select food of a relatively higher nutritional value than larger species (cf Clutton-Brock and Harvey 1983). In the TPR/MTR model (Fig. 12/4), food quality is represented by dietary TPR (8.3.4.3). A somewhat different perspective is given in section 12.3.5b.

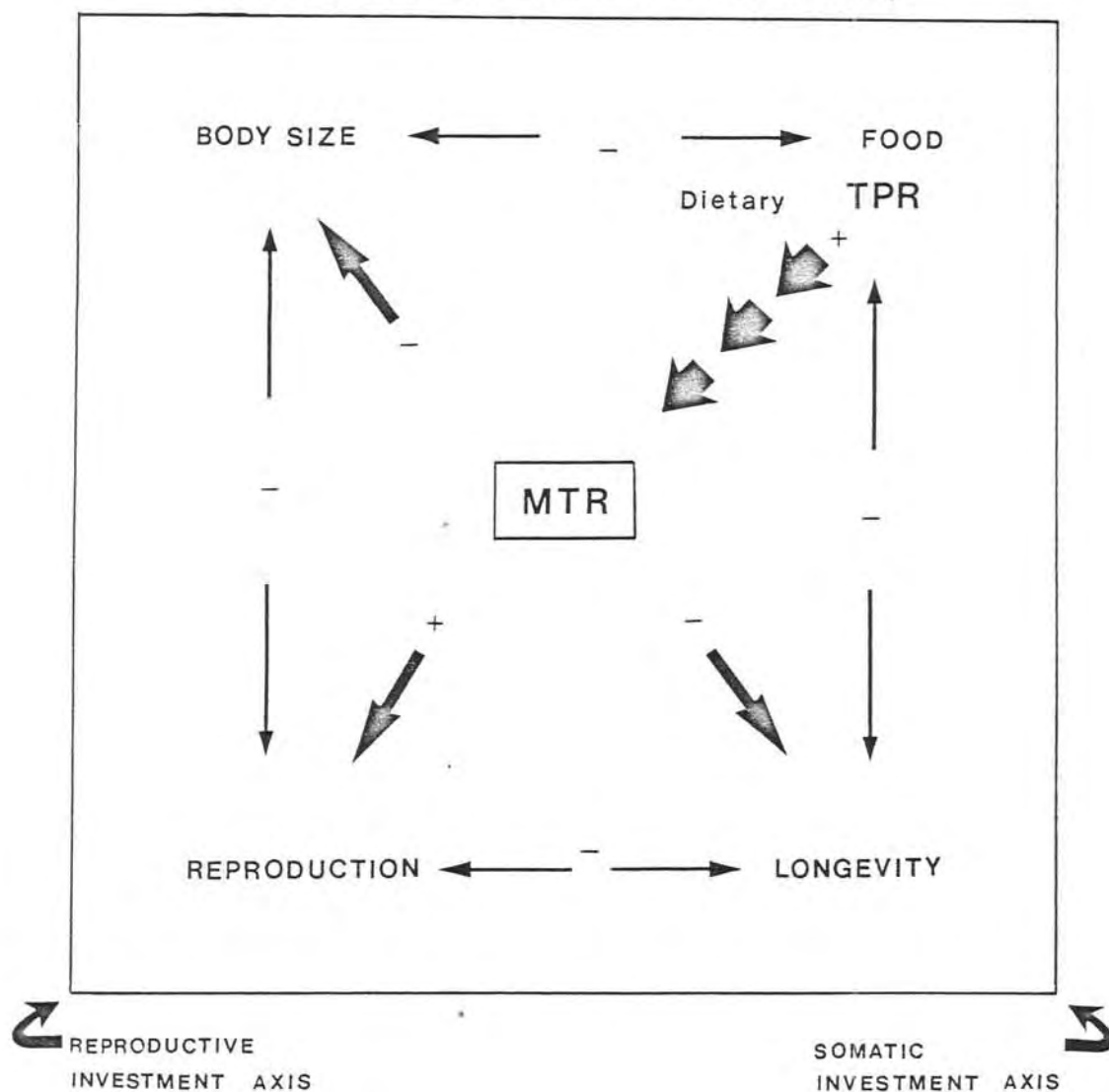
(b) Body size and reproduction

There is general agreement that a low reproductive potential is associated with large body size (Clutton-Brock and Harvey 1983; McNab 1983b). Exceptions occur where high quality offspring are critical for survival (Callow 1977).

FIG.12/4: INTERACTING LIFE HISTORY FEATURES: TPR/MTR MODEL

TPR: TURNOVER POTENTIAL RATIO MTR: METABOLIC TURNOVER RATE

<Positive (+) and inverse (-) interactions>



The lifetime productivity of a female depends on her reproductive life-span, mean interbirth interval and average litter size. These three factors vary according to both absolute body size and metabolic rate, the lowest reproductive rate being associated with the largest body size (Eisenberg 1983). The link between metabolic and reproductive rate is further explored in section 12.3.4.

(c) Reproduction and longevity

The widespread inverse relationship between reproduction and longevity is sometimes attributed directly to the cost of reproduction (12.2.1).

However, it is more likely to be the consequence of the association of high metabolic rates with high reproductive rates (12.3.4).

(d) Longevity and diet

The inverse relationship between unrestricted food intake and longevity has been verified in numerous studies (Berg and Simms 1960, 1961; Ross 1961, 1969, 1972, 1977; Barrows 1972, Walford 1974). Health and female fertility were positively affected by dietary restriction in rats (Berg 1960). However in rotifers, although they had the same lifetime reproductive output, those with an increased life-span due to dietary restriction took a considerably longer time to achieve it (Barrows 1972). This study indicates that the same appears to apply in the bushpig. Those from the Eastern Cape have a higher reproductive rate over a shorter life-span, while those from the Southern Cape have a lower reproductive rate over a longer life-span. This results in approximately similar lifetime reproductive outputs.

The amount and proportion of protein in the diet affects longevity more than the caloric intake, with the longest life-spans being associated with the lowest levels of protein intake (Ross 1961, 1969, 1972, 1977, Leto *et al.* 1976b). The absolute and relative intake of protein apparently affects life-span, but a relatively high protein diet early in life, followed by a low intake later in life, improved life-span compared to animals whose high protein regimen was uniform throughout life (Ross 1977). The protein factor appears to exert its influence irrespective of trophic specialization, presumably through its effect on the rate of metabolic turnover. Herbivores in almost all size classes appear to have a longer potential life-span than similar sized carnivores and insectivores (Eisenberg 1983).

The cause of this relationship is still unknown. One hypothesis suggests that ageing results from the continued use of certain genes, with a loss of or imperfections in the transcription of information. Feeding a low protein diet resulted in lower enzyme activities based on DNA, and assuming that low enzymatic activities per unit DNA indicate reduced use of genetic material, this result would support the hypothesis (Leto *et al.* 1976a). The finding that life-span decreases as

metabolic rate increases is not necessarily incompatible with the above hypothesis. Since metabolism is a steady-state process, this led Sacher (1978) to propose that a species' life-span is inversely related to the rate of entropy production.

12.3.4 Metabolic turnover rate and reproductive versus somatic investment

The inverse relationships discussed in the previous section have a common causal link related to metabolic rate. Both body size and longevity are inversely related to basal metabolic rate (BMR). The first relationship is embodied in the well-known Kleiber curve (Kleiber 1961). Placentals with high rates of metabolism have shorter life-spans than similar-sized species with lower rates (McNab 1983b).

On the other hand production processes are positively correlated with BMR. Mass-specific rates of basal metabolism are correlated positively with post-natal growth rates, fecundity, rates of lactogenesis and intrinsic rates of natural increase of mammalian species (Fenchel 1974, McNab 1980, 1983; Hennemann 1983, Glazier 1985a and 1985b, Derting 1989). Since the rate of ATP production for biochemical synthesis is limited by the rate of metabolism of an organism, these positive correlations are not surprising. The tempo of any biological process which depends upon the speed of biochemical synthesis is thus affected by the rate of metabolism (cf Glazier 1985a).

The above interactions with BMR are mainly based on interspecific comparisons. Intraspecific data for cotton rats (*Sigmodon hispidus*) did not support the expectations based on interspecific data, indicating that BMR *per se* may not have a primary influence on production rates (Derting and McClure 1989). Alternatively, Derting and McClure (1989) introduce metabolic capacity and metabolic scope, correlated positively with BMR, as probably more direct metabolic regulators of maximum rates of production and production potential both intra- and interspecifically. Metabolic capacity represents the maximum amount of energy an animal can mobilize at a particular time and under a specific set of ambient conditions when assimilated energy is not limiting. Metabolic scope is the difference between maximum metabolic rate, i.e.

metabolic capacity, and basal or standard metabolic rate. (Derting and McClure 1989)

What is here termed metabolic turnover rate (MTR: Figures 12/3 and 12/4) is partially correlated with basal or mean metabolic rate, but is not equivalent. It is probably more closely related to Derting and McClure's (1989) concept of metabolic capacity or metabolic scope. MTR is defined as being directly associated with the rate of biosynthesis and appears to be directly dependent on the assimilation rate of production nutrients. According to this definition, the TPR of the diet (8.3.4.3) through its influence on both the reproductive and somatic investment axes (Figure 12/4), is the main determining factor of MTR and thus of life history tactics. This is in contrast to the general view that energy is the determining factor. In terms of the model presented here, given sufficient maintenance energy, it is the availability and rate of assimilation of production nutrients (NPK) which are critical.

The link between diet and metabolic rate was discussed in section 8.3.4.3, where it was contended that a high dietary TPR favours a high metabolic rate. Thus, as shown in Figure 12/4, the TPR of the diet determines the metabolic turnover rate and therefore the sustainable level of reproduction. Conditions allowing and favouring a high reproductive investment require a high MTR, which is not conducive to large body size and longevity (12.3.3). This explains the inverse relationship between the reproductive and somatic investment axes (Figure 12/4).

12.3.5 Diet and life history phenomena

In this section a diversity of life history phenomena will be discussed and interpreted in terms of the TPR-MTR interactive life history model. New perspectives are provided, partly to support the general validity of the model, but also to stimulate further rigorous testing.

(a) Trophic specialization and life history tactics

For a given body size, the TPR of the diet increases along the herbivore, omnivore to carnivore gradient. If carnivores have

sufficient food they effectively have a diet with a high TPR. The expectation, according to the TPR-MTR model, would be that carnivores exhibit higher metabolic rates, have higher reproductive rates and shorter potential longevities. This is borne out by interspecific comparisons (Eisenberg 1983).

McNab (1980) found higher metabolic rates in herbivorous rodents and lower rates in granivores. This is consistent with the TPR-MTR model, as are the associated demographic strategies reported by Grodzinski and French (1983). They found that the herbivores (small animals selecting high quality greenery; i.e. high TPR) had high reproductive rates and low survival, whereas the granivores (low dietary TPR) had low reproductive rates and high survival rates. Omnivores had intermediate reproductive and survival rates. These patterns are also consistent with the observations reported by Taylor and Green (1976) according to which breeding rodent populations consumed more green stuff (fast-growing vegetable matter: high TPR) than non-breeding populations.

(b) Sexual dimorphism in body size

A large herbivore can consume relatively low quality food as well as that of better quality which is available, but a smaller individual cannot make use of food at the lower end of the quality spectrum. Thus, the larger the herbivore, the broader the food quality gradient it can exploit. For larger species there is greater scope for niche differentiation between the sexes in terms of body size dimorphism. This may be the reason why size dimorphism tends to be more pronounced in large sexually dimorphic mammalian species (4.4.3.3).

The optimal body size for a mammalian female is the one allowing the maximum sustainable MTR, i.e. that metabolic rate associated with the highest reproductive rate and degree of fitness (with due regard to offspring quality). Within limits set by opposing constraints, the smaller the body size, the lower are the quantitative food requirements and thus the greater the scope to select a high dietary TPR (within the constraints of the digestive system and the nature of food resource available). Small female body size thus favours maximum reproductive output. For males of sexually dimorphic species, size is considered

critical in terms of fitness (monopolization of females). Large size is selected for and its consequences are higher quantitative food requirements which have to be procured at the cost of food quality.

This often results in differences in diet and habitat selection which amount to a degree of niche differentiation between the sexes of the same species. Males should place a higher premium on somatic investment and females on reproductive investment and should select habitats which favour selection of relatively low and high TPR diets respectively. Females of sexually dimorphic species are therefore expected to be concentrated on ranges of relatively high nutritional quality. Numerous examples support this conclusion, for example, warthog (Cumming 1975), Red deer (Staines *et al.* 1982) and bushbuck (12.3.5c).

(c) Sex ratio patterns

From the foregoing it follows that if food availability is skewed towards either end of the quality gradient, this may affect the distribution of the sexes and their survival and hence the sex ratio. Females tend to preponderate when and where dietary conditions favour a high reproductive rate, i.e. where TPR is high. Bushpig sex ratio records conform to this pattern (11.2.4: Table 11/5), as do those for bushbuck presented in Table 12/2.

| Habitat characteristics | Males n | Females n | Sex ratio | Expected dietary TPR gradient |
|--|------------|--------------|--------------|----------------------------------|
| Indigenous forest (Goudveld) on nutrient-poor sandstone | 168 | 95 | 1,77 | Low High |
| Pine plantations (Goudveld) on nutrient-poor sandstone, but more arid + heliophilous | 90 | 88 | 1,02 | |
| Pine plantations (Witfontein) on nutrient-richer schists and phyllites | 330 | 544 | 0,61 | |

It is not clear whether these results are the outcome of male habitat preference/avoidance, differential mortality or both.

Under conditions where a diet with a high TPR is unavoidable and which generally lead to a shortened life-span, male survival may be particularly impeded. During controlled experiments, 33% food restricted male rats, i.e. at one-third less than *ad libitum* level, had about the same probability of death as females of the same age on an unrestricted diet (Berg and Simms 1960). Females at equivalent food intake levels had a greater longevity than males (Berg and Simms 1961). The significantly lower consumption of vertebrate meat by bushpig males compared to females is effectively selection of a lower dietary TPR and may be relevant to these arguments (8.1.2.2.e).

(d) Differential diet selection during gestation and lactation

The rate of lactogenesis is correlated with and proportional to the rate of adult metabolism. A higher rate of metabolism in both the mother and her offspring appears to synergistically permit a higher rate of conversion of maternal food into offspring tissue (Glazier 1985a). This is in accordance with the TPR-MTR model and may explain some of the features of bushpig diet selection.

The higher dietary TPR of Eastern Cape bushpig females may be a prerequisite for the larger litter sizes compared to the Southern Cape (8.3.4.3). Gestating bushpig females select a notably low TPR diet (high crude fibre content) and store energy in the form of fat deposits, while lactating females select a high TPR diet (8.3.3.2). Not only does the low MTR which we presume to be associated with the low TPR gestation diet favour energy storage, but these stores allow the animal to select a high TPR diet during lactation, since it does not need to concentrate on meeting its energy requirements. A diet high in TPR favours lactogenesis.

In addition, a high dietary TPR can be achieved by consuming fast-growing herbage, which is more available during spring. The advantages of spring for lactation are therefore obvious.

(e) Interspecific similarities in intraspecific life history patterns

In section 11.3.4 two examples were given of life history patterns similar to those of the Eastern and Southern Cape bushpigs. They involved beaver, *Castor canadensis*, populations in Alaska (Boyce 1981) and coyote, *Canis latrans*, populations in north-eastern Canada (Moore and Millar 1984), in habitats of divergent nutritional quality. Another particularly striking example is provided by Red squirrel (*Sciurus vulgaris*) populations studied by Wauters and Dhondt (1989).

In coniferous woodland, both body weight and longevity of females were significantly correlated with lifetime reproductive success. In deciduous woodland, only body weight had a significant effect due to early breeding in some females with poor survival. Whereas body weight was positively related to reproductive success in both coniferous and deciduous woodland, body length (i.e. skeletal size) and age were negatively related to successful reproduction in the deciduous habitat. In the deciduous area a small female was more successful at reproducing than a larger female of the same weight (Wauters and Dhondt 1989).

Dominance, coupled to age, was of greater importance for successful breeding in coniferous than deciduous woodland. Any equivalent higher rank position was attained at an earlier age in deciduous woodland. Thus, in the coniferous woodland only alpha females produced offspring and only old females acquired alpha status. These constraints were more relaxed in the deciduous habitat (Wauters and Dhondt 1989).

It is well-known that deciduousity indicates relatively nutrient-rich site conditions (as in the Eastern Cape) whereas nutrient-poor sites are usually occupied by evergreen vegetation (like conifers) as in the Southern Cape (8.2.3, 8.2.4). The life history trends of coniferous and deciduous woodland Red squirrels are exactly equivalent to those of Southern and Eastern Cape bushpigs. They conform to the TPR-MTR life history model. In addition to reproductive patterns related to body size and survival (Table 12/1), the equivalence extends to the role of dominance and age in the context of life history interaction (10.3.6.2).

(f) Latitudinal trends in life history patterns

The TPR-MTR model deals with variation in food quality over space. However, fluctuations of food quantity over time may also play a role in determining life history tactics. Differentiating between the spatial quality and the temporal quantity components of food availability is often problematic. The difficulty of explaining latitudinal trends in life history patterns is a case in point.

Tropical forms of an organism often begin reproduction later than temperate forms, have reduced litter sizes (Cody 1966) and higher rates of survivorship (Giesel 1976). The larger litter size in the European wild boar compared to the bushpig is a good example. Several explanations have been offered for this widespread phenomenon (Giesel 1976). Relatively low soil nutrient levels and long growing seasons in the tropics typically favour vegetation with a low TPR. The explanation for the lower population turnover rates in the tropics may simply be found herein, as predicted under the postulates of the TPR-MTR life history model. Due to lower prey population turnover under such conditions, the life history characteristics of tropical carnivores could be shaped in an analogous direction.

Alternatively, in the temperate zones, the constraint of uncertain adult and offspring survival places a premium on high r (Murphy 1968). The final differentiation between the two competing models is beyond the scope of the present study.

12.4 Interspecific synopsis of suids

This section attempts to provide a synoptic synthesis of bushpig socioecology and to compare it to other species.

In various sections it has been argued that patterns of food dispersion over space and time (8.2.5: Table 8/3) underlie many crucial aspects of bushpig ecology. Foraging in herbivores is subject to a quantity/quality trade-off, interacting with body size. Food is often available in quantity, but the quality is limiting. Digestive success is therefore critical. For carnivores quality is usually available, but quantity is limiting. Here capture success is critical. Omnivores

occupy a somewhat intermediate position. They have the opportunity of selecting food items from both the plant and animal kingdoms, but they also face a combination of the foraging problems associated with both, and are subject to digestive and search constraints. Furthermore omnivores are not specialized to solve the problems of digestion and capture. The food items which are digestible and procurable are therefore characteristically dispersed and foraging success is critical for an omnivore.

It was suggested that food dispersion has implications for bushpig group size and structure (4.4.1), population densities (11.3.1; 11.3.2), habitat use patterns (6.2.2; 6.3.2) and sociospatial organization (territoriality: 4.4.2.2; monogamy: 4.4.3.2). Although also omnivorous the food resources of the European wild boar are concentrated in time and quality (seasonally pulsed) due to the edaphoclimate conditions of temperate regions. The food resources of the giant forest hog as grazer/browser and the warthog as grazer/rooter are also concentrated (8.2.5). As a result these three suid species tend to occur in larger multimaternal groups and at higher population densities (or biomasses). They are also non-territorial and polygamous, in all these respects thus differing from the bushpig. In passing it is of interest to note possible socioecological analogies between the three African suids and non-suid taxa with similar foraging constraints: the giant forest hog with the elephant, the warthog with a medium-sized grazing antelope and the bushpig, the "canid pig", with a social organization similar to that of the jackal, fox or coyote.

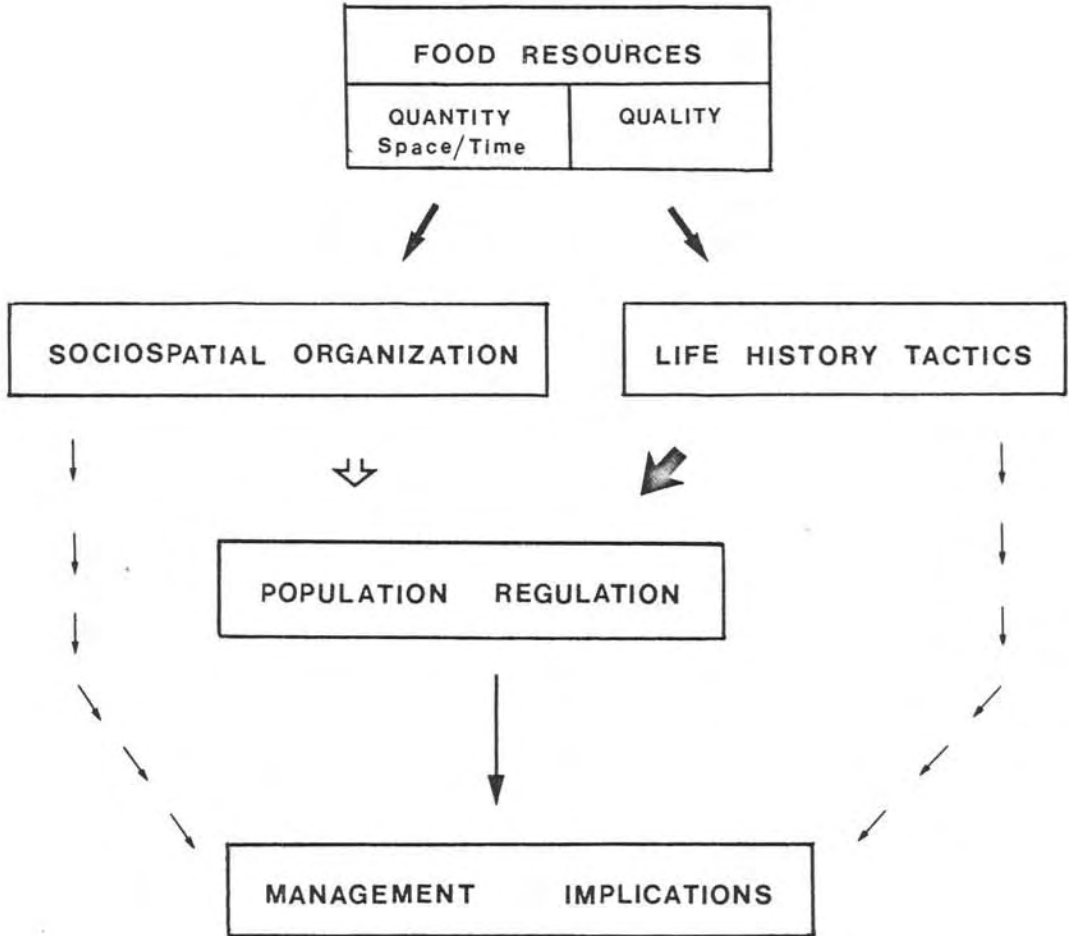
Whereas food quantity is strongly implicated in shaping the species socioecology, food quality, indexed by dietary TPR, is a strong co-determinant of life history tactics, as indicated in this chapter. The expected TPR gradient is paralleled by the fecundity gradient of the three African suid species: giant forest hog < bushpig < warthog (10.4.3). Where dietary TPR is high, high fecundity is favoured. Here one can expect fluctuations in food quantity to exert a greater influence on mortality. We therefore have a pattern where the reproductive rate remains relatively invariant, while the mortality rate fluctuates in response to quantitative fluctuations in food resources. The reverse can be expected where dietary TPR is low. The point was

made in the discussion of population regulation in the form of the buffalo-elephant dichotomy (11.3.5.2). Warthog and Eastern Cape bushpigs evidently fall into "the buffalo-class" (invariant reproduction, variable mortality) and the giant forest hog and Southern Cape bushpigs in the "elephant-class" of population regulation (relatively invariant mortality and variable reproduction).

In the European wild boar, the amplitude of fluctuations in food resource can be so great that both reproductive and mortality rates fluctuate accordingly. This may explain the comparatively large litter size and the sensitive reproductive tracking of food resource fluctuations evident in the European wild boar (10.4.3: Table 10/17; 12.3.5.f)

Concentration of food and fluctuations in its availability, as well as spatial variation in its quality, all play a role in population regulation. These influences may be modified by territoriality, as in the bushpig (11.3.5.3). Thus, both life history tactics and sociospatial organization shape the mode of population regulation (Figure 12/5). All these aspects have implications for the management of wildlife resources.

FIG.12/5: SYNOPSIS OF SOCIOECOLOGICAL INTERACTIONS



13. MANAGEMENT IMPLICATIONS

13.1 Control

13.1.1 Omnivorous suids as agricultural problem animals

Omnivorous suids are predestined to be agricultural problem animals for two main reasons: they occupy the same dietary niche as man and natural foods are scarcer and of poorer quality than those provided by agricultural crops (cf 8.1.3.1, 8.3.3.2, 8.3.3.7). Thus Mackin (1970) found that the amount of damage to agricultural crops depended on the availability of beech and acorn mast rather than population densities of European wild boar *per se*.

The European wild boar causes extensive damage to agricultural crops (Mackin, 1970, Paslawski 1975, Briedermann 1986), which feature prominently in its diet in most areas of Europe (Briedermann 1986). Potatoes and grains such as rye, oats, wheat and barley are the ones mainly involved (Mackin 1970, Ueckermann 1977, Briedermann 1986). When rooting over planted pastures in their search for insects and underground plant organs, the pigs may also seriously reduce pasture production (Mackin 1970, Barrett *op. cit.* Hone 1980, Briedermann 1986).

In many European countries, compensation is payable to the farmer in the event of damage to his crops by wild boar. In Poland, for example, the area of agricultural crops damaged during a single year was estimated to be 37 000 ha (Fruzinski 1985). The cost of compensation and control measures greatly affect the profitability of wild boar harvesting through hunting (Briedermann 1986).

Considerable agricultural losses are also caused by feral pigs in Australia. They amounted to 75 million Australian dollars (ca R67 million) during 1979/1980 (Tisdell 1985). The main crops involved were wheat, sorghum, barley, oilseeds, sugar cane, oats and maize, which were eaten, trampled and rooted out. The pigs also preyed on lambs, damaged fences and watering points, initiated soil erosion by rooting and acted as carriers of diseases of domestic livestock.

Wild boar in Russia were reported to attack weakened sheep and to attack flocks, carrying off lambs (Sludskii 1956). During their study in New South Wales, Australia, Pavlov and Hone (1982) found that lambs were caught by feral pigs in 10 of 42 cases observed (23,8%). Their predatory behaviour entailed running down their prey. Successful chases were always short and fast and usually took place in open habitat. Rowley (1970) however points out that starved lambs occur frequently and are easily taken by predators, so that the impression that a large number of losses are due only to predation, is false. The majority of starving lambs would not survive. Pigs killing them are virtually feeding on carrion. Opportunistic scavenging on afterbirths and dead lambs by feral pigs may initiate killing behaviour (Pavlov and Hone 1982). However, only a small number appear to become habitual lamb predators (Pavlov *et al.* 1981).

Bushpig damage follows much the same pattern, involving crops, pastures, fences and small stock predation. Crops most affected in South Africa are maize, wheat, potatoes, sweet potatoes, pineapples and sugar cane (Thomas and Kolbe 1942, Milstein 1971, Skinner *et al.* 1976, Walker 1986, Cooper and Melton 1988). In addition, damage to a wide variety of crops has been reported from Africa generally, including groundnuts, millet, field peas, beans, cassava roots, pumpkins, marrows, barley, sorghum, tomatoes and other vegetable crops (Thomas and Kolbe 1942, Sowls and Phelps 1968, Dorst and Dandelot 1970, Kingdon 1979, Smithers 1983). According to evidence obtained in this study, maize, wheat, lucerne and pineapples are those most seriously affected in the Cape Province.

Damage to small stock fences, particularly if they are jackal-proof, is considered a serious nuisance (Milstein 1971), especially in the Eastern Cape. In the same region bushpigs are reported to attack and devour small stock in poor condition, particularly new-born lambs and kids. However, this type of damage appears to be sporadic.

Allegations of the bushpig acting as a disease vector (swine fever: Thomas and Kolbe 1942; trypanosomiasis: Sowls and Phelps 1968) and playing an important role as host for tsetse flies remain unverified.

13.1.2 Damage control options

Damage to agricultural crops may be reduced either by reducing the numbers of the problem animals or by protecting the crop itself. Crop protection measures are constrained by economics and population control is difficult to implement. In both cases the input/output ratio must be acceptable. Here follows an evaluation of available crop protection and population control measures for omnivorous suids.

(a) Supplementary feeding

In Europe, supplementary feeding under appropriate circumstances has proved successful in reducing or preventing crop damage by wild boar (Paslowski 1975, Briedermann 1986). This technique is more appropriately termed distraction feeding ("Ablenkfütterung") and serves to hold the animals in natural areas away from agricultural fields, relying on their safety requirements (cf 6.4.2) and pre-empting their food requirements (Briedermann 1986). Vassant *et al.* (1986) demonstrated that supplementary maize can reduce damage to cereal crops by wild boar if supplied regularly and in sufficient amounts in the adjacent forests. Consumption of supplementary food decreased damage in spite of increasing wild boar numbers (Andrzejewski and Jezierski 1978).

According to Briedermann (1986), a daily quota of 5 kg maize is sufficient to attract 10 wild boar away from agricultural fields. This involves ca 1 ton of maize for the required period of about 5 months. Such an input is only economically justifiable if loss compensation payments have to be made and the wild boar harvest yields adequate returns.

No compensation is payable for damage caused by bushpig. Neither is it likely that hunting take-offs could be increased sufficiently by supplementary feeding to make it economically viable. The bushpig's reproductive turnover (13.2.2) and strong sociospatial pressure to disperse make it unlikely that supplementary feeding would be an effective approach to damage control.

(b) Repellents

Visual, olfactory or acoustical repellents are largely ineffective against wild boar since they lose their effectiveness after relatively short periods of operation (Briedermann 1973, Paslawski, 1975, Ueckermann 1977, Briedermann 1986). They are similarly of limited use in the case of bushpigs, but may play an auxiliary role if crops are also patrolled.

(c) Fencing

Although expensive, animal-proof fencing is the only permanent solution. However, since cost limits its application, it usually only displaces the problem to unprotected fields (Ueckermann 1977, Briedermann 1986).

Electric fencing is less costly than pig-proof fencing and can be shifted (Briedermann 1986). It is best suited to smallish fields which need to be protected for a short time (Ueckermann 1977). McKillop and Sibly (1988) have reviewed the behaviour of animals at electric fences and its implications for management. Wright (1972) reports of a case where electric fencing was successful in preventing damage to seed crops. Hone and Atkinson (1983) tested various fence designs. Their results show that electrification significantly reduced the number of feral pigs crossing fences. When not electrified, fine-meshed netting fences were necessary to exclude pigs. They found electrification to be the cheapest and simplest method of modifying existing fences.

The economics of electric fencing depends on its efficiency at stopping pigs, initial and annual costs, life span, area enclosed, perimeter length and the density and value of sheep or crops being protected (Hone and Atkinson 1983). From their limited results, Cooper and Melton (1988) conclude that well-maintained electric fencing can be used to protect crops against bushpigs. Electric fencing can surely be made to work, but there are economic and practical constraints.

(d) **Patrolling of crops**

It is considered impractical to patrol crops on a large scale, especially without the added incentive of hunting. Its success depends on the individual, the shelter afforded to the problem animals by the crop and the weather. Dedicated participants are either not available or expensive (Milstein 1971).

(e) **Trapping**

Bushpigs have been captured with pit traps, box traps and boma traps. Walker (1986) found pit traps to be quite successful especially around small fenced fields. He tested various designs of walk-in-traps (box traps) without much success, since bushpigs were reluctant to enter them. Milstein (1971) also regarded traps as generally ineffective.

In trapping suids there appear to be two main problems:

- (1) They are reluctant to enter traps, especially box traps with relatively small openings; and
- (2) capture success is low when alternative food resources are abundant, e.g. agricultural fields in season (Fox and Pelton 1977). Feral pigs were most easily trapped when native food was scarce (Coblentz and Baber 1987).

Both problems are encountered in capturing bushpigs. Wide entrance boma traps are effective, but capture success is strongly dependent on overall food availability (8.2.6).

(f) **Poisoning**

Attempts to poison bushpigs in Zimbabwe proved unsuccessful (Grzimek 1972 ex Cooper and Melton 1988). However, the use of an effective, tasteless and odourless poison in an acceptable bait could be very effective (Milstein 1971, Coblentz and Baber 1987, Choquenot *et al.* 1990). This method is rather unselective, liable to misuse and illegal. It is not considered an acceptable option for controlling native problem animals.

(g) Hunting

Bushpig hunting may take one of three forms: waiting in fields at night, drive hunts and hunting with dogs during the day. According to a survey reported on by Milstein (1971), 854 bushpigs were destroyed by hunting in South Africa over a 12 month period.

Shooting at night over baits or in fields is hampered by the irregularity of visits by pigs and success is sporadic (Thomas and Kolbe 1942). Even this requires persistent and keen hunters. Drive hunts involve a great effort in terms of manpower and bushpigs are difficult to drive from bush (Smithers 1983).

Hunting with the aid of dogs appears to be the most effective method (Thomas and Kolbe 1942, Milstein 1971). This was confirmed during the present study, since it provided most of the Eastern Cape study material. To be successful, dogs, especially the trackers in the pack, must be experienced and trained to bushpig alone. The problem with this method is that hunts often cross the boundaries of neighbouring properties so that the neighbour's approval is required.

It is the policy of the Department of Environment Affairs (Forestry) to protect all wild animals occurring on State forest land, but section C of Forest Management Instruction 7/5/1 (old file A20/1/1 dated 9 October 1980) makes provision for problem animals to be controlled in exceptional cases. Under this directive "hot pursuit" across State forest boundaries is permissible. It is interpreted as following an animal sighted on the adjoining private property or tracks along the escape route of an animal where circumstantial evidence confirms very recent damage by the species of animal concerned (Departmental files: A20/7/8/2 of 19 December 1983). Such action is subject to prior approval of the Regional Director of the forest region concerned.

Crop damage should not be assessed merely by its visual impact. Losses should be quantified and expressed as a percentage of income or overall operational costs. Although bushpig damage can be of considerable local significance it is not a major agro-economic problem in the Cape Province, nor elsewhere in South

Africa. This is reflected by the change in legal status of the species. In terms of Ordinance 26 of 1957 (Ordinance on Problem Animal Control), bushpigs were classed as "Proclaimed problem animals" in the Cape Province. Since the promulgation of the Nature and Environmental Conservation Ordinance, No. 19 of 1974, they have been considered "unprotected wild animals".

In terms of proclamations issued under this Ordinance, for example Proclamation No. 105/1989 (Cape Province: Hunting seasons, daily bag limits and hunting by the use of prohibited hunting methods), the bushpig may be hunted all year round. Hunting at night, with artificial lights, snares, traps, trap guns and with dogs is permissible.

Before deciding on a method of control, a farmer would need to assess the economic loss caused by bushpigs and weigh this against the cost of control (Cooper and Melton 1988). At present hunting with dogs appears to be the most cost effective measure. However, direct population control provides only temporary relief. Its effectiveness is influenced by population densities, the resulting pressure to fill territorial vacancies, or the crowdedness of interterritorial space. The most cost effective option may sometimes be to do nothing.

13.2 Utilization

13.2.1 Harvesting of *Sus scrofa*

Fruzinski (1985) reviewed statistics on wild boar harvests in certain European countries (animals harvested per annum in parentheses): Russia (54 600 in 1981), Poland (80 000 in 1980), France (60 000 in 1983), Italy (8 000), Yugoslavia (8 000 in 1982), Czechoslovakia (12 000 in 1980), Western Germany (35 000 - 50 000) and central Germany (>100 000). The maximum annual harvest of 127 800 was achieved in central Germany during 1981, an offtake of more than 6 animals/100 ha (Briedermann 1986). Under intensive sustained harvesting, the offtake is generally of the same order of magnitude as the spring (prefarrowing) population density, commonly between 0,5 to 6,0/100 ha/annum (cf Hasselbach 1970, Dietrich 1984, Briedermann 1977, 1986, Vassant *et al.* 1986). In certain

areas, for example central Germany, harvests of between 110% and 180% of the spring populations are considered sustainable and are also realised (Hennig 1981). Rates of increase are on average 150%, ranging between 100% and 200% (Briedermann 1986).

The high reproductive rate of the European wild boar permits high harvest levels from populations with relatively low densities. High growth rates add to biomass productivity of the species (Briedermann 1970b, 1971b, 1973, 1986). A sophisticated approach to harvest regulation is implemented in Germany, which allows the maximum utilization of populations for both meat and trophies.

According to Ueckermann (1977), Hennig (1981) and Briedermann (1986) the overall management goal is a population with a balanced age structure and a tolerable density in terms of damage to agriculture, but at a density allowing sustainable harvest of adults with acceptable trophies. Annual hunting regulations and quotas are set for particular areas according to local management goals and the expected reproductive success. To obtain a maximum return of both meat and trophies, a normal age structure is favoured. This is characterised by a pyramid culminating in 7 year old individuals ("Zielalter"), reflecting the fact that desirable trophies are carried by males of 5 - 8 years of age. If individuals were allowed to become much older many trophy-bearing adults would be lost to natural mortality. A harvesting guide-line to maintain the required age structure, is to take about 75% of juveniles, 15% of yearlings and 10% of adults annually. This provides about 3 - 5% of trophy boars per annum (as a percentage of the total population). Harvest quotas of juveniles and yearlings are adjusted according to annual fluctuations in reproductive success.

13.2.2 Bushpig harvesting

The possibilities of managing bushpig harvesting are much more limited than in the case of the European wild boar.

- (I) Reproductive turnover in the bushpig, and therefore the potential harvestable surplus, is substantially lower (10.4.3). It is also generally true that herbivore populations occupying nutrient-poor

environments are more vulnerable to hunting pressure than those from nutrient-rich environments (cf Bell 1982). The huntable surplus in the Southern Cape is accordingly lower than in the Eastern Cape (10.4.4.2).

- (II) Population densities are comparatively low (11.2.1, 11.3.2), permitting limited harvests per unit area. Density estimation and the determination of population structure are both difficult (11.3.1) and economically unjustifiable.
- (III) As a result of territoriality (4.3.2), bushpigs are spatially spread out. The harvesting of adults nearly always results in depletion of a local population, which must be "recolonised". When territories or home ranges are emptied, the survival of non-territorial animals is improved, thus there is mortality compensation. The rate at which depleted areas are re-occupied is a central factor in determining the potential harvest rate. It depends on (I) the degree of territorial saturation, (II) recruitment pressure, i.e. reproductive success, (III) phase of population density fluctuations and (IV) the proximity of reservoir individuals.

The time taken to complete the recolonisation process after a territory owner has been removed i.e. to re-establish a bonded territorial pair, may often result in the loss of a breeding season. This is not true of species with a non-territorial and more gregarious social organisation, such as the European wild boar. Whereas the shooting of dominants may even have a "stimulatory" effect on wild boar reproduction (10.4.4.3), the opposite tends to be true of bushpig.

Considering these factors it is evident that fine-tuned, intensive regulation of bushpig harvesting is neither practical nor justifiable in terms of cost/benefit. In any event, sustainability is not a concern for landowners interested in damage control. However, it can be achieved to some degree by applying simple common-sense rules.

One is to separate hunting areas from refuges. A refuge is an area of suitable bushpig habitat where no hunting takes place. The longer the perimeter of hunting to adjoining refuge area, the greater the

recolonisation rate and thus the potential harvestable quota per unit of time and hunting area. If the refuge is large enough unrestricted hunting should be possible outside, to the point where the hunting effort exceeds acceptable levels. This approach does not require population density estimation.

Thus, on a farm of say 1 000 ha, surrounded by a refuge, unrestricted hunting should be possible and the annual take-off may substantially exceed the population which the farm itself could support at carrying capacity. Should a number of adjoining farmers, covering a large area, want to hunt bushpigs on their combined properties on a sustainable basis the periphery effect would be reduced. Crude harvest guidelines would be required. The following are tentatively proposed: 1 adult bushpig per 400 ha in the Eastern Cape and 1/700 ha in the Southern Cape. These take account of regional differences in productivity. The underlying assumption is that each breeding pair produces one harvestable recruit into the adult population (2 years and older) per annum.

A large farm could be subdivided into hunting and refuge zones. The optimum size, locality and configuration of refuges would have to be determined empirically, according to the characteristics of the area, taking habitat preferences into account. As a rule refuges should be relatively compact and large enough to contain at least a number of territories.

13.3 Conservation

The bushpig is protected in a number of conservation areas controlled by different agencies. The infrequent hot pursuits allowed into these reserves have little impact on populations. In the Southern Cape and Tsitsikamma forest regions, conservation areas harbour a substantial proportion of the regional bushpig populations. This is not so in the Eastern Cape where there are fewer reserves. On their own they could not safeguard the survival of the bushpig. However, large healthy populations occur on private land. In the Southern Cape bushpig habitats have a low potential for intensive agriculture and there is little pressure for agricultural development.

As noted above, the bushpig has not been classified as a proclaimed problem animal since 1974. Efforts at control have not yet permanently reduced the range of the species in South Africa. In the long-term, human population increases may lead to greater habitat fragmentation and more intensive population control. The maintenance of minimum viable populations will accordingly become increasingly important for the survival of the species. In view of its inherently low population densities, large areas would be required.

Determining minimum viable populations is a complex issue as yet unresolved. It involves biogeographic patterns, genetic considerations and changing environmental conditions (Samson *et al.* 1985). Population fluctuations and patchiness of suitable habitat clearly affect extinction probabilities of species. Genetic considerations are particularly relevant in the management of isolated populations because (I) interdemographic genetic exchange may become restricted as populations or demes become isolated from larger genetic pools and (II) finite isolated populations are subject to increased prospects of genetic drift, inbreeding and extinction (Miller 1979, Samson *et al.* 1985). They emphasise the important role of large conservation areas where the species can be protected.

Bushpig conservation on State forest land is essentially a matter of habitat conservation and law enforcement. The question of whether hunting is permissible and compatible with conservation priorities needs to be addressed in this context. On the ca 100 000 ha of state-controlled indigenous forest and pine plantation in the Southern Cape (including potentially suitable habitat in both the Southern Cape and Tsitsikamma forestry regions) we expect a total bushpig population of only 350 - 450 (11.2.1). According to the "rule of thumb" of 1 harvestable bushpig/700 ha of suitable habitat (13.2.2), about 140 animals at most could be hunted annually. However, substantial unhunted populations should be maintained in and around nature reserves as a conservation priority. Much of the State forest land lies in a long, narrow strip with a width roughly equivalent to only 1 - 5 home range diameters. Control hunting on adjacent private land varies in intensity. In view of these factors, hardly more than half of State forest land could be designated for hunting. The area involved could

accordingly yield something of the order of 70 huntable bushpigs per annum. Economically bushpig hunting would hardly be worthwhile. Taking a broader regional perspective, the populations on State forest land should rather be seen as the reservoir from which populations on private land, depleted by control or recreational hunting, could be replenished.

The bushpig as a species has held its ground in South Africa. No significant contraction in its distribution over the period of historical record is evident (Du Plessis 1969, Skead 1980, 1986). It has benefited rather than suffered from agricultural development. Generally, the extent of suitable bushpig habitat has remained the same and the habitat preference and habits of the species make it difficult to hunt. Its conservation status can thus be considered good. Should the human population increase proceed as predicted, the resulting pressures may alter this in the future. Potentially threatening developments should thus not be neglected in long-term conservation planning.

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