

**SOCIAL STRUCTURE OF THE LIZARD, *CORDYLUS GIGANTEUS***

**BY**

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Thesis presented in partial fulfilment of the requirements for the degree of

**MASTER OF ZOOLOGY**

at the Department of Zoology,  
Faculty of Natural Sciences,  
University of Stellenbosch

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December 2000

## DECLARATION

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

## ABSTRACT

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*Cordylus giganteus* is the largest lizard species of the family Cordylidae and is restricted in distribution to the highveld grasslands of the Free State, South Africa. Previous work on life history and physiological ecology suggested the need for further investigation into the social structure of *C. giganteus*, with the aim of improving knowledge on South African herpetofauna and contributing towards better conservation plans. Observations, recaptures, behavioural experiments and chemical analyses were made to investigate chemical communication, movements around and between burrows, spatial distribution and response to intruders. Sexual variation was found in both femoral gland proteins and lipids, while seasonal variation was found in lipids. Femoral gland proteins do not vary intra-individually. These results suggest alternate roles in communication for femoral gland proteins and lipids. Female *C. giganteus* showed a possible discriminatory ability between their own femoral gland secretion and that of other individuals. Burrow movements were characterised by very little time spent between burrows, high burrow fidelity and limited dispersal during seasons, other than movements associated with mating activity. Lizards remained in very close proximity to burrows. Male and female burrows were distributed in a clumped fashion, while male burrows were distributed randomly and female burrows were distributed randomly with respect to one another. There was a high degree of spatial association of male and female burrows. Male and female resident lizards responded aggressively to experimentally introduced conspecifics of the same sex, but exhibited no differential response towards neighbours or non-neighbours. Males and females exhibited similar levels of aggression towards intruders. The social system of *C. giganteus* can be defined as site defence, with very low frequencies of agonistic interactions. The social system of *C. giganteus* seems to be well suited to other aspects of its life history.

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## UITTREKSEL

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*Cordylus giganteus* is die grootste akkedis spesie van die familie Cordylidae en is beperk in verspreiding tot die hōeveld graslande van die Vrystaat, Suid Afrika. Vorige werk oor die lewensgeskiedenis en fisiologiese ekologie het aangedui dat verdere inligting oor die sosiale struktuur van *C. giganteus* nodig is, met die doel om kennis oor Suid-Afrikaanse herpetofauna te verbeter, en om beter bewaringsstrategieë daar te stel. Observasies, hervangs, gedragseksperimente en chemiese analyses was uitgevoer om aspekte oor kommunikasie, bewegings tussen en om gate, gat verspreiding en reaksie teenoor indringer akkedisse, te bestudeer. Femorale klier afskeidings het seksuele variasie in beide die proteïene en die lipiede getoon, terwyl net die lipiede seisoenale variasie getoon het. Femoral klier proteïene het nie seisoenale variasie binne individue getoon nie. Hierdie resultate dui op alternatiewe funksies vir die femoral klier proteïene en lipiede. Wyfie *C. giganteus* het moontlik tussen hulle eie femoral klier sekreet en die van ander wyfies onderskei. Baie min tyd tussen gate, hoë lojaliteit teenoor gate en beperkte bewegings weg van gate het gat bewegings gekarakteriseer. Net gedurende die paarseisoen was daar meer bewegings tussen gate. Andersins, het akkedisse baie naby hul eie gate gebly. Mannetjies en wyfies gate was naby mekaar versprei, terwyl mannetjies ewekansig teenoor mekaar versprei was, en wyfies ewekansig teenoor mekaar versprei was. Die verspreiding van mannetjies en wyfies het baie van die verspreiding van die ander geslag afgehang, sodat daar 'n groot assosiasie tussen hulle was. Akkedisse wat gate bewoon het, was baie aggressief teenoor indringer akkedisse, maar het geen verskil in reaksie teenoor naburige akkedisse of nie-naburige akkedisse getoon nie. Mannetjies en wyfies het dieselfde aggressiwiteit teenoor indringers getoon. Die sosiale struktuur van *C. giganteus* kan geklassifiseer word as skuilings-beskerming, maar met baie lae frekwensies van sosiale interaksies. Dit blyk dat die sosiale struktuur van *C. giganteus* baie goed pas by ander aspekte van sy lewensstyl.

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## **DEDICATION**

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*Dedicated to my late grandparents, George Frederick van Wyk and Alice le Riche, who always nurtured an interest in my progress as a naturalist. May this follow in the footsteps of my grandfather, a Zoologist for his whole life.*

## ACKNOWLEDGEMENTS

---

I am especially grateful to the following people, who provided various forms of assistance during the study:

Prof. Hannes van Wyk, for accepting me as a student, providing valuable expertise on the study animal and teaching me to become an independent researcher.

Dr. Martin Whiting, for valuable discussions on experimental design and miscellaneous logistic support.

Wynand Louw and his family, for unselfishly accepting me on their farm and allowing me to have access to lizards. I am indebted to them for their perpetual hospitality and logistic support during fieldwork trips.

Alex Searby, for assisting with burrow searching and capturing of lizards.

Louise Visagie, for assisting with burrow searching and capturing of lizards.

Dr. Jonathan Losos, for assisting with burrow searching, lizard capturing and helpful discussions. I also appreciate his continued interest in the project.

Annelise Blignaut from the Biochemistry Department, University of Stellenbosch, for helping me with the protein gel electrophoresis and interpretation of gels.

James Nicholls, for helping with lizard capturing and observations of lizards.

Raina Kutranov, for assisting with capturing of lizards.

Jaques Deere, for assisting with capturing of lizards.

My parents, Grevile and Louie Ruddock, for providing valuable financial assistance during fieldwork trips.

Dr. Alison Leslie, for much needed long-distance logistic support, and with helping me to bleed lizards.

Dr. Michael Cunningham, for helping me with the genetic laboratory work, and for use of his genetics laboratory.

Kate Henderson, for helping me with the genetic laboratory work.

Dr. Edmund Pool, for helping me with the protein gel electrophoresis, and advising me on general biochemical techniques in the laboratory.

Stefan Louw, from the Chemistry Department, University of Stellenbosch, for analysing gland samples, and for useful discussions.

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## CHAPTER ONE

### GENERAL BACKGROUND, OBJECTIVES AND METHODOLOGY

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#### 1.1. BACKGROUND: *CORDYLUS GIGANTEUS*

##### 1.1.1. Classification and description

*Cordylus giganteus*, the large girdled lizard, and also referred to as the sungazer, is the largest lizard of the viviparous genus *Cordylus* and of the lizard family Cordylidae (Figure 1.1.). Andrew Smith first described this lizard in 1844, with further descriptions by FitzSimons (1943), Loveridge (1944) and De Waal (1978). Preliminary analyses of the systematic relationship of the genus *Cordylus* suggest that *C. giganteus* is the sister species to *Cordylus cataphractus* (Olmo and Odierna, 1980; Herselman, 1991).

Sungazers are heavily armoured lizards, with especially spiny tails and prominent occipital spines. Together with *Cordylus cataphractus*, *C. giganteus* is the only *Cordylus* species that has enlarged scales and occipitals. Sungazers are generally dull in colour, with brown to yellow-brown undersides and flanks, and a dark brown to black dorsum. They have no bright colouration and, other than the enlarged occipital spines, they do not possess any elaborate ornamentation. Hatchlings and juveniles have a yellow and orange infusion. As with all other members of the genus *Cordylus*, *C. giganteus* possess epidermal glands on the postero-ventral surface of their hind legs (Van Wyk and Mouton, 1992). Both sexes possess femoral glands (holocrine secretory glands that secrete a waxy exudate through pores) at the posterior part of the hind legs, but only males have a patch of glandular scales, called generation glands, anterior to the femoral glands, and also in the antebrachial region of the forelegs. Other than this, there is no prominent sexual dimorphism in *C. giganteus*, although there is slight female+ dimorphism, i.e. females are slightly larger (Van Wyk, 1992).

##### 1.1.2. Distribution and climate

*Cordylus giganteus* is limited in distribution to the Highveld grasslands of the northeastern Free State, western Kwa-Zulu/Natal, southern Gauteng, and southeastern North-West Province (Figure 1.2.). Although certain surveys have mapped the probable distribution of *C. giganteus* in the highveld (de Waal, 1978; Stolz and Blom, 1981; Jacobsen *et al.*, 1990), it is not known what the current status of populations are in these regions.

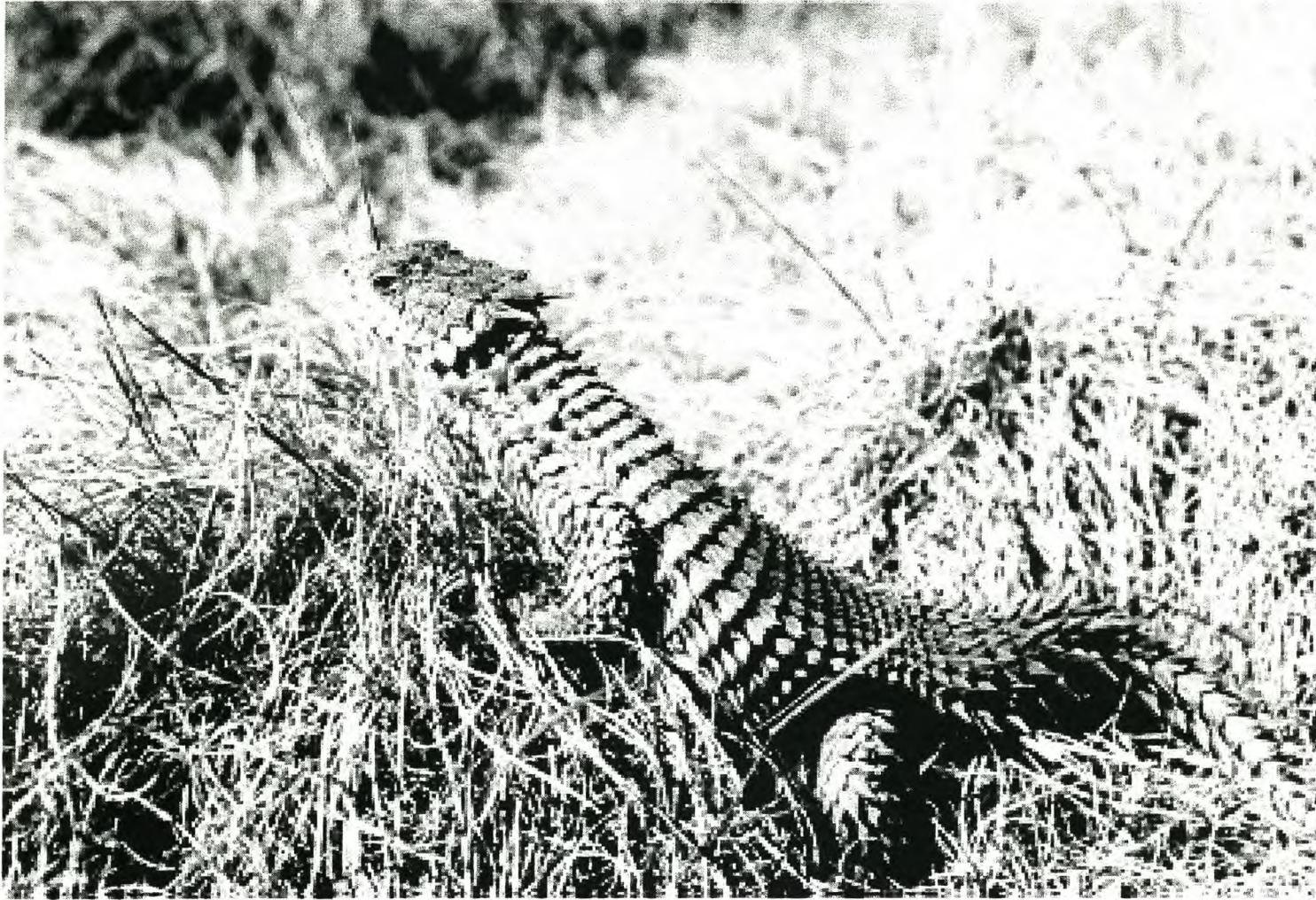


Figure 1.1. The giant girdled lizard, *Cordylus giganteus*, here pictured in its natural habitat (*Themeda* grassland) in the highveld region of the Free State.

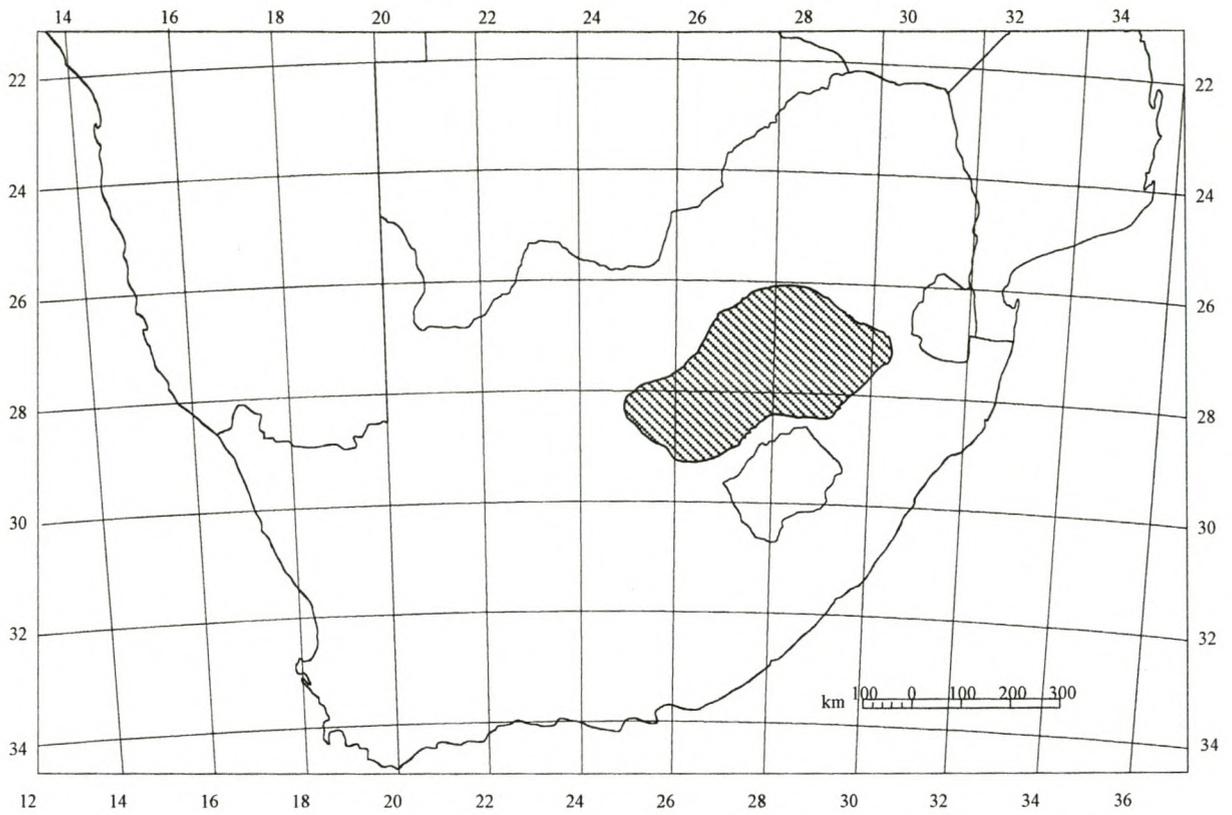


Figure 1.2. Geographical distribution of *Cordylus giganteus* in South Africa, based on reports by de Waal (1978), Stolz and Blom (1981) and Jacobsen *et al.* (1990).

The distribution of *C. giganteus* falls in the summer rainfall region of South Africa, which is characterised by hot summers with prevalent thunderstorms, and cold, dry winters with frost spells overnight. Most of the summer rainfall occurs from November to March, but with a dry period during December and January. The winter dry period usually occurs during June to August. These rainfall and temperature regimes have a marked influence on the seasonal biology of *C. giganteus* (Van Wyk, 1994a, 1994b, 1995; 2000).

### 1.1.3. Habitat

The main vegetation type characteristic of the Highveld region is *Cymbopogon-Themeda* veld (Acocks, 1988). *Themeda triandra* grasslands mainly cover *C. giganteus* habitat, which serves mainly for livestock grazing.

*Cordylus giganteus* is one of only a few species of *Cordylus* that is not rupicolous (Branch, 1998). They live in self-excavated burrows, requiring soils that are deeper than 400mm. Burrows occur in densities of 4-19 lizards per hectare (Stolz and Blom, 1981; Jacobsen *et al.*, 1990; Van Wyk, 1992). Burrows have an average depth of about 50 cm, average length of about 2 m, and taper towards the terminal end (Van Wyk, 1992). Burrows are characterised by their oval entrances with smooth soil leading to the outside, and the presence of a mid-ridge along the floor. Most burrows are occupied by single adult lizards, and where more than one lizard is present, it is mostly adult females with juveniles or hatchlings (Van Wyk, 1992).

### 1.1.4. Conservation status

Due to the limited distribution and habitat of *C. giganteus*, as well as the prevalence of human activities in its range, *C. giganteus* has always had the potential to be a threatened species. *Cordylus giganteus* was listed in the South African Red Data Book (1978) as vulnerable, and this status has been retained until the present.

Potential threats to *C. giganteus* include habitat destruction, industrial development, pollution and to a limited extent the pet and muti trade (Van Wyk, 1992). Since *C. giganteus* occurs mainly on arable farmland, populations are under constant threat of losing habitat, and to a large extent their survival depends on farmers in the region. Other activities that have resulted in habitat destruction include mining and urban development.

Legislation in the form of provincial ordinances do exist to limit illegal trading of *C. giganteus*, as laid down by the Convention on International Trade in Endangered Species (CITES). Since *C. giganteus* is a terrestrial and highly sedentary species, relocation of

threatened populations has been the best conservation measure applied so far. Several relocations of *C. giganteus* have been attempted thus far (Newberry *et al.*, 1985; Petersen *et al.*, 1985; Jacobsen *et al.*, 1990), with reports of success rates of up to 70% survival. However, several relocation attempts with unknown success rates have also been done.

Other than farmer education, relocation is probably the only viable alternative conservation measure for *C. giganteus*, but the lack of follow-up research and monitoring of relocated populations is a worrying factor. Research is needed to determine how the population structure, including the social structure, plays a role in maintaining a stable population after relocation.

### 1.1.5. Previous research

The first study conducted on *C. giganteus* was its description by Smith in 1844. Taxonomic studies were done by FitzSimons (1943) and Loveridge (1944). During this period, however, no major ecological or physiological studies were done on *C. giganteus*.

Branch and Patterson (1975) were the first to document the characteristics of burrows, and mention the winter inactivity of *C. giganteus*. Several studies were conducted during relocation attempts (Stolz and Blom, 1981; Newberry *et al.*, 1985; Petersen *et al.*, 1983, 1985; Jacobsen *et al.*, 1990). Several popular articles have also referred to the behaviour of captive *C. giganteus* (e.g. Schmidt, 1924; Schönfeld, 1973; Seidel, 1979; Switak, 1980; Welzel, 1981). *C. giganteus* has also been the subject of some taxonomic (Olmo and Odierna, 1980; Lang, 1989; Herselman, 1991) and morphological studies (Laforgia and Varano, 1982; Green, 1983; Van Wyk and Mouton, 1992). Marais (1984) provided some notes on feeding and basking behaviour of wild *C. giganteus*.

Although the above-mentioned studies provided information on the biology of *C. giganteus*, there was still a noticeable lack of detailed field research. The most comprehensive study on *C. giganteus* to date is that by Van Wyk (1992), which not only questioned the data of previous studies, but also provided a scientific basis for our knowledge of the life history and ecology of *C. giganteus*. The study based on mark-recapture and autopsies, provided baseline seasonal information on reproduction, feeding, energy dynamics, growth, population dynamics and activity. Reproduction is seasonal in both sexes, yet males exhibit a postnuptial spermatogenic cycle with a bimodal plasma testosterone profile. Females, on the other hand, ovulate during spring, and give birth to two or three young in early autumn; however, the data indicates that reproduction may be a biennial and sometimes even triennial phenomenon in *C. giganteus* females. This could also be affected by the status

of energy reserves (fat bodies) in different females, which vary seasonally, and between females as well. The variation in reproductive and energy status of females was very evident, and breeding seasons were characterised by two or three categories of reproductive status in females. *Cordylus giganteus* eat mainly insects, and especially coleopterans. Most growth of lizards occurred during the summer months, and sexual maturity of males and females was reached in about the fourth year after birth. It seems that growth is a distinctly seasonal pattern in *C. giganteus*, with cessation of growth during the winter months. Mortality is also the highest during summer, with hatchlings and juveniles suffering the most mortality. The age structure of *C. giganteus* is characterised by the low relative abundance of juveniles in populations. As mentioned before, there is slight female+ dimorphism, yet no noticeable colouration or ornamentation differences between the sexes. Thermoregulation activity of lizards is regulated primarily by behavioural means. Summer activity was characterised by a bimodal activity pattern on sunny days, but unimodal on cool/overcast days. Winter activity was non-existent (May-August), when lizards enter their burrows for hibernation. Burrows play an important role in thermoregulatory activity and as a refuge. The life history of *C. giganteus* seems to correspond partially to a K-selected life history.

## 1.2. OBJECTIVES

The baseline work by Van Wyk (1992) indicated several new directions that should be investigated, should effective conservation measures be applied to protecting *C. giganteus* populations. Data from the reproductive cycle of males and females, and burrow movements, highlight new questions about the underlying social mechanisms that ensure mating and maintenance of social structure. It was also thought that the social structure of *C. giganteus* may play an important role in ensuring survival of populations, especially in a long-lived, sedentary and terrestrial species. Therefore, the eventual aim of this study was to contribute to knowledge of the biology of *C. giganteus*, which can also help to ensure more effective relocation attempts. And the specific objective of this study was to determine the social structure of *C. giganteus*.

Apart from conservation implications for *C. giganteus*, this study is also of intrinsic value as well. Behavioural studies on southern African herpetofauna, and specifically lizards, are generally lacking. This paucity is especially noticeable in phylogenetic reviews of lizard behaviour (Carpenter and Ferguson, 1977; Stamps, 1977; Martins, 1994). Therefore, this study will contribute to our understanding of lizard behaviour in general, and add to our knowledge of southern African lizards. Furthermore, models on social behaviour can be

tested, since *Cordylus* lizards exhibit very little or no sexual dimorphism. More specifically, our knowledge on large-bodied, long-lived, terrestrial lizards can be improved, since this class of reptiles seems to exhibit unique characteristics (Van Wyk, 1992; Bull, 1995).

The social structure of an animal species includes aspects such as communication, mating system, social behaviour, spatial distribution, behavioural endocrinology and kin dynamics within a population (Whitehead, 1997). The main purpose of this study was to test various basic hypotheses regarding some of these aspects in *C. giganteus*. The whole study is introduced with a review of our current knowledge regarding cordylid social behaviour, as well as behavioural theory, in chapter two. The following three chapters investigate chemical communication by looking at the chemical composition of glandular secretions (chapter three and four) and behavioural response to the secretions (chapter five). In chapter six, the spatial distribution and movements of lizards between and around burrows are investigated, to obtain an idea of the extent of movements made by *C. giganteus*. The nature of behavioural interactions is investigated in chapter seven, which focuses on social behaviour in *C. giganteus*. Chapter nine summarises and concludes the results of the whole study. Hypotheses regarding each study are outlined in each chapter.

### **1.3. GENERAL METHODOLOGY**

#### **1.3.1. Study area**

The study area was chosen due to its use in a previous study (Van Wyk, 1992). The study site is situated on a dairy farm in the eastern Free State, South Africa (28°01'S, 28°05'E). The lizard population studied is distributed over an area of 500 × 500m (Figure 1.1.), and is surrounded by cultivated farmland. *Cordylus giganteus* habitat on this farm is used for grazing for sheep and cattle. The lizard population in the study area was used for gland sampling, DNA tissue sampling and behavioural studies.

#### **1.3.2. Burrow marking and lizard capture**

Initially, with the help of assistants, the study site was searched for *C. giganteus* burrows, which can be recognised by their oval shape, raised middle portion on the floor of the burrow entrance and flattened grass outside the burrow entrance (Van Wyk, pers. comm.; pers. obs.). Positions of burrows were then marked by inserting iron stakes (1.2 m) next to burrows and attaching numbered nursery flag markers to them, making burrow positions clearly visible during summer months when the grass is especially long. One half of the study

site was mapped (burrow positions) using a 1:2000 “dumpy level”, and the rest of the burrows by triangulation, using a tape measure (Santyaufibreglass measuring tape, 50 m).

Adult lizards were captured by placing anchored loops (iron tent pegs and nylon rope) at the burrow entrances. Lizards became caught in the loop and could then be extracted by lowering their occipital spines to prevent them from jamming themselves in the burrow. Juveniles (one year and older, judged by SVL, Van Wyk, 1992) and hatchlings were caught by placing mist netting over the burrow entrances where adult females were caught (juvenile lizards remain in burrows of birth for a few years after birth). In some cases, hatchlings were caught by placing cardboard with mirror sticky tape at the burrow entrances, on which hatchlings became stuck; following capture, they were carefully removed from the tape. Body measurements of lizards were standard and included: total length (nearest 0.5 mm), snout-vent length (SVL) (nearest 0.5 mm), head width (nearest 0.5 mm), head length (nearest 0.5 mm) and mass (nearest g). Adult and older juvenile males can be distinguished from females by the presence of generation glands on the postero-anterior region of the hind legs, and antebrachial region of the forearms. Each lizard was also assigned a number for easy identification of samples, etc. Pet identification tags (P.I.T.) (Identipet), each with a unique identification code, were injected into the postero-femoral region of the hind leg of adult and older juveniles (3 years and older), while younger juveniles were uniquely toe clipped. These procedures allowed future identification of individual lizards.

### **1.3.3. General statistical procedures**

Statistical procedures followed Zar (1984), and the statistical computer software programmes SigmaStat<sup>®</sup> (Jandel Scientific) and STATISTICA<sup>®</sup> (StatSoft, Inc.) were used to analyse data. Data were tested for normality with the Kolmogorov-Smirnov test for normality, and with Bartlett's test for homogeneity of variances. Data that did not conform to normality and equality of variances, behavioural data and interval data, were subjected to non-parametric statistical analysis; otherwise, parametric tests were done. Unless otherwise stated, a significance level of  $\alpha = 0.05$  was used throughout all studies.

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## CHAPTER TWO

### BIOLOGICAL CORRELATES OF SOCIAL STRUCTURE IN LIZARDS

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#### 2.1. INTRODUCTION

Animal behaviour can be defined as the activities an animal performs during their lifetime, and includes locomotion, feeding, breeding, predator avoidance and social behaviour (Miller and Harley, 1994). Social structure is defined as the relationships of conspecifics with one another, and includes competition, dominance, mate acquisition, parental care and communication (Whitehead, 1997). The social structure of a population influences, or is influenced by, various aspects of a species' biology, from gene flow through to predation (Wilson, 1975), so much so that various correlations can be drawn between social structure and other aspects of a species' biology (Whitehead, 1997). Within the Reptilia, social structure seems to be less complex than in higher vertebrates, and therefore provides a good model to study social correlates (Brattstrom, 1974). Of all the reptiles, lizards have been studied the most (Stamps, 1977), since they exhibit a rich repertoire of display behaviours (Carpenter and Ferguson, 1977; Carpenter, 1978; Tokarz, 1995).

Social structure in cordylids has been poorly studied (Mouton and Van Wyk, 1997), which is especially noticeable in recent and even old phylogenetic and behavioural reviews (Carpenter and Ferguson, 1977; Stamps, 1977, 1983; Mason, 1992; Martins, 1994). Only a handful of behavioural studies have been done (Burrage, 1974; Wirminghaus, 1990; Cooper *et al.*, 1996, 1999; Whiting, 1999; Whiting and Bateman, 1999; Ruddock *et al.*, 2001, *J. Herpetol.*, in press), which is not enough to make definite conclusions on the type of social behaviour exhibited by genera of this family. The cordylid clade represents a unique combination of genera, including viviparous and oviparous genera (Mouton and Van Wyk, 1997), with some showing pronounced sexual dimorphism and others none or very little (Mouton and Van Wyk, 1993; Cordes *et al.*, 1995; Mouton and Van Wyk, 1997). Habitat types vary from rupicolous to terrestrial (Mouton and Van Wyk, 1997; Branch, 1998), while members of all genera of the Cordylidae are ambush, or sit-and-wait, foragers (Cooper *et al.*, 1997), although plasticity in foraging mode has been reported in *Platysaurus broadleyi* (Greeff and Whiting, 2000). Prey-chemical discrimination (PCD) may be absent in cordylids (Cooper and Van Wyk, 1994; Cooper *et al.*, 1995). Cordylids also exhibit a variety of body

forms, ranging from the stocky, heavily armoured *Cordylus* species to the more graceful crag lizards, and on the other extreme, the snake-like *Chamaesaura* (Branch, 1998). Probably the most unique diversification in cordylid lizards is the variety of epidermal glands found in them, which, in contrast to other morphological features, does show sexual dimorphism in at least some genera (Van Wyk and Mouton, 1992).

It is obvious from the above-mentioned that there are a variety of adaptations in the Cordylidae (Mouton and Van Wyk, 1997). Therefore, the purpose of this review is to investigate ecological, behavioural, morphological and physiological correlates of social structure in lizards, and then to apply this framework to the Cordylidae, so that predictions can be made about their social structure. This study on *C. giganteus* can then serve as a test of these predictions.

## 2.2. TYPES OF SOCIAL STRUCTURE IN LIZARDS

Hinde (1976) proposed a conceptual framework for describing social structure on three levels: interactions between individuals; content, quality and temporal patterns of interactions; and content, quality and patterning of relationships. Social structure can therefore be described and examined on many levels. In this review, social structure in lizards will be described on two levels: 1) type of mating system, and 2) use of space.

Mating systems have been divided into two categories in lizards: polygynous and non-polygynous, although this dichotomy may really be a reduction from a continuum (Stamps, 1983). In polygynous systems, males mate with and monopolise more than one female, or mate promiscuously, while in non-polygynous systems males usually mate with only one female, be it a lifetime partner (monogamy), or many different partners at different times (Emlen and Oring, 1977). These mating systems are determined by mechanisms underlying male reproductive success, whether it is female choice of male mating partners, or intrasexual competition between males for females.

Use of space in lizards varies from free ranging to defence of a home range or territory, to defence of a site or personal space (Stamps, 1977). According to this classification, lizards can also be described as territorial (defence of resources within a specific area, from conspecifics) or non-territorial (no defence of resources from conspecifics) (Stamps, 1977; Stamps, 1983). Territorial lizards typically display aggressive behaviour towards intruding conspecifics, which takes the form of a wide array of behaviours (Carpenter and Ferguson, 1977). In crowded situations, territorial and non-territorial lizards may often form dominance hierarchies (Rose, 1985).

The rest of this review is devoted towards describing and explaining the relationship between these social systems and ecological, behavioural, morphological and physiological aspects of lizards.

## **2.3. CORRELATES OF SOCIAL STRUCTURE**

### **2.3.1. Foraging mode**

Foraging modes of animals have typically been divided into two classes: active (search) foraging, and ambush (sit-and-wait) foraging (Huey and Pianka, 1981). Active foragers typically search for their food or prey items, while ambush foragers wait for passing prey items to come by. Foraging mode seems to be tightly coupled to the ability to discriminate prey chemicals, with active foragers possessing this ability, while ambush foragers do not (Cooper, 1995).

Foraging mode puts constraints on the type of social system in lizards. Indeed, within lizard taxa, there seems to be a definite dichotomy of foraging modes. Most members of the families Agamidae, Chamaeleonidae, Gekkonidae and Iguanidae are sit-and-wait foragers, rely heavily on visual cues, and are territorial with little home range overlap, while most members of the Lacertidae, Scincidae, Teiidae and Varanidae are active foragers, rely less on visual cues and are non-territorial with overlapping home ranges (Krekorian, 1976; Stamps, 1977b; Rose, 1985; Cooper, 1995). Ambush foraging allows territorial lizards to remain on the same spot while surveying a territory, while this is not possible in an actively searching lizard. Generally, active foragers will also have larger home ranges than ambush foragers will (Rose, 1985).

Foraging mode seems to be tightly coupled with several aspects of lizard biology, including reproductive mode (Mouton and Van Wyk, 1997), prey chemical discrimination (PCD) ability (Cooper, 1995) and energetics (Schmidt-Nielsen, 1972; Taylor, 1973). It is therefore not surprising that these factors co-vary in many lizard social systems (Stamps, 1977b).

### **2.3.2. Reproductive mode**

Lizards have traditionally been classified into two types of reproductive modes: oviparous (egg laying) and viviparous (live bearing) (Guillette, 1993). The origin of these reproductive modes seems to be closely associated with climate, with viviparous forms having originated in colder climates while oviparous forms originated in warmer climates (Blackburn, 1982).

The implications of reproductive mode for lizards for female lizards are widespread. Viviparity results in the impairment of movement in gravid females (Garland and Losos, 1993), draining of energy reserves during reproduction (Derickson, 1976) and increased basking time to facilitate development of embryos (Guillette, 1993). Such factors place constraints on movements, making a territorial social system a more likely option in viviparous lizards. Indeed, viviparity seems to be more closely associated with a sit-and-wait feeding strategy, which in turn is more amenable to a territorial social system (Cooper *et al.*, 1990). Sheltered sites also provide refuge during parturition, which could result in a social system with specific site defence.

The basic implication of reproductive mode is the constraints it places on movements by female lizards, thereby also restricting associated social behaviour.

### **2.3.3. Communication mode**

Lizards have a relatively complex system of social communication, including a wide diversity of visual displays (Carpenter and Ferguson, 1977) and various glands associated with chemical communication (Mason, 1992). In general, lizards are thought to be primarily visually orientated (Mason, 1992).

Individual recognition seems to be an important component of territorial and dominance social systems in lizards (Glinski and Krekorian, 1985). Mechanisms of recognition include individual colour patterns and individual-specific displays (McKinney, 1969; Stamps, 1973; Crews, 1975; Jenssen, 1971, 1977; Stamps and Barlow, 1973; Jenssen & Hover, 1976; Carpenter, 1978, 1982; Qualls and Jaeger, 1991), and odour and pheromones (Graves and Halpern, 1991; Alberts, 1992; Alberts and Werner, 1993).

Although both visual and chemical communication serves the same endpoint (recognition of conspecifics), these communication modes seem to be associated with specific defence types. Site defenders lack the vast array of colour patterns and displays found in home range defenders, and generally seem to rely largely on chemical cues to communicate information (Carpenter and Ferguson, 1977; Stamps, 1977). There even seems to be a general taxonomic dichotomy with regard to communication mode: Iguanians, agamids, teiid and lacertid lizards are primarily visually orientated, possess a wide variety of visual displays, and exhibit territorial and home range defence; on the other hand, geckos, skinks and anguids rely heavily on olfactory and chemical cues, generally lack colour and exhibit non-territoriality or site defence (Carpenter and Ferguson, 1977). The general picture emerging is that members of the Cordylidae also rely heavily on chemical cues (Cooper *et al.*, 1996, 1999), but visual

communication is also important in some genera (Mouton and Van Wyk, 1993; Whiting, 1999; Whiting and Bateman, 1999). Although these generalisations can be made, it must be remembered that lizards often make use of both communication modes for particular situations, it is the degree of use that differs.

The inference from the above-mentioned is obvious. Lizards that exhibit display behaviour and high frequencies of social interactions are more likely to be territorial and polygynous, whereas lizards exhibiting few displays and frequencies of interactions, are more likely to be non-territorial or site defenders.

#### **2.3.4. Use of space**

Spatial distribution has been studied extensively in lizards and strongly indicative of the type of social system. Home range data are available for a large number of species (Rose, 1985), with definite patterns emerging.

In territorial social systems, population density can largely be regulated by social interactions (Bustard, 1970; Philibosian, 1975), such that there is a minimum density allowed by a particular social system. In territorial species, one would expect individuals to be spaced regularly, while in non-territorial species a random distribution might emerge. Agonistic encounters between lizards in a population may increase with an increase in density, which eventually disperses individuals into a regular spatial distribution (Ruibal and Philibosian, 1974; Jennings and Thompson, 1999). This apparent association between social system and spatial distribution seems logical, but spacing of individuals is also affected by the nature of the habitat (M'Closkey *et al.*, 1990; Whiting *et al.*, 1993), such that measuring spatial distribution in species may not accurately reflect the underlying social system. For example, Stamps (1988, 1990) found that juvenile *Anolis aeneus* were aggregated when habitat patchiness was controlled.

Home range data is often used to describe social systems in lizards (Rose, 1985). Low home range overlap between males and between females suggests territoriality (Rose, 1982; Smith, 1985;), while large overlap suggests a dominance hierarchy (Ferner, 1974). Large overlap between males and females, on the other hand, suggests a polygynous, or promiscuous mating system, where males extend their home ranges to include as many females as possible (Ferner, 1974; Stamps, 1977b). Although home range data reflects the type of social system, use of space is also largely affected by food abundance (Simon, 1975), such that limitation of resources can also affect social interactions (Stamps, 1977a; Greenberg and Crews, 1990), because food can also be a defended resource in territories (Rose, 1982).

It is noteworthy that, although home range and spatial data often serve as an accurate means of inference of social system, exceptions may occur. Social activity may not always be uniformly spread throughout the home range, since it is also a function of resources like food, basking spots and shelters (Rose, 1985). Extensive home range overlap can occur even if lizards are territorial (Eifler and Eifler, 1998). The general pattern mentioned above still holds.

### **2.3.5. Habitat**

Lizards inhabit a variety of different habitat types, which differ with regard to degree of openness, abundance of resources, availability of refuges and availability of perching sites. Many of these factors seem to be important selective forces in the evolution of social systems in lizards, directly or indirectly (Hixon, 1987; Baird *et al.*, 1997; Melville and Swain, 2000).

Habitat type is an important factor determining the potential for a social system, eventually influencing the potential for sexual selection (Baird *et al.*, 1997). The nature of the immediate environment affects directly the transmissibility of displays (Fleishman, 1988a & b; Baird *et al.*, 1997), and therefore the potential for a particular social system to evolve. For example, territoriality requires an open habitat with sufficient perches for individuals to survey their territories. In more closed/complex habitats, extensive home range overlap may occur because of the nature of the habitat preventing individuals detecting one another. Types of social systems may even differ within a species depending on the habitat, such as in *Anolis aeneus*, where dominance hierarchies as well as territoriality occurred in different habitats (Stamps, 1973).

Abundance of resources such as food seems to be important in determining the spatial distribution of lizards, and therefore the potential for a social system to evolve. Limited resources results in increased competition between conspecifics (Stamps, 1977a), which can lead to the formation of dominance hierarchies to regulate agonistic interactions (Greenberg and Crews, 1990). Food abundance has been shown to directly influence the size of territories in several lizards (Simon, 1975; Simon and Middendorf, 1976; Eifler, 1996), and social behaviour can even be abandoned during times when resources are scarce (Nagy, 1973). Generally, the dispersion and abundance of food seems to influence the type of social systems (Stamps, 1977b), such that a uniform food distribution results in territorial systems, while non-uniform food distribution will cause clumping, and dominance hierarchies, to occur (Brown and Orians, 1970). On the other hand, when resources are abundant, or not a limiting

factor for a lizard population, defence of these resources is not necessary, leading to a non-territorial social system (Torr and Shine, 1996).

Some lizard species exhibit specific site defence, where a shelter site or refuge is aggressively defended from conspecifics, such as in geckos or skinks (Stamps, 1977b). These species generally exhibit morphology that makes them more vulnerable to predators than other lizard families, by constraining their escape abilities. Predator refuges are therefore a viable alternative as a predator escape mechanism, but shelter sites may become a limited resource as well. This would then result in a social system of specific site defence, where predator-safe refuges are defended from conspecifics (Stamps, 1983a). However, in the case of geckos, aggregations may occur.

Since the first developments in evolutionary theory, the importance of the environment in determining the direction of evolution has been recognised. The nature of an organism's habitat affects many aspects of its biology, which directly or indirectly influences its social system. It must be remembered, however, that others features of an organism may be under greater selective pressure from the habitat, and in so doing actually constrain the social system.

### **2.3.6. Morphology**

The phenotype of animals is under constant pressure from various selective forces, which equips individuals with adaptive morphological traits (Darwin, 1859). Within lizard taxa, colour and relative body size seem to be important morphological traits in social interactions, and are largely associated with social behaviour.

Sexual dimorphism is a term used to describe differences in morphology between sexes of a species. Sexual dimorphism in size and colouration is common in lizards (reviewed by Fitch, 1981), and is influenced by many factors including resource partitioning between males and females, and intrasexual selection among males (Schoener, 1977). As far as size is concerned, larger males constitutes male-plus dimorphism, while larger females is female-plus dimorphism (Fitch, 1981); most lizards are dimorphic rather than monomorphic (Schoener, 1981). Stamps (1983) proposed a model for polygyny in lizards, that predicts that intrasexual selection among males should be more intense in territorial species than in non-territorial species, which would result in greater sexual dimorphism in territorial than non-territorial species. Therefore, one would expect greater sexual dimorphism in polygynous species than non-polygynous species. A comparison of territorial and non-territorial species reveals that territorial lizards have a higher average dimorphism in size (Stamps, 1983). In

polygynous mating systems, larger body size of males seems to be positively correlated with reproductive success (Bull and Pamula, 1996; Abell, 1997; Jenssen and Nunez, 1998; Whiting, 1999; Lewis *et al.*, 2000). This is augmented by territorial behaviour, where males actively defend resources, such as females.

Although sexual dimorphism is seen as an accurate indicator of social system, this may not be the case in lizards where both males *and* females exhibit aggressive behaviour towards individuals of the same sex (Mahrt, 1998). In such cases larger body size may be selected for in both sexes, resulting in less sexual dimorphism.

In several lizard species, there is often more than one type of male colour morph, or more than one size male, which in most cases seems to be related to dominance (Hover, 1982; 1985; Thompson and Moore, 1987, 1991; Carpenter, 1995; Baird *et al.*, 1997; Smith and Zucker, 1997). In these cases, specific colour morphs and larger males tend to dominate others, resulting in sexual selection for these traits due to increased reproductive success.

It is apparent that the presence of sexual dimorphism in a species is associated with territoriality and usually a polygynous mating system, although sexual dimorphism can arise in non-territorial lizards with dominance hierarchies, due to intrasexual selection. A general familial pattern with regard to colour variation also arises. Iguanids, agamids, teiid and lacertid lizards generally exhibit brighter colours and more ornamentation, and exhibit territorial and home range defence. Geckos, skinks, anoles and probably cordylids generally lack colour and exhibit non-territoriality or site defence (Carpenter and Ferguson, 1977).

Morphology also puts constraints on the type of social system. Body size largely determines the home range size a lizard can maintain, at least over the spectrum of foraging groups (Turner *et al.*, 1969), although maintenance of a larger home range can depend on energetics as well (Rose, 1982). Furthermore, limb morphology influences locomotor performance in lizards (Garland and Losos, 1993; Melville and Swain, 2000), which affects antipredatory behaviour. Where heavy body armour is an adaptation to predator avoidance, constraints are also put on movements and extension of skin for ornamentation (Mouton and Van Wyk, 1992). Therefore, where the costs of morphological and energetic constraints outweigh the benefits of maintaining a territory or multiple mates, one would expect a species to have site defence as a social system.

As mentioned before, the morphology of an animal is under various selective pressures, such that the interrelatedness of factors may become complex, masking the underlying correlation between morphology and social system. Morphology and display

behaviour in lizards may not even be as tightly coupled in evolution as previously thought (Wiens, 2000).

#### **2.4. BASIC MODEL OF CORRELATES OF SOCIAL STRUCTURE**

Although this review has attempted to classify social systems according to other co-varying aspects, it is appreciated that the relationships so far discovered in the great amount of studies on lizard behaviour, are often not one-to-one, but incorporate a combination of various aspects. Indeed, the value of elucidating these relationships is in inferring social systems from *combinations* of characteristics, i.e. whereas using the presence of only one biological aspect to infer a social system may be ambiguous, the presence of several aspects will be more accurate in inferring the social system. Table 2.1 summarises the correlates investigated in this review, and presents a very basic model to infer social system from the corresponding biological factors. However, demonstration of each aspect would require many further studies, so definite conclusions cannot be drawn from it.

Table 2.1. Simple relationships between ecological, morphological, behavioural and physiological factors and the corresponding social system. This table represents a model for investigation, since there may be many exceptions.

FACTORS	DESCRIPTION	SOCIAL SYSTEM
Foraging mode	Ambush	Territorial/site defence
	Search	Non-territorial
Reproductive mode	Viviparous	Territorial/site defence
	Oviparous	Non-territorial?
Communication mode	Visual	Territorial/site defence
	Chemical	Site defence
Habitat	Open	Territorial
	Closed	Non-territorial/site defence
	Food uniformly distributed	Territorial
	Food clumped	Dominance hierarchy
Morphology	Sexual dimorphism present	Territorial/polygynous
	Sexual dimorphism absent	Non-territorial/both sexes territorial
	Colourful	Territorial/polygynous
	Dull (non-colourful)	Non-territorial/site defence
	Well-developed limbs	Territorial/non-territorial
	Short, stocky limbs	Site defence
	Male colour morphs	Dominance hierarchy/polygynous
	No male colour morphs	Non-territorial/site defence
Use of space	Home range overlap	Non-territorial/site defence
	No/little home range overlap	Territorial
	Uniformly distributed	Territorial
	Clumped distribution	Dominance hierarchy
Refuge	Inhabits refuge (site fidelity)	Site defence
	No specific refuge (no site fidelity)	Territorial/non-territorial

## **2.5. TESTING THE MODEL: SOCIAL STRUCTURE IN *CORDYLUS GIGANTEUS***

As mentioned above, the use of a basic model is in testing its predictions. This study on *C. giganteus* will serve as a test of the general correlations explored in this brief review. Furthermore, knowledge gained from this study can aid in our understanding of the complex relationships between social system and other biological factors in lizards.

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## CHAPTER THREE

### PROTEIN VARIATION OF FEMORAL GLAND SECRETIONS

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#### 3.1. INTRODUCTION

Lizards possess a variety of epidermal glands including pre-cloacal, cloacal, femoral and generation glands (Simon, 1983; Van Wyk and Mouton, 1992). Femoral glands are holocrine epidermal glands that occur on the postero-ventral margin of the hind legs of most lizard families (Maderson, 1970; Quay, 1986) and secrete a solid, waxy exudate in the form of a secretion plug (Cole, 1966). Femoral glands are more active in the breeding season and males are known to produce more secretion than females (Mason, 1992). Single-layer “glandular scales” have been described as “generation glands” in sphaerodactyline and eublepharine gekkonoids (Maderson, 1972), while pre-cloacal “glandular scales” have been reported in agamids (Moody, 1980). Single- and multi-layered glandular scales have also been reported in cordylids, just anterior to the femoral gland, in the pre-cloacal, dorsal body and anterior antebrachial regions (Lang, 1991; Van Wyk and Mouton, 1992). Femoral glands have been implicated in chemical communication (Cole, 1966), but little is known about the function(s) of generation glands.

Both femoral and generation glands are well developed in cordylid lizards (Van Wyk and Mouton, 1992). Generation glands in cordylids are taxonomically diverse, and are represented by “protruding” and “pit” type glands in *Platysaurus* and *Pseudocordylus*, and are absent or poorly developed in females of some species (see Van Wyk and Mouton, 1992 for histological details). Femoral glands seem to be active throughout the year, with a slight increase in activity during the breeding season (Van Wyk, 1990). Conversely, indications are that generation gland layers in some cordylids may be deposited during skin shedding events (Van Wyk, pers. comm.).

To date, several studies have investigated the chemical composition and variation of lizard femoral gland secretions. It has been shown that the femoral gland secretion consists of proteins/polypeptides (80%) and lipids (20%) (Alberts, 1990), and that protein profiles vary individually, intersexually and between clutches (Alberts, 1991; 1992; 1993). This evidence suggests that femoral glands have a social function, such as individual recognition and mating. Variation in chemical composition of glandular material is used as evidence for a communication function for these glands (Alberts, 1990). Such studies, however, have only

focused on iguanids such as *Dipsosaurus dorsalis* (Alberts, 1990, 1991; Alberts *et al.*, 1993) and *Iguana iguana* (Weldon *et al.*, 1990), and only on femoral glands.

Due to the nature of the habitat of *C. giganteus* (highveld grassland), visual communication is probably very constrained (Van Wyk, pers. comm.), and chemical communication is therefore a viable alternative. *Cordylus giganteus* possesses both femoral and generation glands on the postero-ventral margin of the hind-legs, as well as generation glands on the antebrachial region of the forelegs in males (FitzSimons, 1943; Loveridge, 1944; Van Wyk, 1992). *C. giganteus* therefore possesses an array of possible glandular sources, including femoral, generation and possibly cloacal glands, situated in close proximity (Van Wyk and Mouton, 1992). The eventual aim of these studies is to determine the levels of variation of chemical composition of each source, and therefore how they all, singly or synergistically, contribute towards information transfer between conspecifics. Studies by Cooper *et al.* (1996, 1999) on the cordylid *Cordylus cordylus* have already provided evidence that these glandular sources play a role in sex and individual recognition.

Therefore, analysing the chemical composition of glandular secretions of *C. giganteus* can indicate the potential for chemical communication. The main objective of this study was to analyse individual, sexual and seasonal protein variation of the femoral gland secretions of *C. giganteus*.

## **3.2. MATERIALS AND METHODS**

### **3.2.1. Sample collection**

Femoral gland secretions were collected from lizards by exerting manual pressure on the area surrounding the glands on the hind legs and extracting the secretion plugs with forceps. The tips of the forceps were covered with masking tape and replaced for each lizard. Femoral gland samples were placed in numbered microfuge tubes and immediately placed on ice. Samples were then transported to the University of Stellenbosch and stored at -70°C.

For the seasonal analysis of gland secretions, 11 male and 14 female femoral gland samples were collected during three months of the year: April 1998 (autumn), October 1998 (spring) and February 1999 (late summer). To investigate individual variation, 39 male and 50 female femoral gland samples were collected during February 1999. Lizards were identified by scanning (Mini Portable Reader, Destron/Fearing Corp.) their hind legs for their P.I.T. tags (see chapter one for details of recaptures). For analysis of individual variation, data was used from one season only, February 1999, when the most lizards were sampled.

### 3.2.2. Protein gel electrophoresis

Protein gel electrophoresis was used to separate the gland secretions into their various protein components according to relative molecular weights. For this purpose, polyacrylamide protein gel electrophoresis (Laemmli, 1970) was used to determine the protein-banding pattern of each lizard's glandular secretions.

Femoral gland secretions were weighed to the nearest 0.1 mg and homogenised in adjusted volumes of treatment buffer (0.125 M Tris-Cl, pH 6.8; 4% (v/v) SDS; 20% (v/v) glycerol; 10% (v/v) 2-mercaptoethanol) to obtain a final concentration of 3.3 µg/µl. Fifteen µl of these prepared samples were then loaded onto 15% (v/v) reducing polyacrylamide gels (Mini VE gel apparatus, Hoefer Scientific Instruments, San Francisco), together with Bromophenol-blue (10% of sample volume) as tracking dye. Gels were run at 20 mA until the tracking dye reached 5 mm from the bottom of the gels, usually after 2 hrs. Molecular weight standards (Amersham Life Science, Buckinghamshire, England) were run alongside samples, with molecular weights of 220, 97.4, 66, 46, 30, 21.5 and 14.3 Kilo-Daltons, to allow for comparisons between gels.

Subsequently, gels were stained in Coomassie-Blue (0.125% (v/v) Coomassie-Blue; 50% (v/v) methanol; 10% (v/v) acetic acid) on a Belly Dancer (Heidolph Duomax 1030, Labotec) overnight, and destained in 50% (v/v) methanol and 10% (v/v) acetic acid for 4 hrs.

### 3.2.3. Data analysis

#### *General*

The protein banding patterns of individual lizards were compared to a standard set of bands identified among all the samples. Molecular weight standards were used to identify these bands between gels. Hereafter a presence-absence matrix was created where bands were scored as either being present (1) or absent (0) for each lizard.

#### *Protein band frequencies*

From the presence-absence matrix, protein band frequencies among individuals were calculated by summing the number of individuals having a particular protein band. Frequencies were then compared between males and females for each season, using a Chi-squared test.

### ***Similarity coefficients***

Similarity coefficients (Lynch, 1990) were calculated between all possible pairs of individuals. This coefficient reflects the degree of band sharing between individuals, and is calculated according to the formula:

$$S = \frac{2(AB)}{A + B}$$

where        A = total number of bands in individual A's banding pattern  
              B = total number of bands in individual B's banding pattern  
              AB = number of protein bands shared by both individuals A and B

The index varies from 0 to 1, from when no bands are shared to where the banding patterns are identical.

Mean similarity coefficients were calculated for intra- and intersexual similarity, as well as for intra- and inter-individual similarity over seasons. To test for sexual variation in similarity, mean inter- and intrasexual similarity were compared with one-way ANOVA where data were parametric, and with Kruskal-Wallis ANOVA on ranks where data were nonparametric. To test for seasonal variation in similarity, the same tests were used to compare inter- and intraindividual similarity over seasons. To test if gland protein similarity is related to spatial proximity, similarity coefficients between all individuals were plotted against the distance between each pair of individual's burrows (see chapter one for mapping of burrow positions), and tested for significant correlation with Pearson's Product correlation coefficient.

## **3.3. RESULTS**

### **3.3.1. Protein banding**

Twenty-four protein bands were identified in the femoral gland secretions of *C. giganteus*. Molecular weights of bands varied from 14.3 to 66 KD, and differences in intensity of bands within individuals and between seasons were evident, although no quantitative analysis was done on this. Figure 3.1 illustrates the banding patterns of 9 individuals.

### **3.3.2. Individual variation**

Banding patterns of individual lizards varied considerably, with very few individuals having identical profiles. Frequency of occurrence of the different protein bands amongst

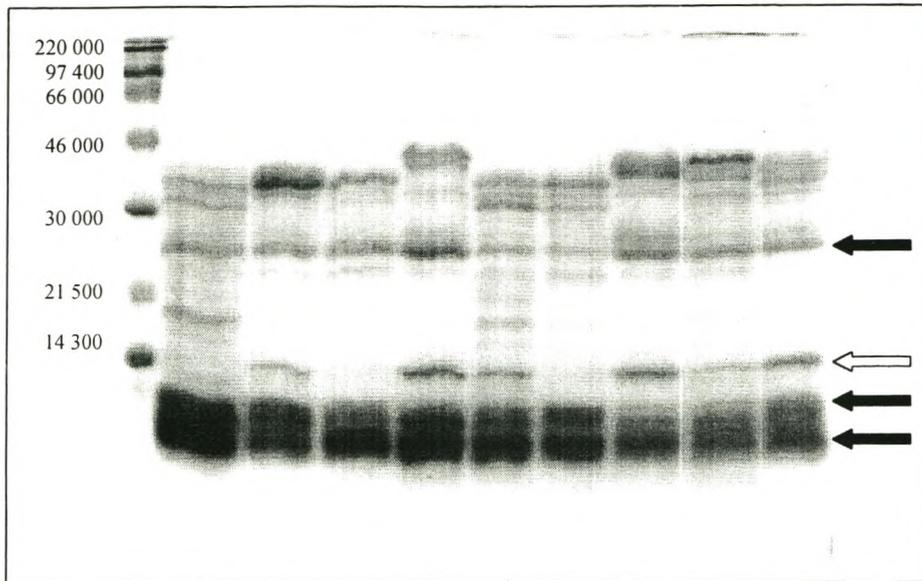


Figure 3.1. A representative SDS-Polyacrylamide gel, with the protein banding profiles of nine different individuals. Sizes of the molecular weight markers in Daltons (lane one) are given on the left. The closed arrows indicate those bands that were found in all individuals, while the open arrow indicates the band that was present in all males.

individuals revealed that three bands were present in all individuals analysed (males and females), while four bands were present in all males. Other bands varied in their abundance (see Figure 3.1). There was no pattern with regard to source of greatest variation (in terms of uniqueness of band), and bands varied over all molecular weights.

Mean similarity ( $\pm$  SD) for the entire population was  $0.632 \pm 0.123$  ( $n = 90$ ; range: 0.300-1.000), during February 1999. Except for 5 pairs of individuals out of 4095 possible pairings, no two pairs had identical profiles; this involved seven out of a total of 90 individuals, i.e. 7.7% of individuals analysed had protein profiles identical to another, while 92.3% had unique profiles.

### 3.3.3. Sexual variation

Variation in protein banding between the sexes was evident in similarity indices calculated for intra- and intersexual pairs. Males had a higher intrasexual similarity than females during autumn (April 1998) and late summer (February 1999), but there were no significant differences during spring (October 1998) (Table 3.1). Females had a significantly lower intrasexual similarity during late summer (February 1999) (Table 3.1).

Frequencies of the different bands in individuals did not vary significantly between males and females over all three time of the year (April:  $\chi^2_{16} = 12.88$ ,  $p = 0.682$ ; October:  $\chi^2_{17} = 9.05$ ,  $p = 0.939$ ; February:  $\chi^2_{20} = 30.46$ ,  $p = 0.063$ ), i.e. protein bands occurred in similar relative proportions in males and females (Figure 3.2). There were no bands that were found exclusively in either males or females.

### 3.3.4. Seasonal variation

Mean similarity indices calculated for the same individuals (intra-individual) between all three times of the year were not significantly different for both males and females (Table 3.2). However, intraindividual similarity was significantly greater than inter-individual similarity over the three times of the year (Table 3.3). Six out of a total of 24 individuals (25%) had identical profiles over all three months, while 13 out of 24 individuals (54.2%) had identical profiles over two months, i.e. 19 out of 24 individuals (79.2%) had identical profiles over at least two months. These results indicate that individual lizard femoral gland secretion protein profiles remain stable seasonally. A representative SDS-Polyacrylamide gel showing the protein profiles of three individuals over the three months is shown in Figure 3.3.

Table 3.1. Comparison of the similarity coefficients (protein band similarity) calculated within and between sexes for *C. giganteus*, for three different times of the year. The last two columns indicate statistical significance of comparisons for each month, and superscripts indicate statistical significance of post-hoc comparisons.

MONTH	PAIRING	N	SIMILARITY COEFF.		
			( $\pm$ SD)	STATISTIC	p
April	Male-male	11	0.694 $\pm$ 0.091 <sup>b</sup>	H=10.40	0.006
	Male-female	25	0.639 $\pm$ 0.095 <sup>a</sup>		
	Female-female	14	0.644 $\pm$ 0.131 <sup>a</sup>		
October	Male-male	11	0.645 $\pm$ 0.113	H=0.59	0.743
	Male-female	25	0.624 $\pm$ 0.123		
	Female-female	14	0.628 $\pm$ 0.127		
February	Male-male	39	0.687 $\pm$ 0.104 <sup>c</sup>	H=256.15	<0.001
	Male-female	89	0.620 $\pm$ 0.124 <sup>b</sup>		
	Female-female	50	0.602 $\pm$ 0.121 <sup>a</sup>		

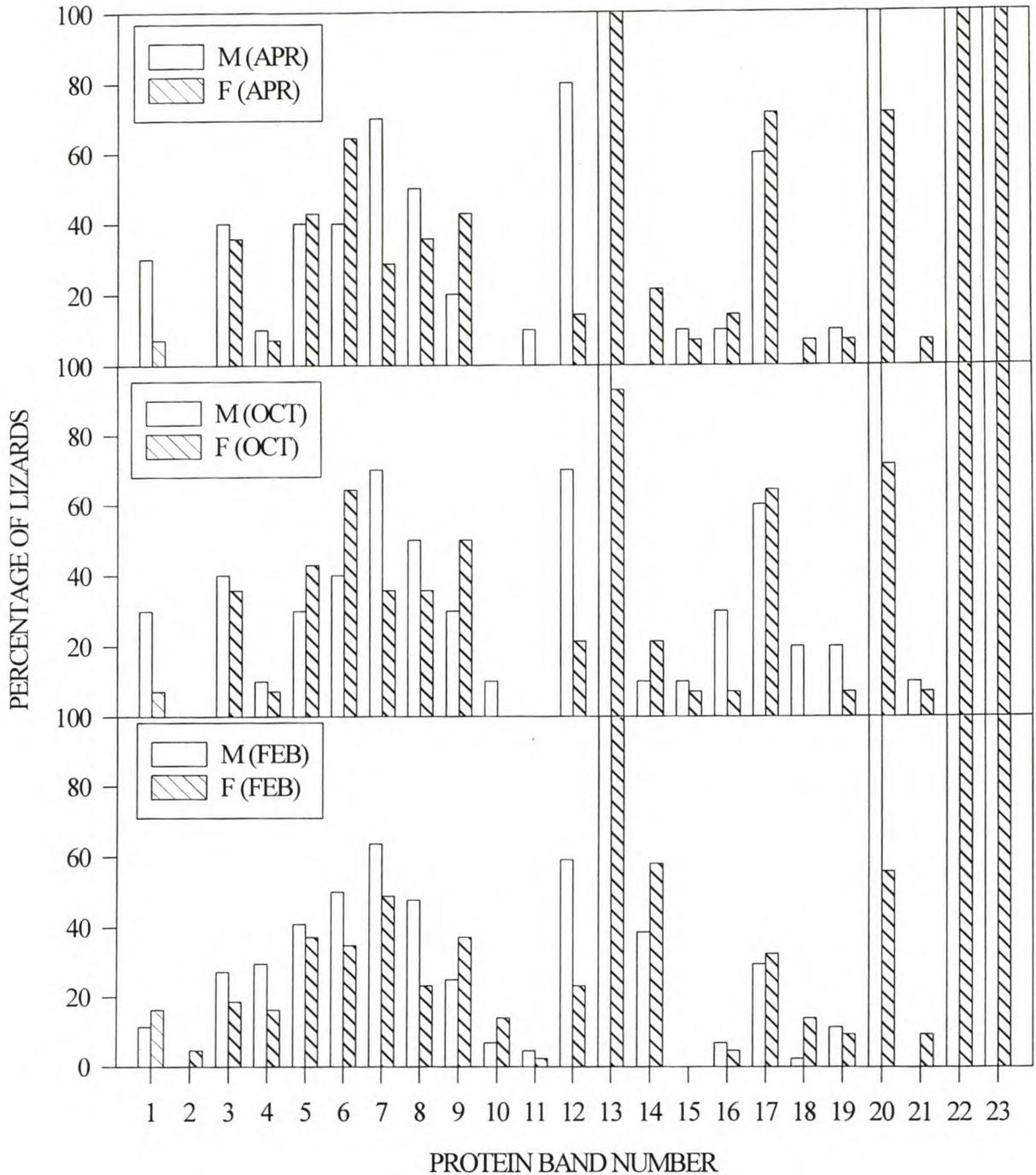


Figure 3.2. Comparison of the frequencies (in percentage) of male and female *C. giganteus* that had the numbered protein bands (numbered from 1 to 23, in order of decreasing molecular weight), for April and October 1998, and February 1999. There were no significant differences in proportions of bands between males and females for all three times of the year (see text for details).

Table 3.2. Comparison of mean similarity coefficients between three times of the year, for intra- and inter-individual similarity of male and female *C. giganteus*. The last two columns indicate statistical significance of comparisons.

SEX	COMPARISON	MONTH PAIR	N	SIMILARITY COEFF. ( $\pm$ SD)	STATISTIC	p
Males	Intra-individual	Apr-Oct	11	0.943 $\pm$ 0.071	H=0.06	0.973
		Apr-Feb	11	0.955 $\pm$ 0.057		
		Oct-Feb	11	0.942 $\pm$ 0.091		
	Inter-individual	Apr-Oct	11	0.709 $\pm$ 0.117	F=0.17	0.842
		Apr-Feb	11	0.698 $\pm$ 0.111		
		Oct-Feb	11	0.672 $\pm$ 0.125		
Females	Intra-individual	Apr-Oct	14	0.953 $\pm$ 0.041	H=0.46	0.793
		Apr-Feb	14	0.931 $\pm$ 0.075		
		Oct-Feb	14	0.940 $\pm$ 0.073		
	Inter-individual	Apr-Oct	14	0.681 $\pm$ 0.085	H=2.31	0.314
		Apr-Feb	14	0.687 $\pm$ 0.077		
		Oct-Feb	14	0.666 $\pm$ 0.066		

Table 3.3. Comparisons of mean similarity coefficients between and within individuals over the three times of the year (April, October, and February), for male and female *C. giganteus*. The last two columns indicate statistical significance of comparisons.

SEX	COMPARISON	N	SIMILARITY COEFF.		STATISTIC	p
			( $\pm$ SD)			
Males	Intra-individual	11	0.947	0.071	U=241.50	<0.001
	Inter-individual	11	0.693	0.113		
Females	Intra-individual	14	0.941	0.064	U=788.00	<0.001
	Inter-individual	14	0.678	0.678		

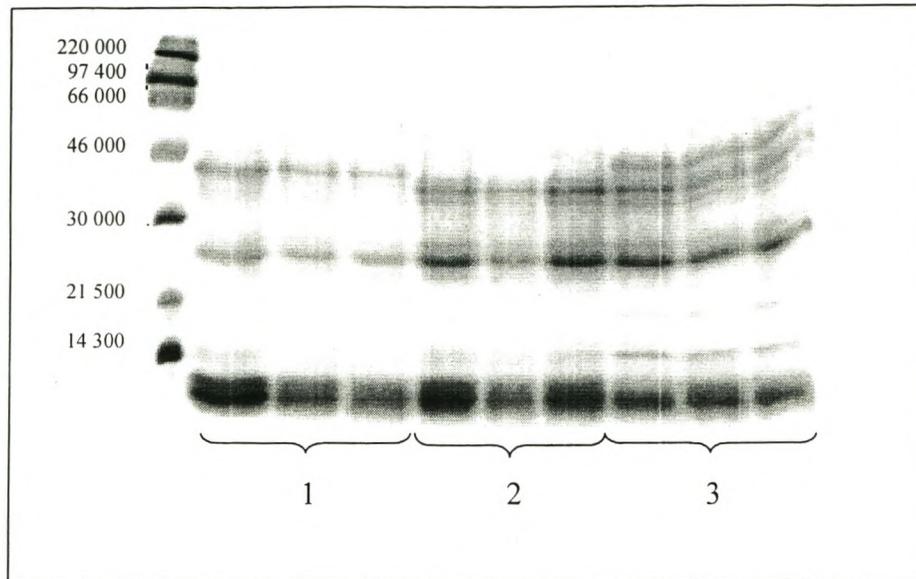


Figure 3.3. A representative SDS-Polyacrylamide gel, with the protein banding profiles of three different individuals sampled in three different months (April, October and February). Lanes 2-4 are individual one, lanes 5-7 are individual two and lanes 8-10 are individual three (indicated on Figure). Sizes of the molecular weight markers in Daltons (lane one) are given on the left.

### 3.3.5. Spatial variation

There was no significant correlation between burrow distance and femoral gland secretion similarity between all individuals (Pearson Product correlation coefficient = -0.029,  $p = 0.137$ ); similarity between individuals seemed to remain constant over all distances between burrows (Figure 3.4).

## 3.4. DISCUSSION

This study shows that protein variation in femoral gland secretions is evident in *C. giganteus*. These results therefore support the basic premise that communication chemicals should show some form of variation, specific to individuals, or defined groups of individuals (Alberts *et al.*, 1993). However, although variation of glandular chemicals is a prerequisite for chemical communication, it only indicates the potential for chemical communication in *C. giganteus*. Most behavioural studies have focused on responses to whole body odours or substrate deposits (Mason, 1992), but this may mask the relative contribution of individual components, especially specialised structures like epidermal glands.

The mean similarity of femoral gland proteins (based on presence/absence of components) reported in this study is significantly lower than that reported for femoral gland lipids and other compounds, which show seasonal variation in relative abundance of compounds (chapter three). This is consistent with Alberts *et al.* (1992), who also found seasonal variation of lipids in *Iguana iguana* (Iguanidae). Since femoral gland proteins have a high melting point (Alberts, 1990), they can last longer when exposed to prolonged heat, making femoral gland proteins more suitable for range marking of defended sites (chapter seven), than other lower molecular weight compounds. Proteins can be detected by the vomeronasal system (Halpern, 1987), which could possibly function in acute discrimination of secretions (Mason, 1992).

The most obvious form of variation in the protein composition was differences in the number of lizards that possessed certain bands. At least three bands were present in all individuals, while other bands varied in their relative abundance amongst individuals. While the femoral gland secretions of other *Cordylus* species were not examined in this study, it may be that variation among species plays a role in species recognition, at least to the extent that conspecifics can detect the presence of another conspecific at a burrow. Interspecific differences in femoral gland proteins have been reported in several iguanids, with more closely related species having more similar banding profiles (Alberts, 1991). Individual

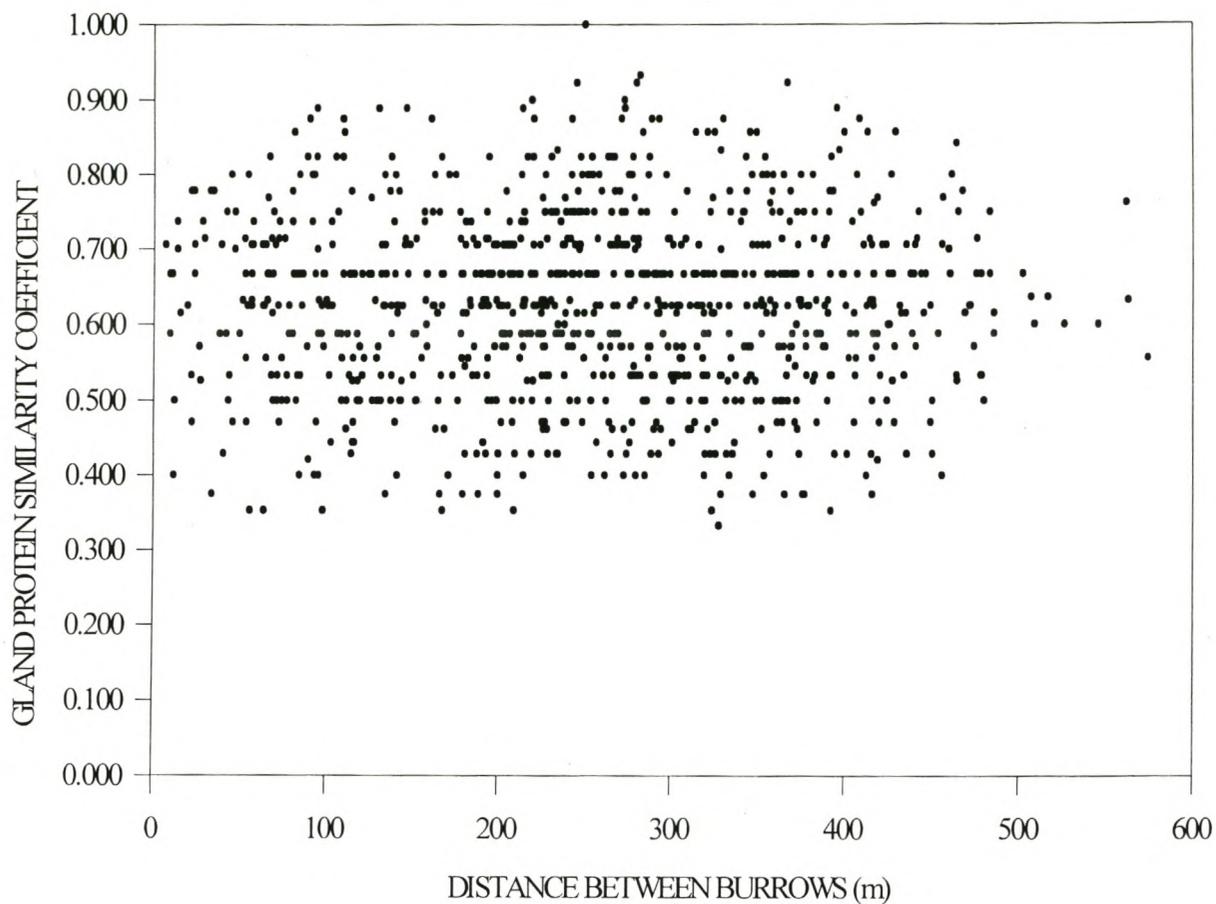


Figure 3.4. Scatter plot of distance between burrows and femoral gland protein similarity coefficients for *C. giganteus* individuals, during February 1999.

protein banding profiles were seasonally stable, indicating that an individual's femoral gland protein composition stays relatively constant over time. Not all individuals had identical profiles over all three months. This is in contrast to the findings of Alberts *et al.* (1993), who found identical profiles in 39 individuals sampled in different months. These differences may be due to different staining techniques; silver staining has been shown to be highly sensitive in comparison to Coomassie Blue (Morissey, 1981). Therefore, since bands often varied in intensity between months and individuals, the staining may not highlight certain bands, leading to non-identical profiles in some individuals (differences in band intensity were also reported by Alberts *et al.* (1993)). On the other hand, these seasonal differences may be real in *C. giganteus*, and possibly be affected by diet (Halpin, 1980; Albone, 1984) or even reproductive status (Fergusson *et al.*, 1985). *C. giganteus* does show seasonal differences in wet stomach mass (Van Wyk, 2000), so reduced intake during certain months could alter the composition of femoral gland secretions. Femoral glands have also been shown to be targets of androgenic control (Chiu *et al.*, 1975; Fergusson *et al.*, 1985), and productivity varies seasonally in some lizards (Van Wyk, 1990; Alberts *et al.*, 1992), but whether this affects actual protein composition is unknown. It may be more likely that lipids and other volatile compounds are affected more, due to greater seasonal variation in relative composition (Alberts *et al.*, 1992; this study, chapter three). The other potential source of sex recognition is the generation glands, which are found only in males (Van Wyk and Mouton, 1992).

High individual variation and constant femoral gland secretion profiles over time suggest that *C. giganteus* have individual signatures and may therefore function in individual recognition between conspecifics. Since *C. giganteus* are also highly site-specific and spend most of their time at a home burrow (chapter six), the protein chemical signal can be deposited around a burrow, and therefore serve to mark a lizard's refuge. This would be important in a highly site-specific lizard, where burrow identification is essential. This is supported by considerable tongue-flicking at grass around burrow entrances by resident lizards (chapters four and seven), a sign that residents constantly determine the identity of burrows or the presence of other lizards. *Cordylus cordylus* has the ability to discriminate between its own substrate deposit and that of other individuals (Cooper *et al.*, 1999). Other lizards have also been shown to be able to distinguish between their own and other femoral gland secretions (Alberts, 1992; Alberts and Werner, 1993).

Sexual variation of proteins in the femoral gland secretions of *C. giganteus* was lower in males than females, at least in two of the three months analysed. Whether these sexual differences are functionally significant is not clear. In the only other study addressing protein

variation at the level of individuals, Alberts *et al.* (1993) reported higher intra-sexual than intersexual similarity in *Iguana iguana*. It can be argued that the protein portion of femoral gland secretions could function in sex recognition, but this depends on the detectability of the differences (Alberts, 1993), and in what proteins the differences lay. However, individual variation in *C. giganteus* femoral gland proteins would probably negate sexual variation, even if significant differences were found, because of the high degree of uniqueness of each individual's secretion. It is more plausible that lipids and other volatile substances play a role in sex recognition in femoral glands, since there are much greater sex differences in these compounds (chapter three). Sex recognition of substrate deposits has also been reported in *Cordylus cordylus* (Cooper *et al.*, 1996).

The results suggest a high degree of intraspecific variability in the protein composition of *C. giganteus* femoral gland secretions, and that the gland proteins probably serve to identify individuals, rather than sex. A comprehensive genetic study is required to detect any relation to genetic similarity, and therefore if these glands can also function in kin recognition.

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## CHAPTER FOUR

### VOLATILE COMPOUND VARIATION OF FEMORAL GLAND SECRETIONS

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#### 4.1. INTRODUCTION

Together with proteinaceous material, femoral gland secretions contain at least 20% lower molecular weight compounds by weight as well (Alberts, 1990). A wide diversity of these compounds have been identified in femoral gland secretions of the lizard *Iguana iguana*, and include fatty acids, mono-, di- and tri-glycerides, alcohols, sterols and ketones (Alberts *et al.*, 1992). Many such compounds have also been identified in glandular or skin secretions of snakes (Oldak, 1976; Mason *et al.*, 1987, 1989; 1990; Simpson *et al.*, 1988; Mason, 1993), turtles (Eisner *et al.*, 1977; Weldon and Tanner, 1990; Seifert *et al.*, 1994) and crocodiles (Weldon *et al.*, 1990). Such low molecular weight compounds are well suited as pheromones due to their relatively high volatility and therefore usefulness in transmitting chemical signals between individuals (Hadley, 1985). However, most pheromonal studies on squamates have focused on contact pheromones, and the role of volatile substances are still speculative (Mason, 1994).

As for any chemical signal, for pheromones to be useful in chemical communication there should be variation in the chemical composition thereof (chemical communication hypothesis (Alberts *et al.*, 1993)). In *Iguana iguana*, seasonal variation in lipids is manifested in the relative amounts of lipids in the femoral secretion, which is greater during the breeding season than in the non-breeding season (Alberts *et al.*, 1992). Several studies also indicate the role of hormones in regulating the functioning of epidermal glands (Chiu *et al.*, 1970; Fergusson *et al.*, 1985; Alberts, *et al.*, 1992), confirming that epidermal gland lipids vary seasonally. However, other than several studies investigating skin lipid variation between sexes and seasons in garter snakes (*Thamnophis sirtalis parietalis*) (Mason *et al.*, 1987), or variation between snake species (Oldak, 1976), there are not many detailed studies focusing on lipid variation of glandular secretions in lizards.

Although some of the above-mentioned studies have described levels of variation and composition of femoral gland secretions, detailed analyses of seasonal and sexual variation are lacking, and studies have been limited to only two species, *Iguana iguana* and *Dipsosaurus dorsalis* (Alberts, 1990, Weldon *et al.*, 1990; Alberts, 1991; Alberts *et al.*, 1993). Since *C. giganteus* is restricted to the grassland vegetation of the highveld in South Africa,

chemical communication could be a viable alternative in a habitat where visual communication is limited. Therefore, *C. giganteus* provides a good model to examine the composition and levels of variation of volatile compounds in their gland secretions.

The objective of this study was to identify and analyse the variation of dichloromethane (CH<sub>2</sub>Cl<sub>2</sub>) extractable compounds in the femoral gland secretions of *C. giganteus*, and to further investigate the chemical communication potential of these glands.

## **4.2. MATERIALS AND METHODS**

### **4.2.1. Sample collection and analysis**

Femoral gland samples were collected as described in chapter three. Portions of frozen samples were placed in Pyrex glass vials and taken to the Ecological Chemistry Laboratory at the University of Stellenbosch. Samples were analysed with a Carlo Erba 4160 Gas Chromatogram and Carlo Erba QMD 100 GC-MS (Louw, unpublished M.Sc. thesis). Relative abundances (peak areas, in terms of relative concentration) of the various compounds were generated for each lizard's gland sample used in subsequent data analyses. To standardise comparisons between individuals, peak areas of each compound were expressed as a percentage of the total peak area, for each individual.

### **4.2.2. Sexual and seasonal variation in compounds**

The femoral gland secretions of male and female *C. giganteus* were collected at three different times of the year: April 1998 (11 males, 12 females), October 1998 (five males, five females), and February 1999 (five males, five females), and compound profiles obtained for each individual at each of the three times of the year. These months correspond to autumn, spring and late summer respectively. Data for similar compounds were pooled into their major groups (fatty acids, alcohols, ketones, hydrocarbons and steroids), and comparisons made between sex and season. Although the most appropriate test for this data is a two-way MANOVA with SEX and SEASON as independent factors, and the various compounds as dependant variables, the number of compounds outnumber the sample size, making this test invalid. Therefore, univariate tests were done on each compound for sex and season. To compensate for repeated univariate tests on the same null hypothesis, Bonferroni adjustment of significance levels was applied separately to comparisons between sex ( $\alpha = 0.003$ ) and between months ( $\alpha = 0.005$ ).

To test for sex differences, the relative proportions of each major group were compared between males and females for each month, with *t*-tests (parametric data) or Mann-

Whitney tests (non-parametric data). To test for seasonal differences, the relative proportions of each major group were compared between the three months for each sex, with one-way repeated measures ANOVA (parametric data) or one-way ANOVA on ranks (non-parametric data), and Tukeys and Dunn's tests used for post-hoc comparisons, respectively.

#### **4.2.3. Sexual and seasonal variation in secretion composition**

This analysis determined the relative proportions, by weight, of proteins versus lipids and other volatile compounds in gland secretions, and if there is sexual and seasonal variation. Glandular secretions of 31 individuals (14 males and 17 females) collected during the mating season (October, 1998) and 38 individuals (17 males and 21 females) collected during the non-mating season (February, 1999), were used.

Femoral gland samples were weighed to the nearest 0.1 mg and placed in adjusted volumes of dichloromethane (300µl dichloromethane per 1mg secretion), which was extracted and replaced successively with a pipette over three days. The dichloromethane was then removed and the secretions allowed to dry. Post-extraction mass of gland samples was determined and the mass difference (from original mass) calculated.

Mass differences of gland samples were expressed as percentages of the total original mass of the gland secretion. To test for sex and seasonal differences in relative composition, a two way ANOVA with SEX and SEASON as independent factors was performed on the data, and Tukeys test used for post-hoc comparisons.

#### **4.2.4. Individual variation**

A presence-absence matrix of compounds was created, where compounds were scored as either present (1) or absent (0) for each of 23 individuals (11 males and 12 females) sampled in April 1998. Similarity coefficients (Lynch, 1990) were calculated between all possible pairs of individuals. This coefficient reflects the degree of band sharing between individuals, and is calculated according to the formula:

$$S = \frac{2(AB)}{A + B}$$

where: A = total number of bands in individual A's banding pattern

B = total number of bands in individual B's banding pattern

AB = number of protein bands shared by both individuals A and B

The index varies from 0 to 1, from when no bands are shared to where the banding patterns are identical.

Similarity indices were calculated for all possible pairs of individuals, and mean indices for intra-sexual similarity and inter-sexual similarity tested for significant differences with one-way ANOVA on ranks, and post-hoc comparisons with Dunn's test.

## 4.3. RESULTS

### 4.3.1. General

From a total of 173 volatile compounds found in the femoral gland secretions of 23 individuals, only 53 were identified by mass spectrometry (Table 4.1). These included free fatty acids, alcohols, ketones, hydrocarbons and steroids. Unidentified compounds constituted a mean ( $\pm$  SD) percentage of  $6.75 \pm 2.71\%$  per individual, so only the 53 identified compounds were used in subsequent analyses. Unidentified compounds were excluded for two reasons: 1) they would probably not contribute significantly to results due to the small proportion of the total compounds they constitute, and 2) even if they show sexual and seasonal variation, subsequent interpretations would be difficult without knowledge of their identity. Therefore, it was assumed that the variation shown by the 53 identified compounds are representative of all the compounds.

Steroids (including unidentified steroids) made up the greatest proportion in both males and females throughout the year, constituting up to 50 % of the gland secretion (see Figure 4.3 and 4.4). Thereafter, fatty acids and hydrocarbons constituted the second and third most in proportion respectively, followed by alcohols and ketones. Saturated fatty acids were always higher in proportion than unsaturated fatty acids throughout the year, in both sexes. Prominent compounds (constituting more than 5% of the total peak area per individual in most cases) included hexadecanoic acid, octadecanoic acid, squalene, cholest-5-en-3 $\beta$ -ol, cholesta-5,7-dien-3 $\beta$ -ol and lanost-8-en-3 $\beta$ -ol.

### 4.3.2. Sexual variation in compounds

Some of the major groups of compounds showed significant sexual variation, but differences varied between seasons as well (Figure 4.1). No significant sexual variation was found in both acids (April:  $t_{21} = -0.772$ ,  $p = 0.449$ ; October:  $t_8 = 0.787$ ,  $p = 0.454$ ; February:  $t_8 = -0.322$ ,  $p = 0.753$ ) and alcohols (April:  $t_{21} = 2.179$ ,  $p = 0.041$ ; October:  $t_8 = -1.00$ ,  $p = 0.347$ ; February:  $U_8 = 21.0$ ,  $p = 0.222$ ), which remained in similar proportions in males and females. Hydrocarbons constituted a significantly greater proportion in males than females in April

Table 4.1. List of 53 compounds identified from 173 compounds detected in the femoral gland secretions of *C. giganteus*. Compounds are listed according to major groups and retention index ( $R_t$ ).

GROUP	COMPOUND	( $R_t$ )
Acids	Tetradecanoic acid	29.58
	Pentadecanoic acid	33.75
	(Z)-9-Hexadecenoic acid	37.26
	Hexadecenoic acid	37.71
	Hexadecanoic acid	38.38
	Heptadecanoic acid	42.06
	Heptadecanoic acid	42.77
	(9Z,12Z)-9,12-Octadecadienoic acid	45.88
	(Z)-9-Octadecenoic acid	46.28
	Octadecanoic acid	47.56
	Nonadecanoic acid	51.91
	(Z,Z,Z)-8,11,14-eicosatrienoic acid	53.33
	Eicosanoic acid	56.4
	Heneicosanoic acid	60.76
	Docosenoic acid	63.73
	Docosanoic acid	65.01
	Tricosanoic acid	69.29
Tetracosenoic acid	72.13	
Tetrasanoic acid	73.22	
Alcohols	1-Dodecanol	-
	2-Heptadecenal	34.51
	1-Hexadecanol	34.77
	$\alpha$ -Tocopherol	90.03
Hydrocarbons	Dodecyl propanoate	-
	Branched hydrocarbon	-
	Squalene	75.56

Table 4.1. (cont.) List of 53 compounds identified from 173 compounds detected in the femoral gland secretions of *C. giganteus*. Compounds are listed according to major groups and retention index ( $R_t$ ).

GROUP	COMPOUND	( $R_t$ )
Ketones	2-Heptadecanone	35.64
	2-Nonadecanone	44.81
	2-Heneicosanone	53.97
	2-Tricosanone	62.77
	2-Tetracosanone	67.13
	2-Pentacosanone	71.07
Steroids	Steroid 1	76.72
	Steroid 2	78.46
	Steroid 3	79.11
	Steroid 4	79.59
	Steroid 5	80.47
	Steroid 6	81.3
	Steroid 7	83.31
	Steroid 8	83.96
	Cholest-5-en-3 $\beta$ -ol	88.9
	Steroid 9	89.57
	Cholesta-5,7-dien-3 $\beta$ -ol	90.68
	Steroid 11	92.03
	Steroid 12	93.18
	Steroid 13	94.65
	Ergost-5-en-3 $\beta$ -ol	95.53
	Cholest-4-en-3-one	96.46
	Steroid 16	98.24
	Lanost-8-en-3 $\beta$ -ol	100.6
	Steroid 18	101.4
	Steroid 19	102.7
Steroid 20	103.9	

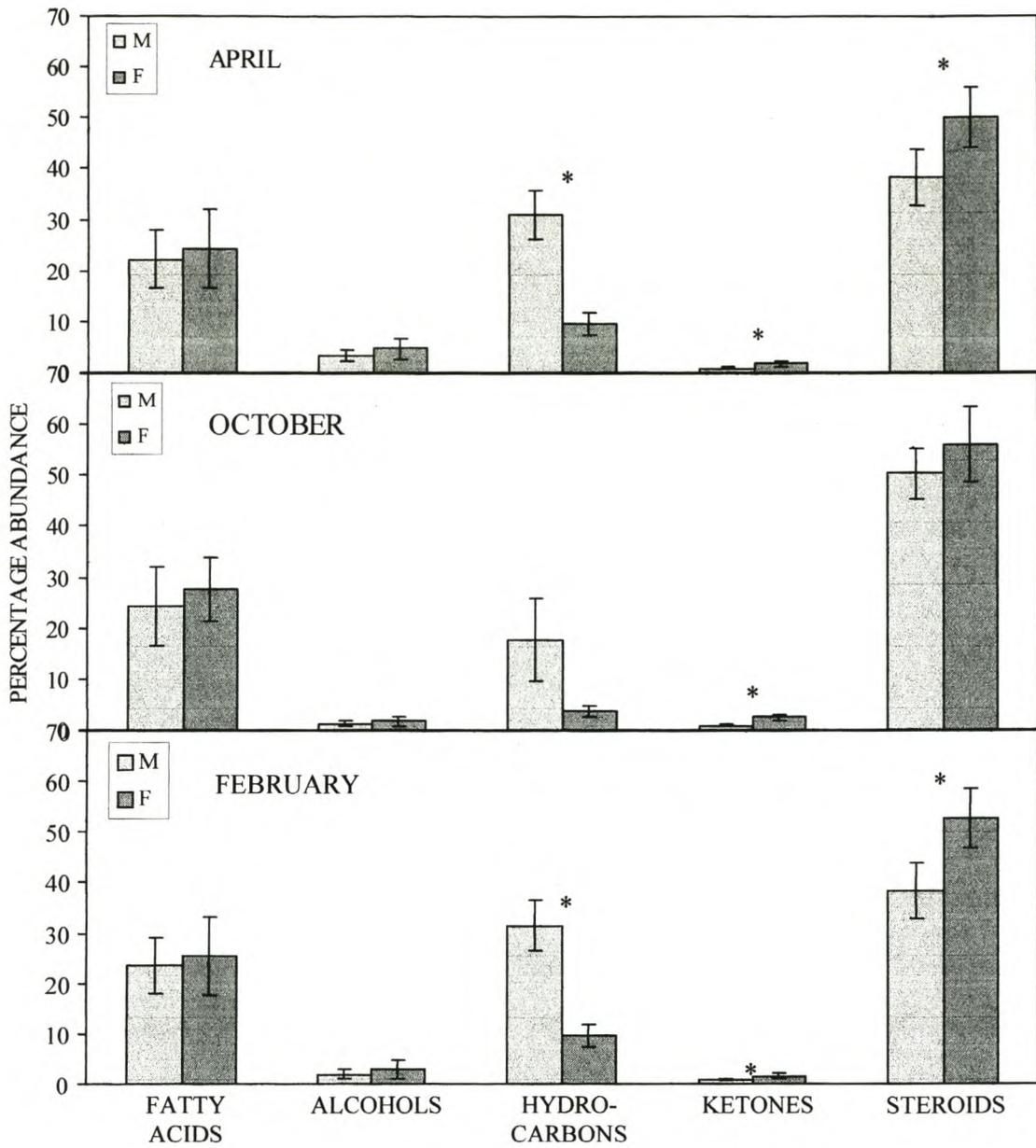


Figure 4.1. Comparison of the mean ( $\pm$ SD) proportions (%) of the major groups of compounds between male and female *C. giganteus* in April, October and February.

\*  $p < 0.05$  for two-sample tests

( $U_{21} = 198.0$ ,  $p < 0.001$ ) and February ( $t_8 = 7.817$ ,  $p < 0.001$ ), but not in October ( $U_8 = 40.0$ ,  $p = 0.008$ ); this was probably largely due to the larger proportion of squalene in males than females (see Figures 4.3 and 4.4). A reverse pattern was found in steroids, which were greater in proportion in females in April ( $t_{21} = -4.90$ ,  $p < 0.001$ ) and February ( $t_8 = -3.99$ ,  $p = 0.003$ ), but not in October ( $t_8 = -1.41$ ,  $p = 0.197$ ). These sexual differences were largely due to the greater proportions of the two cholesterols (cholest-5-en-3 $\beta$ -ol and cholest-5,7-dien-3 $\beta$ -ol) in females, although lanost-8-en-3 $\beta$ -ol was always greater in proportion in males (Figures 4.3 and 4.4). Ketones constituted a greater proportion in females at all three times of the year (April:  $U_{21} = -72.0$ ,  $p < 0.001$ ; October:  $t_8 = -6.913$ ,  $p < 0.001$ ; February:  $t_8 = -4.769$ ,  $p = 0.001$ ).

### 4.3.3. Seasonal variation in compounds

#### *Males*

While no significant seasonal variation was found in fatty acids ( $F_{20} = 0.200$ ,  $p = 0.821$ ) and ketones ( $F_{20} = 0.101$ ,  $p = 0.905$ ), alcohols, hydrocarbons and steroids showed significant seasonal variation (Figure 4.2). Alcohols showed a smaller decrease in proportion ( $H_2 = 10.979$ ,  $p = 0.004$ ) than hydrocarbons ( $F_{20} = 9.833$ ,  $p = 0.001$ ) in October, while steroids increased in proportion in October ( $F_{20} = 10.98$ ,  $p < 0.001$ ). Again, squalene seemed to account for most of the seasonal variation in hydrocarbons, while cholest-5-en-3 $\beta$ -ol, cholesta-5,7-dien-3 $\beta$ -ol and lanost-8-en-3 $\beta$ -ol contributed most to seasonal variation in steroids (Figure 4.3).

#### *Females*

No significant seasonal variation was found in fatty acids ( $H_2 = 0.959$ ,  $p = 0.619$ ), ketones ( $F_{20} = 3.873$ ,  $p = 0.039$ ), alcohols ( $F_{20} = 5.74$ ,  $p = 0.011$ ) or steroids ( $F_{20} = 1.48$ ,  $p = 0.253$ ) (Figure 4.3). Only the hydrocarbons showed significant seasonal variation ( $F_{20} = 13.24$ ,  $p < 0.001$ ), also decreasing in proportion in October (Figure 4.3). As in males, squalene seemed to account for most of the seasonal variation in hydrocarbons (Figure 4.4).

### 4.3.4. Sexual and seasonal variation in secretion composition

Results are summarised in Table 4.2. While there was a significant main effect of SEASON ( $F_1 = 11.40$ ,  $p = 0.001$ ), the main effect SEX was non-significant ( $F_1 = 0.646$ ,  $p = 0.425$ ). No significant interaction of main effects was found ( $F_1 = 0.357$ ,  $p = 0.552$ ).

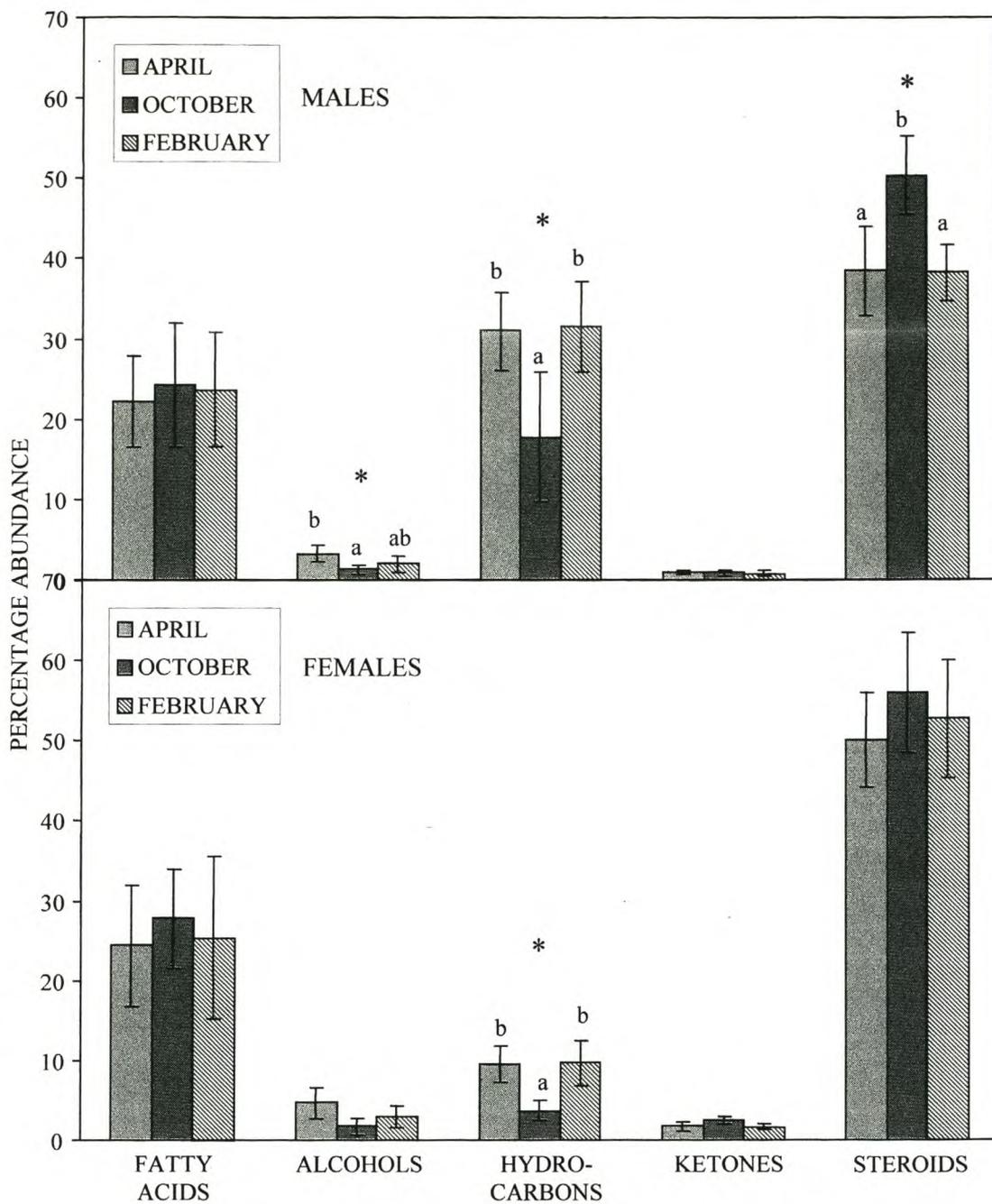


Figure 4.2. Comparison of the mean ( $\pm$ SD) proportions (%) of the major groups of compounds between April, October and February for male and female *C. giganteus*.

\*  $p < 0.05$  for three-sample tests

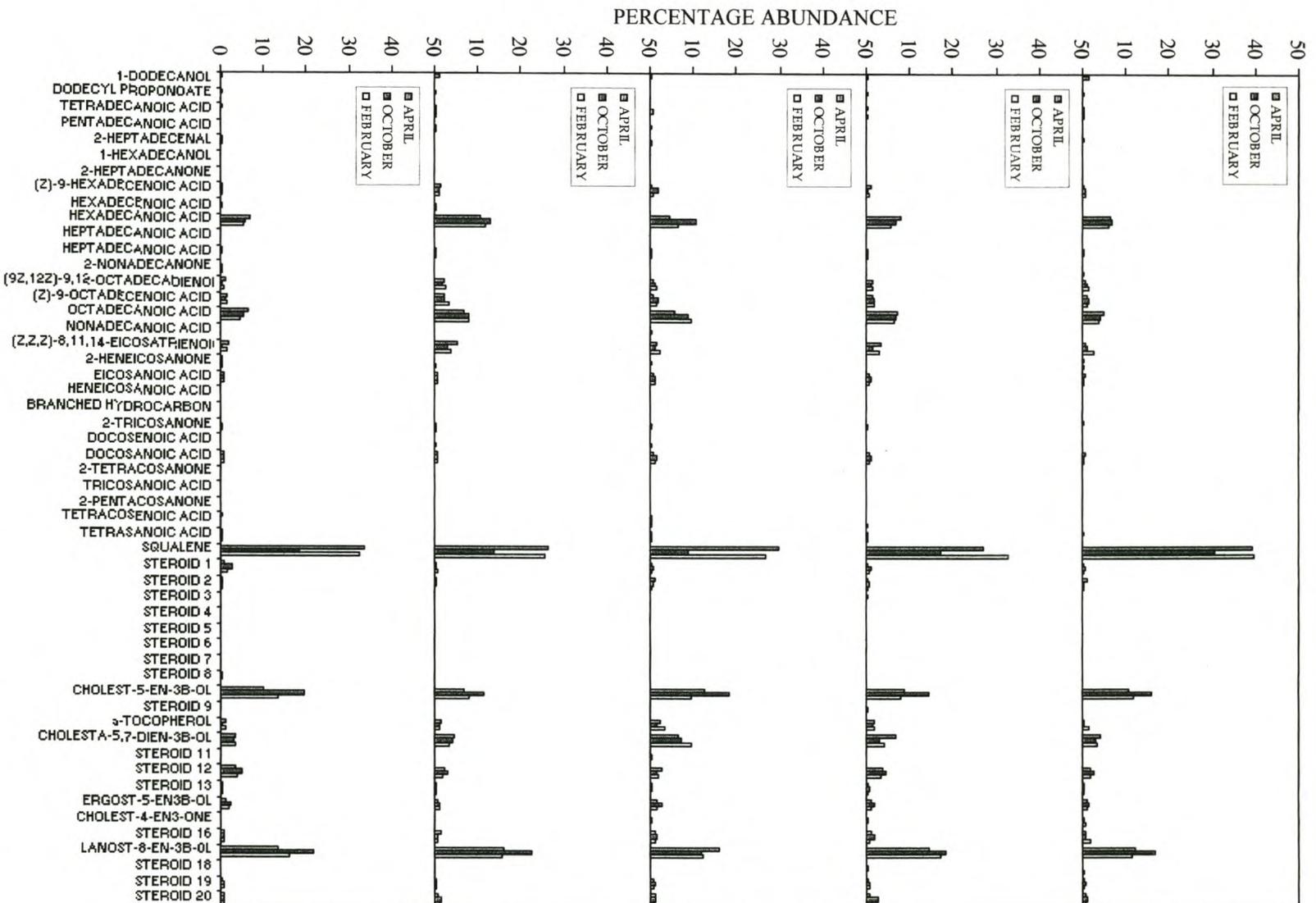


Figure 4.3. Profiles for the 53 compounds (% abundance) of five male *C. giganteus* for three times of the year (April, October and February).

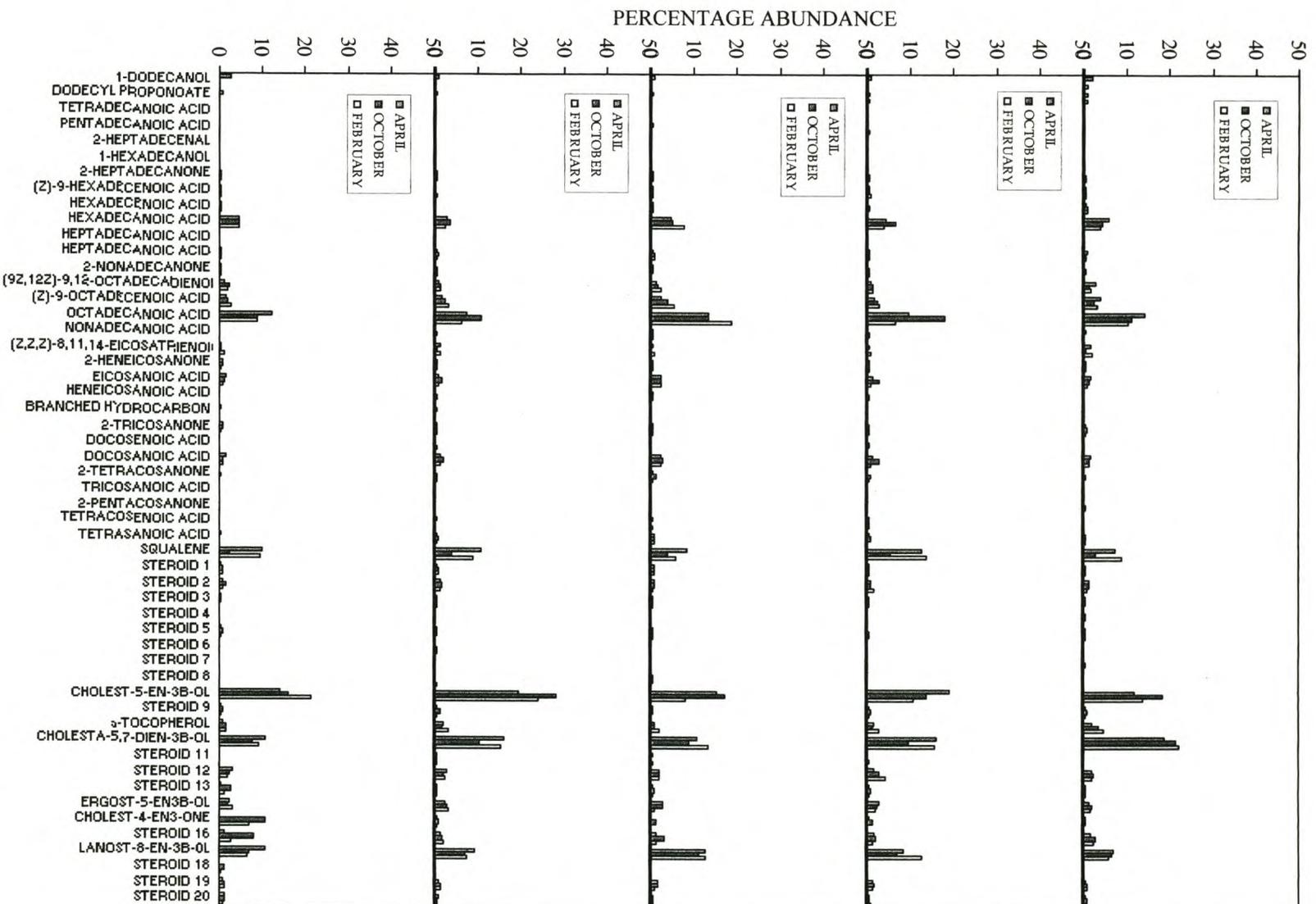


Figure 4.4. Profiles for the 53 compounds (% abundance) of five female *C. giganteus* for three times of the year (April, October and February).

Table 4.2. Relative composition (percentages) of dichloromethane extractable compounds during the mating (October) and non-mating (February) seasons. Shown are mean percentages ( $\pm 1$  SE). Different subscripts indicate significant seasonal differences ( $p < 0.05$ ).

	OCTOBER	FEBRUARY
Males	33.00 $\pm$ 4.31 <sup>b</sup>	22.74 $\pm$ 2.22 <sup>a</sup>
Females	38.18 $\pm$ 4.88 <sup>b</sup>	23.51 $\pm$ 3.01 <sup>a</sup>
TOTAL	38.30 $\pm$ 4.57 <sup>b</sup>	24.66 $\pm$ 2.24 <sup>a</sup>

Therefore, in both males and females, volatile compounds contributed significantly more to the total weight of gland secretions in October than in February (Table 4.2).

#### 4.3.5. Individual variation

In terms of presence-absence of volatile compounds, *C. giganteus* showed a mean ( $\pm 1$  SD) similarity of  $0.92 \pm 0.03$ . A comparison between sexes revealed a significantly greater intrasexual similarity in females ( $0.94 \pm 0.02$ ) than males ( $0.91 \pm 0.03$ ), and males were not more similar than intersexual similarity ( $0.91 \pm 0.02$ ), whereas females were ( $H_{(2)} = 49.3, p < 0.0001$ ).

#### 4.4. DISCUSSION

The compounds identified in the femoral gland secretions of *C. giganteus* are consistent with those found in *Iguana iguana* (Weldon *et al.*, 1990; Alberts *et al.*, 1992;). In addition, the presence of several alcohols and ketones are reported for the first time in lizards. Although fatty acids constituted a considerable proportion of secretions, steroids were the most abundant (up to 50 %) compound in males and females in. These, and other compounds, have been identified in the gland secretions of a variety of reptile taxa (e.g. Oldak, 1976; Eisner *et al.*, 1977; Simpson *et al.*, 1988; Weldon *et al.*, 1990; Weldon and Tanner, 1990), but many of these compounds have also been found in the skin of snakes and lizards (e.g. Mason *et al.*, 1986, 1987; Weldon and Bagnall, 1986; Mason and Gutzke, 1989). The presence of these major groups of compounds in gland secretions and skin therefore seems to be conservative across reptile taxa, with either or all compounds always being present.

The mode of action and dispersal of airborne semiochemicals impose certain restraints on the chemical properties of these messengers (Hadley, 1985). This means that the size and nature of chemicals determines the efficiency of their transfer in the environment. Wilson and Bossert (1963) even predicted that the majority of pheromones should contain between five and 20 carbons and have molecular weights between 80 and 300, because smaller molecules are more volatile and therefore can be transmitted more easily. The chemical nature of lipids makes them highly volatile in comparison with other compounds (Hadley, 1985), and it is probably for this reason that they are found in most gland and skin secretions. The femoral gland secretions of *C. giganteus* contain a variety of fatty acids, with chain lengths from  $C_{14}$  to  $C_{40}$ , with the most abundant being hexadecanoic acid ( $C_{16}$ ) and octadecanoic acid ( $C_{18}$ ). Although the fatty acids as a whole did not vary between sexes and season, their abundance in relation to one another may vary. Steroids are generally much less volatile, and therefore

could function in close-range signalling, whereas the fatty acids could be involved in long-range signalling.

Alcohols and ketones are utilised more widely in signalling than fatty acids (Hadley, 1985); only sexual variation was evident in ketones in *C. giganteus*, with females having a greater proportion, whereas the alcohols showed some seasonal variation in males. Alcohols are known to be used as sex pheromones in lepidopterans and coleopterans, but ketones are used more as predator deterrents (Hadley, 1985).

The most prominent variation in the femoral gland secretions of *C. giganteus* was that of the hydrocarbons (mainly squalene) and the steroids. These two groups seem to covary, with a decrease in hydrocarbons being accompanied by an increase in steroids, and vice versa. The seasonal steroid profile in both males and females also seems to follow the hormonal profile of *C. giganteus*. Female lizards maintain greater levels of steroid hormones (progesterone and oestrogen) during the year (Van Wyk, 1994), which could explain the greater proportion of steroids in females, and at the same time result in decreased levels of squalene, which is an important precursor molecule in the synthesis of steroids (Zubay, 1993). On the other hand, males showed an increase in steroid proportion during the mating season, which could be linked to increased levels of the steroid hormone testosterone during this time of the year (Van Wyk, 1995), and explains the lower levels of squalene. Lower annual levels of steroid hormones in males than in females could therefore be linked to the pattern of squalene/steroid abundance in the femoral gland secretions. If so, the levels of these compounds in the femoral gland secretion may simply reflect the blood plasma hormonal profile of a lizard, and these compounds could be transferred into the gland secretion by simple diffusion processes. Histological evidence has shown that lipids are present in the cells surrounding the secretory tubule of the femoral gland in cordylid lizards (Van Wyk, pers. comm.), suggesting that lipids could be actively secreted into the secretion during its passage through the pore of the femoral gland to the exterior, which indicates a positive role of these compounds in contributing to the composition of the gland. On the other hand, the levels of steroids could also be affected by steroid hormones targeting the femoral glands (Dufaure and Chambon, 1978; Boeyens *et al.*, 1992). Whatever the mechanism, seasonally altering levels of these compounds in the femoral gland secretion could contribute to seasonally different profiles in the gland secretion. This in turn could alter the behavioural responses of conspecifics towards individuals secreting femoral gland secretions. Possible information carried by the gland composition profile could be reproductive status (Chiu *et al.*, 1970; Fergusson *et al.*, 1985; Alberts, *et al.*, 1992; this study) and sex (this study). There

appears to be a link between internal and external communication in many species, because the steroids used as sex hormones are often also released to the environment as pheromones (Shorey, 1976). Garstka and Crews (1981) have reported a hormone/pheromone system in male garter snakes.

Originally it was thought that single-compound systems are the rule with pheromonal signalling, but since Silverstein *et al.* (1966) demonstrated the importance of a multi-component pheromone, it seems that combinations of compounds are more important than the presence of single compounds. Relative quantities of compounds often determine the eventual effectiveness of pheromones as sex attractants (e.g. Yushima *et al.*, 1974). In view of this, the variation in relative abundance of compounds in *C. giganteus* indicates that signals elicited by the femoral glands provide differing information from males and females, and from the same individual at different times of the year.

The functions of compounds may also lie in their chemical properties, which can aid in increasing signalling efficiency (Hadley, 1985). Many of the unidentified and trace compounds in the femoral gland secretions of *C. giganteus* may have such a role. It has even been hypothesised that the protein in femoral gland secretions functions as a protective capsule for lipids in the secretion (Alberts, 1993). It may also be that the function of the volatile compounds lies in their relative proportion in the gland secretion. These compounds constituted a greater proportion of the secretion in the mating season, which may increase the relative volatility of the secretion during this time, due to the greater abundance of low molecular weight compounds. In turn, this would make the secretion more detectable during the mating season (Alberts, 1993), when males and female *C. giganteus* move the most between burrows (Van Wyk, 1992; chapter six). Males could then determine the reproductive status (see above) of a female, since there are reproductively active and non-reproductive females during the mating season (Van Wyk, 1994). This is very likely, since femoral gland activity is affected directly by hormones (Chiu *et al.*, 1970; Fergusson *et al.*, 1985; Alberts, *et al.*, 1992). Ultraviolet visual sensitivity has also been investigated as a possible means for lizards to detect gland secretions (Alberts, 1989).

Although lipids varied between individuals, the amount of variation was much less than with proteins (see chapter three), adding to the evidence that femoral gland proteins could function to allow individual recognition, and femoral gland lipids function for secretion detection (Alberts, 1993), indication of reproductive status (Chiu *et al.*, 1970; Fergusson *et al.*, 1985) and social status (Alberts, *et al.*, 1992), if they were to be used as communication chemicals. This is consistent with the chemical properties of these two signal components.

Proteins are high molecular weight molecules with low volatility and high melting points (Alberts, 1990), and therefore can withstand extreme environmental conditions. These chemical properties make femoral gland secretions very suitable for range marking, or in the case of *C. giganteus*, marking of individual burrows, and the greater level of individual variation provides each lizard with a unique identification of its home burrow. Lipids are also lower molecular weight molecules with higher volatility and lower melting points than proteins (Alberts, 1990); this allows for better secretion detection over distance, which may facilitate movements between burrows by male *C. giganteus*. If the compounds were directly linked to the physiological state of the individual, they would be excellent indicators of reproductive or social status of individuals in a population.

It is therefore likely that the components identified in the femoral gland secretions of *C. giganteus* have a multi-functional role in signalling. The more volatile and less variable compounds (fatty acids, ketones and alcohols) likely aid in long-range detection of the secretions, while less volatile and more variable compounds (hydrocarbons and steroids) could function in signalling the social or reproductive status of an individual. It is less costly for lipids to be incorporated into gland secretions that follow the physiological status of the individual, rather than actively producing these chemicals in the gland and secreting them into the secretion. Consequently, information transferred by the gland lipids are an accurate indicator of these states, and could provide honest signals of quality and reproductive status. This in turn is amenable to a social structure where reproductive behaviour is confined to short periods, with limited movements between burrows, as is the case with *C. giganteus* (Van Wyk, 1992; this study).

Even though the evidence for use of airborne chemical cues in lizards is still scant and speculative (however, see Bull *et al.*, 1993), the variation in volatile compounds reported here, and in other studies, suggests that these compounds may have a positive role in chemical communication in *C. giganteus*. Furthermore, although this study has provided valuable insights into the functional significance of lipids in chemical communication in lizards, in order to evaluate general patterns, more information regarding social and reproductive status with respect to gland lipids is required.

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## CHAPTER FIVE

### BEHAVIOURAL RESPONSES TO FEMORAL GLAND SECRETIONS

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#### 5.1. INTRODUCTION

The social role of glands in animals is best determined by testing behavioural responses of individuals to the glandular material. Within the Reptilia, most studies have been conducted on ophidians and saurians (reviewed by Mason, 1992), and results are increasingly beginning to elucidate specific functions of reptilian glands. The behavioural responses of lizards to chemical cues elicited by glandular material has become a subject of much research since the 1980s. Researchers have realised that lizards, as with most other reptiles, also rely on chemical cues in addition to visual cues to transfer information to other individuals (Carpenter and Ferguson, 1977; Burghardt, 1970), or to recognise prey (Cooper, 1995).

Possible chemoreceptors of lizards include taste buds, the olfactory apparatus and the vomeronasal organs (Simon, 1983). Schwenk (1985) described the presence of taste buds in a wide array of lizard taxa, and suggests that the tongue should not be overlooked as a chemosensory organ, due to the abundance of taste buds on lizard tongues. Tongue-flicking has become a useful indicator of perception of chemical cues, since it is functionally related to the vomeronasal system (Distel, 1978; Graves and Halpern, 1990). Tongue-flicking has been used in a number of studies to show discrimination between different chemical cues. It has long been speculated for a long time that chemoreception in lizards is an interaction between the three systems (Cowles and Phelan, 1958).

Behavioural responses of lizards to chemical cues include aggression, courtship, avoidance behaviour, trailing and aggregation (Simon, 1983; Mason, 1992). Studies have focused on mother-offspring interactions (Fitch, 1954; Evans, 1959; Burghardt, 1970), conspecific and interspecific responses (Duvall *et al.*, 1980; Cooper and Vitt, 1984a, b; Cooper and Vitt, 1986; Cooper and Garstka, 1987), responses to unfamiliar situations (DeFazio *et al.* 1977; Bissinger, 1981) sex recognition (Cooper *et al.* 1986; Mason and Gutzke, 1990; Cooper *et al.*, 1996), conspecific aggression (Cooper and Vitt, 1987; Mason and Gutzke, 1990), pheromonal self recognition (Graves and Halpern 1991; Alberts, 1992; Alberts and Werner, 1993; Cooper *et al.* 1999), trailing and aggregation (Cooper and Gartska, 1987; Bull *et al.* 1992), and kin recognition (Werner *et al.*, 1987; Main and Bull, 1996; Léna

and Fraipont, 1998). The possible pheromonal roles of the glandular exudates have not all been determined yet, as lizards possess a wide array of possible sources of chemical cues. Some studies have even investigated the response of lizards to isolated fractions of glandular material (e.g. Cooper and Garstka, 1987). It has been proposed that the lipid fraction of femoral gland secretions allows detection of the chemical (Wilson and Bossert, 1963), or that lizards can perceive chemicals in the ultraviolet spectrum (Alberts, 1989).

Cole's review on lizard femoral glands suggested four hypotheses for the functions of femoral glands (see Cole (1966) for list of hypotheses). More recent behavioural studies (on iguanids) have provided evidence for territorial marking (Alberts, 1992; Alberts and Werner, 1993), yet there are no further studies on specific responses to femoral gland secretions and none to date on generation gland secretions. Such studies are needed to determine the specific functions of glands, in relation to their composition. Since these glands are well developed in cordylids, it is highly likely that they would play a role in chemical communication. Although it has been demonstrated that the cordylid *Cordylus cordylus* can distinguish between male and female substrate deposits (Cooper *et al.*, 1996), and between their own and other substrate deposits by tongue-flicking (Cooper *et al.*, 1999), this does not indicate whether it is femoral, generation or cloacal glands that serve these functions.

*Cordylus giganteus* possesses several potential sources of pheromones, including femoral, generation and cloacal glands (Van Wyk, 1992; Van Wyk and Mouton, 1992). Since residents occupy burrows for long periods of time (chapter six), it is suspected that chemical marking of burrows may occur. It would therefore be advantageous for residents to be able to distinguish their own chemical signals from that of other individuals. The objective of this study was to determine whether female *C. giganteus* use their femoral gland secretions for determining burrow identity chemically<sup>1</sup>. I tested the hypothesis that these glands are used for self recognition in females, i.e. can female *C. giganteus* distinguish between their own femoral gland secretions and that of another female?

## 5.2. MATERIALS AND METHODS

### 5.2.1. General procedures

Previous work on *Cordylus cordylus* (Cooper *et al.*, 1996, 1999) established that lizards responded to substrate deposits on ceramic tiles presented to them. Therefore, since *C. giganteus* belongs to the same genus and the tiles are appropriate for smearing femoral gland

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<sup>1</sup> Due to the tedious and time-consuming nature of field experiments, it was only possible to test females in the time allocated to these experiments during field trips.

secretions, tiles (15 × 10cm) were used to present femoral gland secretions to lizards. Secretions were smeared with a forceps onto the width of the tiles, over an area of approximately 3 × 1 cm and smeared secretion plugs (femoral glands) were also chosen to be of roughly the same size for each treatment (see below). Microfuge tubes containing the secretions were transported to the study site on ice and smeared onto tiles (except control tiles) prior to placing tiles at burrow entrances. All tiles were cleaned beforehand with odourless soap, and control tiles presented as is.

Observations of lizards were done by viewing a mirror mounted above the burrows of the test lizards with a 15-60× telescope (Tasco 15×30×40×60, Japan) placed 20 to 30 m from the burrow. At least two days prior to trials, mirror mountings were assembled at the burrows and pieces of cardboard, roughly the same size as the mirrors, were mounted. This allowed lizards to become accustomed to the presence of a foreign object outside their burrow entrances before trials.

Test tiles were carefully placed within 20 cm of the burrow entrance of the test lizard, in a manner that reduced disturbance to lizards still in their burrows. Upon emergence, the number of tongue-flicks performed by the test lizard was recorded over a focal period of 10 min., from the first tongue-flick directed towards the tile. Tongue-flicks were recorded as air tongue-flicks (tongue touches no object), grass tongue-flicks (touching grass around the burrow entrance), tile tongue-flicks (touching the tile) and secretion tongue-flicks (touching the secretion smeared onto the tile). Any behavioural responses other than tongue-flicks were also recorded. Tiles were removed from burrow entrances immediately after the trial was completed. Presentation of treatments for each experiment was done in a block design in partially counter-balanced order, for ten adult females.

### **5.2.2. Self recognition**

This experiment was done to determine if there was a difference in response of females to femoral gland secretions produced by self and that produced by other females. Therefore, each lizard was presented with three treatments: blank tile (control), tile with own secretion, and tile with secretion of an other female. The blank tile was used as a control to determine if lizards simply tongue-flick a foreign object outside their burrows. The other individual was chosen randomly from any lizard further than 50 m from the test lizard's burrow, to avoid possible neighbour recognition confounding the results. Only females (n = 10) were used in this experiment, because to the considerable amount of time used to obtain

data as a result of the high alertness of some of the lizards. Consecutive trials for each lizard were separated by at least two days to avoid habituation to tiles.

### 5.2.3. Data analysis

Counts of tongue-flicks towards each treatment were averaged to get mean tongue-flick rates for each treatment. Where data did not violate parametric assumptions, one-way repeated measures ANOVA was used to test for significant difference between treatments for each of the different types of tongue-flicks as well as for total tongue-flicks. Where data violated parametric assumptions, Friedman Repeated Measures on Ranks was used. Bonferroni adjustment of significance levels for repeated tests for applied ( $p = 0.007$ ).

## 5.3. RESULTS

### 5.3.1. General

Due to the high level of vigilance of lizards, they often took a great amount of time to emerge from burrows and start investigating tiles. Some lizards did not emerge even after 2 hours of observation, and had to be discarded from the experiment. Lizards generally approached the tiles with much caution, and always used tongue-flicking to investigate. No behaviour other than tongue-flicking was observed.

### 5.3.2. Self recognition

Mean number of tongue-flicks performed by female *C. giganteus* ( $n = 10$ ) towards the different treatment tiles are summarised in Table 4.1. Within all the different categories of tongue-flicks, there were no significant differences in the number of tongue-flicks towards the different treatments. Although non-significant, the greatest difference in mean tongue-flicks was in tongue-flicks directed at objects other than tiles (grass and air), with more tongue-flicks towards tiles with the secretion of other lizard.

## 5.4. DISCUSSION

The results indicate no discriminatory ability in *C. giganteus* females, and at most are only suggestive. Differential tongue-flicking rates usually indicate a discriminatory ability in lizards, with more tongue-flicks being directed towards less familiar odour sources (Graves and Halpern, 1991; Alberts and Werner, 1993). Self-recognition of femoral gland secretions has been demonstrated in *Iguana iguana* (Alberts, 1992) and *Dipsosaurus dorsalis* (Alberts and Werner, 1993), with highly significant results. However, test lizards in these experiments

Table 5.1. Comparison of the mean ( $\pm 1$  SE) number of tongue-flicks (TF) performed by female *C. giganteus* towards a blank tile (Blank), tile labelled with own secretion (Self), and tile labelled with secretion of other lizard (Other).

	SECRETION SOURCE	TONGUE FLICKS	RANGE	STATISTIC	p
Air TF	Blank	2.00 $\pm$ 0.71	0-5	$\chi^2=1.04$	0.654
	Self	2.11 $\pm$ 0.81	0-6		
	Other	7.78 $\pm$ 3.53	0-33		
Grass TF	Blank	1.90 $\pm$ 1.06	0-8	$\chi^2=3.25$	0.285
	Self	1.11 $\pm$ 0.56	0-4		
	Other	1.78 $\pm$ 0.46	0-4		
Total TF (non-tile)	Blank	3.90 $\pm$ 1.70	0-13	$\chi^2=1.46$	0.531
	Self	2.90 $\pm$ 1.13	0-10		
	Other	8.60 $\pm$ 3.64	0-36		
Tile TF	Blank	3.00 $\pm$ 1.18	0-12	F=2.267	0.136
	Self	0.56 $\pm$ 0.34	0-3		
	Other	2.44 $\pm$ 1.25	0-12		
Secretion TF	Self	1.56 $\pm$ 0.65	0-5	F=0.232	0.644
	Other	1.22 $\pm$ 0.40	0-3		
Total TF (tile)	Blank	3.00 $\pm$ 1.18	0-12	F=1.244	0.315
	Self	1.90 $\pm$ 0.85	0-8		
	Other	3.30 $\pm$ 1.20	0-12		
TOTAL TF	Blank	6.90 $\pm$ 2.58	0-20	F=3.75	0.046
	Self	5.33 $\pm$ 1.13	1-11		
	Other	13.22 $\pm$ 3.70	2-36		

were kept under controlled conditions and trials were conducted in prepared enclosures. These studies provide evidence for a range-marking or territory-marking function of femoral glands in these lizards. The ability to discriminate between own secretions and that of other individuals means that lizards can identify their own range or refuge, which would be important in a territorial social system. *Cordylus giganteus* show high levels of site fidelity and remain at the same burrow for long periods of time (chapter six), so femoral self-recognition would be advantageous for burrow recognition. Lizards often tongue-flicked their burrow surroundings upon emergence in the morning, indicating that burrow residents possibly test the odours around their burrow entrances to confirm burrow identity or the presence of other lizards.

No significant results were obtained for total tongue-flicks directed towards the different treatments, and there were no significant differences within the different categories of tongue-flicks (see Table 1). However, the greatest difference in mean tongue-flicks was found in tongue-flicks directed to objects other than tiles. In view of the nature of this field experiment, these differences could prove significant with greater sample size, since they contributed most to the difference in total tongue-flicks (however, Cooper *et al.*, 1996, 1999 obtained highly significant results with samples sizes of  $n = 10$ ). The use of non-substrate tongue-flicks has been demonstrated in studies on *Cordylus cordylus* (Cooper *et al.*, 1996; 1999), where results showed that lizards could discriminate substrate deposits of males and females, and own/other individuals. It is still unclear what the role of air tongue-flicks is, although there is speculation that it allows detection of chemical cues through volatile substances (Cowles and Phelan, 1958). In the case of *C. giganteus*, however, differences in tongue-flicks were mainly due to the difference in air tongue-flicks, which would suggest that, if *C. giganteus* could discriminate, discrimination is based on these tongue-flicks and not substrate tongue-flicks. Differences in air-tongue-flicks towards familiar and unfamiliar secretions were found in *Iguana iguana* (Alberts and Werner, 1993). Comparison of unfamiliar secretions with range marks or own body odours also suggests a discriminatory ability in lizards (Alberts, 1992).

Although various studies (Cooper *et al.*, 1996, 1999; Graves and Halpern, 1991) provide evidence for discrimination, these experiments used whole body odour (or whole body substrate deposits) as the treatments, so it may also be that other chemical sources such as skin chemicals (Weldon and Bagnall, 1987; Mason and Gutzke, 1990) or cloacal glands (Cooper and Vitt, 1986, 1987; Cooper and Garstka, 1987; Cooper and Trauth, 1992) play a role in discrimination as well. Whatever the case, even if studies using substrate deposits and

body odours show discriminatory abilities in lizards, they do not indicate which glands are involved, so behavioural studies should also focus on specific glands.

As mentioned above, greater sample size could create a clearer picture, but results could also have been confounded by conditions associated with field experiments. Results could have been confounded by the time of day during which experiments were performed (*C. giganteus* lizards may be more 'motivated' in the morning than in the afternoon, as deduced from daily activity patterns (Van Wyk, 1992)). Furthermore, the long emergence time from burrows of some lizards may indicate a higher level of alertness in some that may result in abnormally increased numbers of tongue-flicks directed towards a strange object. Although a field study may provide interesting information on natural tongue-flicking behaviour of lizards, environmental factors like wind, temperature and sunshine, and biological factors like motivation of lizards and age of secretion may also influence the results. It may also be that discriminatory ability of lizards is heightened only during the mating season. As this study was conducted after the primary mating season, it could be that female lizards are less 'motivated' due to lower levels of oestrogen (Van Wyk, 1994) at this time of the year. Femoral self-recognition would be more important during the mating season as well, since lizards spend more time moving around between burrows (Van Wyk, 1992; this study). Experimental studies with hormone treated female snakes and natural observations of breeding females (Duvall, 1981) also provide evidence for discriminatory ability being a function of hormonal status.

The results of this study also suggest that more attention needs to be paid to field studies of behavioural response to gland secretions, and whether tongue-flicking can still be used as an accurate indicator of discriminatory ability in view of the high variation in number of tongue-flicks recorded in behavioural experiments. Although tongue-flicking is known to be functionally related to the vomeronasal system (Burghardt, 1970; Gravelle, 1980; Simon, 1983), it is not known how accurately tongue-flick rate predicts the level of perception of chemical cues by lizard. It must also be remembered that captive conditions place many unknown stresses on test animals, that may influence results (e.g. Visagie *et al.*, unpublished data; test lizards (*Cordylus cataphractus*) did not tongue-flick tiles during trials).

In summary, overall results are not convincing enough to suggest a discriminatory ability in female *C. giganteus*. A clearer picture may emerge with greater sample size, but field conditions and high alertness of lizards could also confound results. More attention should be paid to experimental design and conditions associated with field circumstances.

Finally, generation glands, which only occur in male *C. giganteus* (Van Wyk and Mouton, 1992), still have to be used in behavioural tests to help elucidate their function in cordylid social systems. The diversity and close association of epidermal glands in cordylid lizards represents a unique opportunity to study the evolution and functional significance of these glands.

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## CHAPTER SIX

### SPATIAL DISTRIBUTION AND BURROW MOVEMENTS

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#### 6.1. INTRODUCTION

The area within which an individual animal moves is known as a home range, and includes food, refuge(s), basking spots and mates (Rose, 1982). Home range data can provide interesting information on the behaviour and ecology of populations. Measures of home ranges can indicate possible functions of these areas, and how movements of individuals serve to maintain breeding success, the social structure, and eventually ensuring stable populations. Variation between species, populations and over seasons is related to individual fitness, and it is this that determines the value of home ranges in home range studies. Home ranges can vary as a function of sex, energetic requirements, reproductive season and density (Rose, 1982).

Since it is impossible to monitor all the movements of an animal, sampling methods have been employed to estimate home range size, based mainly on recaptures/sightings of marked individuals. Two main methods have been used: polygon methods (Turner, 1971) and probability density functions (Jorgensen and Tanner, 1963; Tinkle, 1967; Jennrich and Turner, 1969; Waldschmidt, 1979). These methods represent movements of individuals in terms of areas, or probability distributions, and from this comparisons can be made with regard to differences between male and female movements, differences between seasons and extent of spatial overlap between individuals. Studies on lizards have shown that home ranges generally differ between sexes (Ferner, 1974; Parker, 1974; Davis and Ford, 1983; Smith, 1985; Van Sluys, 1997; Janssen and Nunez, 1998), between seasons (Nagy, 1973; Ferner, 1974; Parker, 1974; Kjekorian, 1976; Van Sluys, 1997), and as a function of body size (Turner *et al.*, 1969; Kjekorian, 1976; Swallow *et al.*, 1996). However, studies have also shown that home range varies as a function of body size over foraging groups (insectivores vs. herbivores), but not within foraging groups (Turner *et al.*, 1969; Christian and Waldschmidt, 1984).

Home range overlap is also used as an important indicator of resource availability and use of resources (Rose, 1982). Percentage overlap and/or number of individuals overlapped are frequently used to define the mating system or social system of lizards (Tinkle, 1967; Ferner, 1974; Kjekorian, 1976; Davis and Ford, 1983; Smith, 1985; Nicholson and

Spellerberg, 1989). High overlap suggests a hierarchical social system, while low overlap may suggest a more territorial system.

Distinction has also been made between home range, territories and core areas within home ranges. Territories are defended areas within the home range and can be the same size as the home range (Stamps, 1977); home ranges may also contain core areas where the highest degree of activity occurs (Christian *et al.*, 1986). These core areas may not be associated with home range movements or territorial encounters.

Spatial ecology encompasses how individuals of a population are positioned in their habitat, relative to one another. Three main types of spatial distribution are recognised (random, clumped and uniform), but they only refer to points along a continuum, and spatial patterns will vary accordingly (Krebs, 1989). Most non-random spatial patterns observed in animals are associated with heterogeneous distribution of resources, which leads to aggregations of individuals, but increased vigilance in groups also plays a role (Moody *et al.*, 1997). Social factors often lead to more uniform spacing of individuals (Eifler, 1996).

*Cordylus giganteus* remain within an area not more than 2 m from their burrow entrances, and movements further than this are either for feeding or to other burrows, most probably for mating (Van Wyk, 1992). Movements can be analysed on two levels: 1) micro-movements around the burrow entrance and macro-movements between burrows; 2) movements within a season, and movements over several seasons. Therefore, the movements of *C. giganteus* to a large extent are determined by relative positions of burrows, and a more accurate indication of "home range movements" would be given by number of burrows visited, and distance from home burrow, rather than home range area, since the area calculated would have no biological significance in terms of use of space. The homogeneity of the habitat in which *C. giganteus* lives provides an excellent opportunity to investigate spatial distribution of lizard burrows where environmental resources may not be limiting. *Cordylus giganteus* is a relatively sedentary species, exhibiting limited movements (Van Wyk, 1992). Burrow movements may therefore have important social implications. The purpose of this study was to record movements around the burrow entrance and between burrows, and spatial distribution of lizards in the population, with the aim of comparing these parameters between sexes, and in the case of between-burrow movements, between successive seasons.

## 6.2. MATERIALS AND METHODS

### 6.2.1. General

To investigate the spatial distribution of lizard burrows, spatial data obtained during mapping of the study area (see chapter one) were used. To analyse micro-movements (i.e. around burrow entrances) of lizards during the breeding season, observations of lizard positions at their burrows were made during October 1998. To analyse macro-movements (i.e. between burrows) of lizards over successive seasons, data on recaptures by Van Wyk (1992) over three seasons were used. Micro- and macro-movements were analysed in terms of within-season movements and between-season movements.

### 6.2.2. Spatial distribution

#### *Burrow spacing*

Positions of burrows were mapped as described in chapter one. X and Y coordinates of burrows were then determined and the map redrawn on a computer, with the sex of lizards indicated at each burrow (see Figure 8.1). Distances between all pairs of burrows were calculated using Microsoft® Excel for Windows 95, and nearest neighbours (first, second, third, to nth nearest neighbour) could then be determined for each individual in the population.

#### *Data analysis*

Statistical tests for testing deviation of spacing from randomness followed Donnelly's (1978) modification of Clarke and Evans' (1954) test. An index of aggregation,

$$R = \frac{r_c}{r_A}$$

where  $R$  = index of aggregation

$r_c$  = expected distance to nearest neighbour corrected for lack of boundary strip

$r_A$  = mean distance to nearest neighbour

was calculated for nearest neighbour distances, and tested for significant deviation from a random pattern ( $R = 1$ ) with a z-statistic:

$$Z = \frac{(r_A - r_c)}{S_r}$$

where  $z$  = standard normal deviate  
 $s_r$  = standard error of expected distance to nearest neighbour corrected for lack of boundary strip

With a clumped pattern,  $R$  approaches zero, and with a regular pattern  $R$  approaches an upper limit of 2.15. This test determines the nature of male-female, male-male, and female-female spatial distribution.

To test for spatial association of males and females, a presence-absence contingency table of nearest neighbours was created and analysed with the chi-square test for significant association or random mingling (Krebs, 1978).

Frequencies of male and female first to fifth nearest neighbour were calculated respectively for males and females, and the relative proportions of male and female nearest neighbours compared with the chi-square test.

### **6.2.3. Within-season movements**

#### ***General***

An observation tower was constructed from scaffolding in a position that allowed me to observe at least 22 burrows, which included 7 adult males and 9 adult females. The top of the tower was covered in white shade-cloth to prevent lizards being affected by my presence. Lizards were observed with a 60× telescope (Tasco 15/30/45/60×). During recaptures, lizards were marked with a unique paint code on their head, to allow visual identification. Scan observations were conducted over the whole day during a two-week period in October 1998. Scans were conducted every 30 min and the following information recorded: burrow number, lizard identity, distance of lizard from burrow entrance, and any possible interactions (see chapter one for details of lizard and burrow marking). At least three iron pegs (20 cm) were inserted in the ground at 0.5 m from burrow entrances at 90° with respect to each other, to aid the observer in estimating the distance of a lizard from its burrow entrance. A total of 64 h of scan sampling was performed during this period. Weather conditions at this time of the year were sunny and hot with occasional thunderstorms in the afternoons.

In addition to observations during October 1998, recaptures and censuses of the study area during the 1998-1999 seasons were also used to provide additional data on burrow movements.

### ***Data analysis***

Distance data were converted to mean distance from burrow entrance, and compared between sexes. Mean distance from burrow entrance was also compared to mean nearest neighbour distance to determine use of space between burrows.

#### **6.2.4. Between-seasons movements**

##### ***General***

Van Wyk (1992) sampled lizards over a period of four years (1985 - 1988), with up to fifteen recaptures per lizard. With each recapture, burrow location was recorded. This data therefore provided information on long-term movements over three seasons. This data did not provide information on local movements around burrows, but gives an indication of burrows occupied over several seasons. To determine the number of recaptures that would give the most accurate indication of burrow movements, recaptures were plotted against number of burrows occupied, and the asymptote determined for each season and for the entire study period.

Relative burrow positions were measured and plotted following Van Wyk (1992), and from this the X and Y co-ordinates of burrows determined. From this data, nearest neighbour distances could be calculated and used in subsequent analyses.

##### ***Data analysis***

Movements between burrows was analysed in terms of 1) number of lizards that moved between burrows; 2) number of burrows occupied per lizard; 3) number of successive burrow changes per lizard; 4) burrow fidelity; and 5) extent of movement (how far each lizard moved in terms of which  $n^{\text{th}}$  nearest neighbour visited). Burrow fidelity was measured as the proportion of recaptures that lizards spent in respective burrows. For a fixed number of burrows occupied, counts of burrow occupancy were tallied from most used to least used, standardised to a fixed number of recaptures per lizard and summed from burrow most used to burrow least used. The null hypothesis tested (no burrow fidelity) was that each burrow would represent equal proportions of recaptures, so for each number of burrows occupied, the observed counts were compared to the expected counts if there was no burrow fidelity. Extent of movement was measured by assigning each nearest neighbour a numerical rank in order of relative distance from the initial burrow used, providing an index of relative maximum distance moved; furthest distance moved was then compared between sexes with

the Mann-Whitney rank test. Bonferroni adjustment of significance levels were applied where applicable.

The above-mentioned parameters were then compared between sexes for each season, and for the entire study period (1985-1988).

### 6.3. RESULTS

#### 6.3.1. Spatial distribution

Burrows occupied by male and female *C. giganteus* were distributed in a slightly clumped fashion, whereas males were distributed randomly with respect to one another, and females were distributed randomly with respect to one another (Table 6.1).

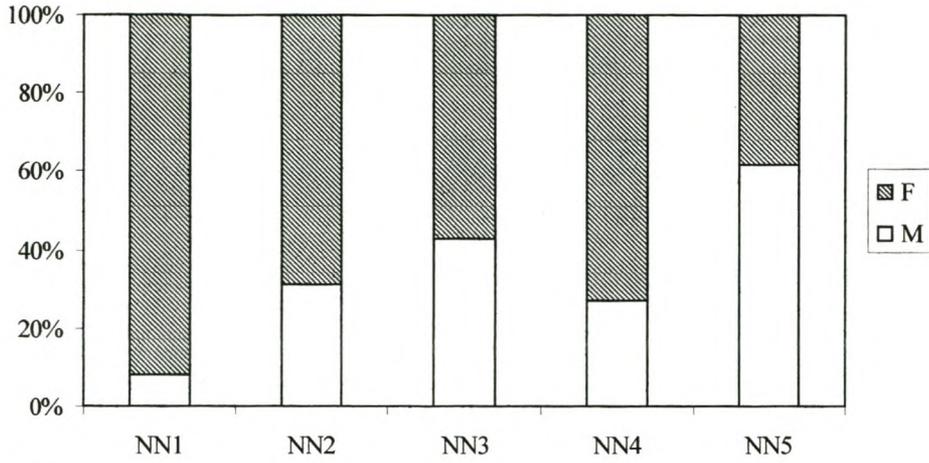
There was a highly significant association of males and females in terms of first nearest neighbours ( $\chi_1^2 = 32.0$ ,  $p < 0.001$ ), with there being considerably more male-female nearest neighbours than male-male and female-female nearest neighbours (Figure 6.1, first nearest neighbours). In several groupings ( $n = 8$ ), the associations consisted of one male grouped with two females (Figure 6.2). Furthermore, females had proportionally more female nearest neighbours than males had male nearest neighbours. This pattern changed gradually from first to fifth nearest neighbours for both males and female (Figure 6.1). There were no significant associations between male and female *C. giganteus* in terms of second nearest neighbour ( $\chi_1^2 = 0.23$ ,  $p = 0.634$ ) or third nearest neighbour ( $\chi_1^2 = 0.35$ ,  $p = 0.554$ ).

#### 6.3.2. Within-season movements

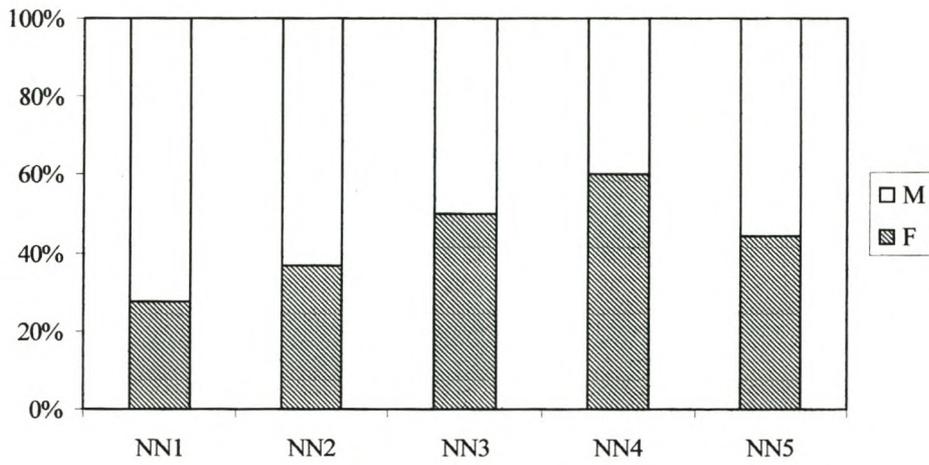
Burrow movements were characterised by very little time actually moving between burrows, but lizards remained at destination burrows for up to two days before returning to their home burrows, i.e. very little time was spent between burrows and areas surrounding home burrows. Lizards only moved from burrow to burrow, i.e. lizard activity always remained confined to burrows and burrow entrances. Burrow movements between male- and female-occupied burrows were further characterised by a pattern of burrow swapping, i.e. males and females that visited each other would swap burrows for the duration of the burrow visits, only remaining together at one burrow for a very short time. Lizards all returned to their home burrows after burrow visits, during the two week observation period. Movements at the burrows (micro-movements) were mainly position shifts related to basking and feeding, with occasional movements further than usual to catch prey items. Basking positions were often maintained for extended periods of time, i.e. lizards would be almost completely stationary for long periods during the day.

Table 6.1. Statistics of spatial distribution of a population of *C. giganteus* lizards. R = index of aggregation; z = critical statistic. The spacing differs significantly from randomness if  $|z| > 1.96$ .

	R	z	SPACING
Male-male spacing	1.14	1.58	Random
Female-female spacing	0.96	0.50	Random
Male-female spacing	0.86	-2.42	Clumped



(a). Males



(b). Females.

Figure 6.1. Percentage of *C. giganteus* male and female nearest neighbours for each sex, from first to fifth nearest neighbours.

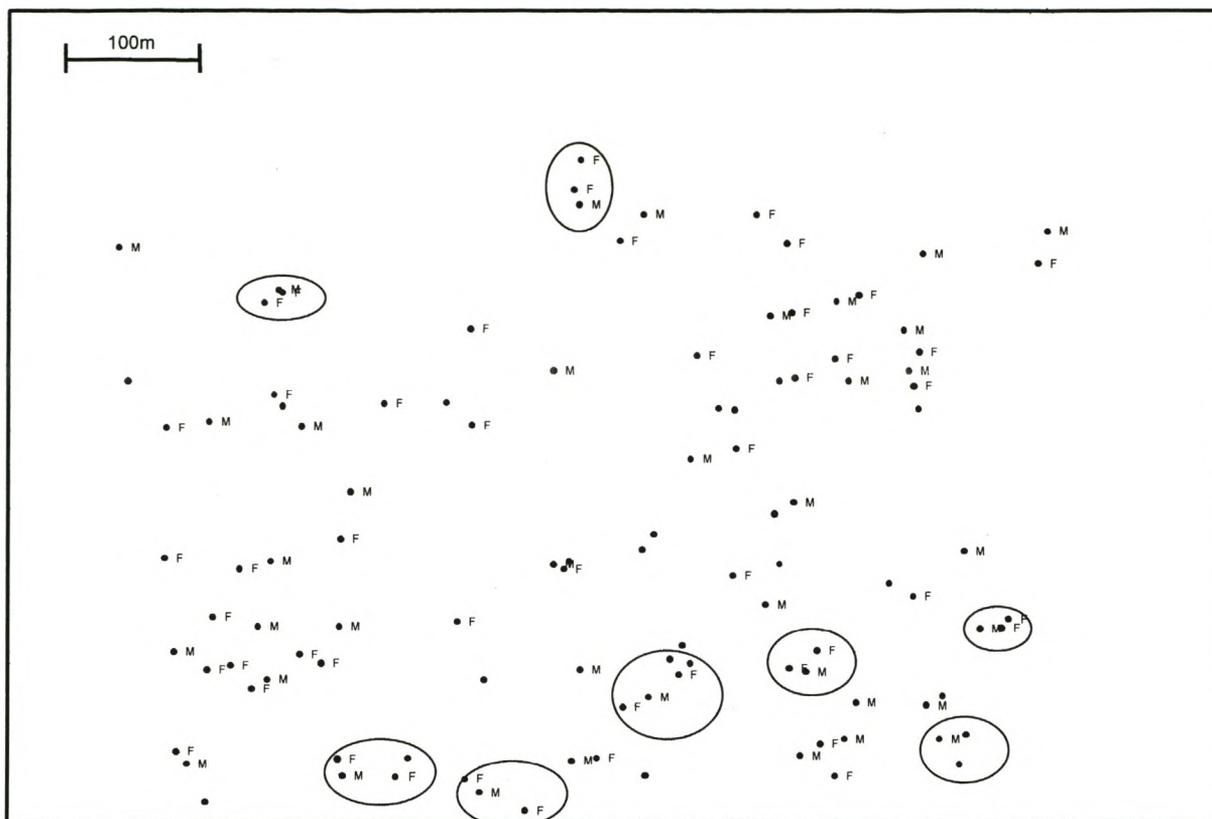


Figure 6.2. Map of the spatial distribution of *C. giganteus* burrows in the study area. Burrow labels indicate the sex of lizards at each burrow, while unlabeled burrows indicate unoccupied burrows or burrows where lizards were not captured. Oval shapes indicate cases where male *C. giganteus* are associated with two female *C. giganteus* (see text for details).

Males ( $n = 7$ ) maintained a mean ( $\pm$  SD) distance of  $0.47 \pm 0.23$  m from the burrow entrance, which was significantly further than the mean distance of  $0.41 \pm 0.17$  m maintained by females ( $n = 9$ ;  $T = 167818.50$ ,  $p < 0.0001$ ). Overall, lizards also maintained a mean distance ( $0.43 \pm 0.20$  m) that was significantly smaller than half the mean distance ( $7.78 \pm 3.49$  m) between nearest neighbours in the study site ( $T = 13960.00$ ,  $p < 0.0001$ ).

Movements between burrows during October 1998 are presented in Table 6.2. Of all the lizards ( $n = 41$ ) observed and censused during October 1998, 68.3% moved from their own burrow to other burrows. Of all the males ( $n = 18$ ), 72.2% moved between burrows, and 65.2% of females ( $n = 23$ ) moved between burrows. There was no significant difference in the proportion of males or females that moved between burrows (macro-movements) ( $\chi_1^2 = 0.02$ ,  $p = 0.889$ ), so males moved around just as much as females. Most visits by lizards were to a single lizard of the opposite sex, although a few males ( $n = 4$ ) visited two burrows occupied by two different females; these female burrows were always first and second nearest neighbour burrows. The second female was visited in the following breeding season. No females visited more than one male burrow. However, there was no significant difference in the mean number of burrows visited per male ( $1.31 \pm 0.117$ ) or per female ( $1.00 \pm 0.000$ ) lizard ( $T = 218.5$ ,  $p = 0.169$ ); therefore males and female lizards maintained a general pattern of visiting only one lizard of the opposite sex, at least during the mating period. Most visits by lizards were to the nearest neighbour (Table 6.2.), with only a few lizards visiting as far as the third nearest neighbour. Only one male travelled as far as the sixth nearest neighbour, i.e. burrow visits were therefore confined to nearest neighbour male-female pairs.

### 6.3.3. Between-seasons movements

For analyses of movements during each season, a minimum of three recaptures was necessary, while a minimum of five recaptures was necessary for analyses of movements over the whole study period (1985-1988).

There was no significant correlation between snout-vent length (SVL) and number of burrows occupied the whole period (males:  $r = -0.246$ ,  $p = 0.199$ ; females:  $r = -0.030$ ,  $p = 0.879$ ).

With respect to the proportion of lizards that moved, nearly half of the recaptured lizards moved each season, while more than 75% had moved over the entire period (Table 6.3). Other than the 1985/1986 season, a significantly greater proportion of males than females moved; over the entire period, proportionally more males than females moved as well. On average, lizards generally occupied more than one burrow per season, and over the

Table 6.2. Summary of within-season burrow movements by *C. giganteus* during October 1998 (during the breeding season). NN = nearest neighbour.

	TOTAL	TOTAL	%	$\chi^2$	p	MEAN	VISITS TO:					
	MOVED	STAY	MOVE			VISITS	NN1	NN2	NN3	NN4	NN5	NN6
Males	13	5	72.2	0.02	0.890	1.0±0.1	10	6	0	0	0	1
Females	15	8	65.2			1.0±0.0	10	4	1	0	0	0
TOTAL	28	13	68.3				20	10	1	0	0	1

Table 6.3. Summary of the proportion of lizards that moved (i.e. captured in more than one burrow) during the respective season and over the entire period. Chi-square and p values for comparisons between males and females are given in the last two columns.

SEASON	SEX	NO. LIZARDS			$\chi^2$	p
		MOVE	STAY	% MOVE		
1985	Males	16	12	57.1	0.99	0.319
-	Females	14	20	41.2		
1986	TOTALS	30	32	48.4		
1986	Males	16	4	80.0	4.58	0.032
-	Females	15	15	50.0		
1987	TOTALS	31	19	62.0		
1987	Males	9	9	50.0	7.07	0.008
-	Females	11	18	37.9		
1988	TOTALS	20	27	42.6		
1985	Males	38	4	90.5	5.96	0.015
-	Females	40	17	70.2		
1988	TOTALS	78	21	78.8		

whole period had occupied more than two burrows (Table 6.4). Once again, other than the 1985/1986 season, males occupied significantly more burrows than females, as well as over the whole period. The same pattern was evident with the number of successive movements (burrow changes): other than the 1985/1986 season, males changed burrows more often than females, and over the entire period (Table 6.5). Although most lizards remained at their initial burrow, with a considerable proportion that went as far as second nearest neighbour, some dispersed further than nearest neighbour 40 during some seasons (1985/1986:  $n = 2$ ; 1987/1988:  $n = 2$ ). Most lizards had moved as far as nearest neighbour one after all three seasons. Although in none of the seasons did males disperse significantly further than females (1985/1986:  $U = 361.0$ ,  $p = 0.299$ ; 1986/1987:  $U = 191.5$ ,  $p = 0.032$ ; 1987/1988:  $U = 228$ ,  $p = 0.674$ ) (Figure 6.3), over the entire period males had dispersed considerably further than females (1985-1988:  $U = 678.0$ ,  $p = 0.007$ ) (Figure 6.4). When lizards occupied more than one burrow, one burrow was always used more often than the others, and in all cases the proportion of use differed significantly from an equal proportion of use between all burrows (Table 6.6). However, burrow fidelity did not differ between males and females, with both sexes occupying similar numbers of burrows in equal proportions.

In summary, a considerable proportion of the population shifted occupancy between burrows each year, culminating in the majority of lizards having shifted occupancy over all the years. More males than females tended to move each season, and occupy more burrows on average. Male- and female-occupied burrows were clumped in distribution, but randomly distributed within sexes; females seemed to be clumped around males. Males also shifted occupancy more often and tended to disperse further in the long term. Finally, male and female lizards tended to make most use of a single burrow more often than other burrows, when they had occupied more than one burrow, during successive seasons and also over more than one season.

## 6.4. DISCUSSION

Although in most cases area is used as a measure of home range size to evaluate the movements of individuals in a population (Rose, 1982), this study indicates that home range area may not always be biologically applicable. As shown in this study, movements of *C. giganteus* are concentrated almost exclusively around burrow entrances ("micro-movements"), while movements between burrows ("macro-movements") occur infrequently and constitute a negligible amount of time in relation to total time spent moving, and therefore

Table 6.4. Summary of the mean number of burrows occupied per lizard during the respective seasons and the entire period. T and p values for comparisons between males and females are given in the last two columns.

SEASON	SEX	N	NO. BURROWS		
			( $\pm$ SD)	T	p
1985	Males	28	1.68 $\pm$ 0.72	1104.50	0.255
	Females	33	1.44 $\pm$ 0.56		
1986	TOTALS	61	1.52 $\pm$ 0.63		
1986	Males	22	2.10 $\pm$ 0.79	187.50	0.026
	Females	29	1.57 $\pm$ 0.63		
1987	TOTALS	51	1.68 $\pm$ 0.73		
1987	Males	17	1.56 $\pm$ 0.62	452.00	0.048
	Females	28	1.45 $\pm$ 0.63		
1988	TOTALS	45	1.41 $\pm$ 0.60		
1985	Males	44	2.69 $\pm$ 1.20	787.50	0.004
	Females	56	1.98 $\pm$ 0.88		
1988	TOTALS	100	2.19 $\pm$ 1.09		

Table 6.5. Summary of the mean number of successive movements by lizards between burrows during the respective seasons and the entire period. T and p values for comparisons between males and females are given in the last two columns.

SEASON	SEX	N	NO. MOVEMENTS		
			( $\pm$ SD)	T	p
1985	Males	28	0.93 $\pm$ 1.02	1,093.00	0.224
	Females	33	0.59 $\pm$ 0.82		
1986	TOTALS	61	0.70 $\pm$ 0.90		
1986	Males	22	1.65 $\pm$ 1.23	176.00	0.014
	Females	29	0.80 $\pm$ 1.00		
1987	TOTALS	51	1.68 $\pm$ 0.73		
1987	Males	17	0.72 $\pm$ 0.83	446.50	0.042
	Females	28	0.59 $\pm$ 0.87		
1988	TOTALS	45	0.54 $\pm$ 0.81		
1985	Males	44	2.93 $\pm$ 1.99	758.50	0.002
	Females	56	1.74 $\pm$ 1.77		
1988	TOTALS	100	2.19 $\pm$ 1.09		

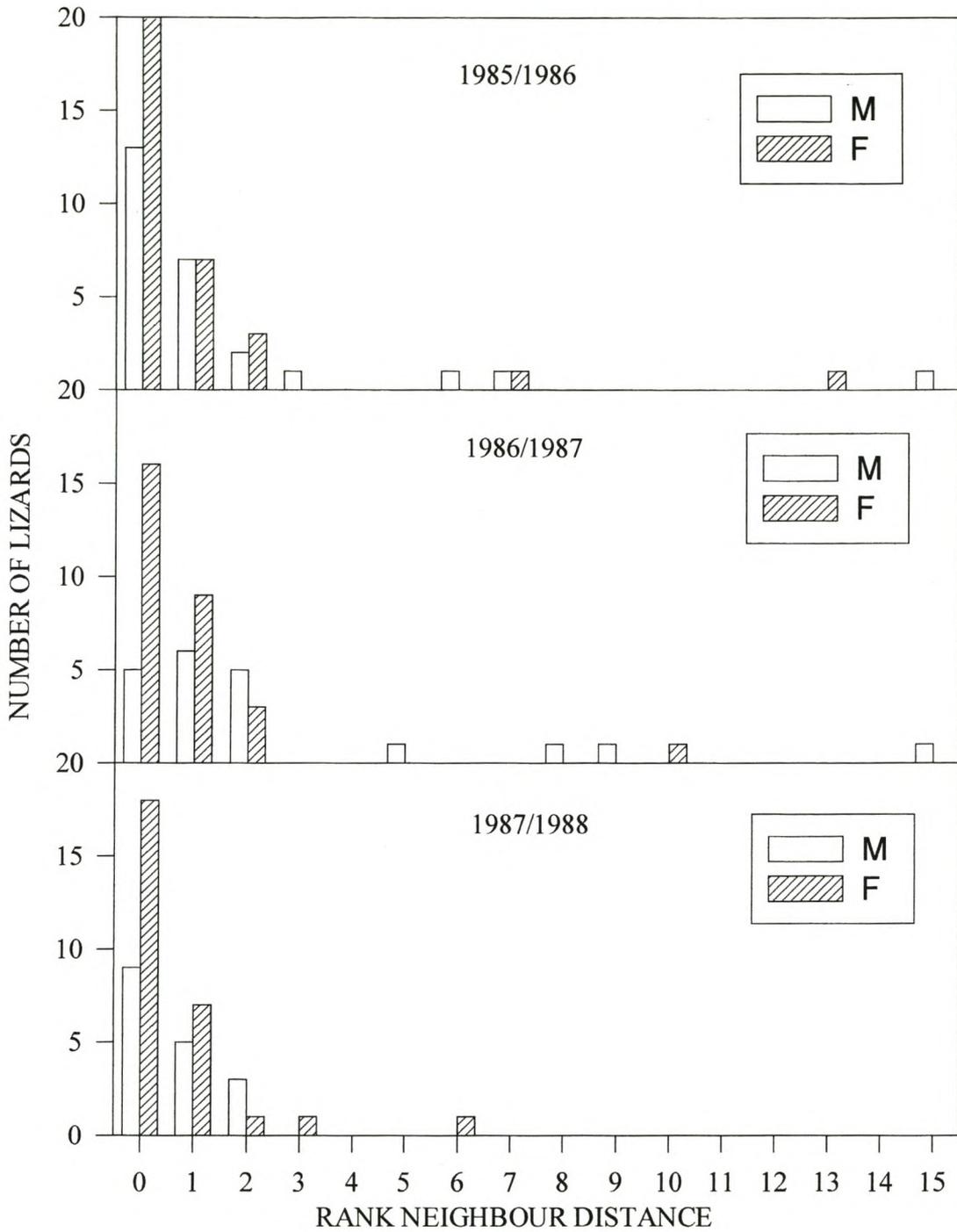


Figure 6.3. Relative dispersal distances of male and female *C. giganteus* in terms of number of lizards and furthest ranked neighbour burrow visited, for each of the three seasons. Dispersal beyond nearest neighbour fifteen is not shown.

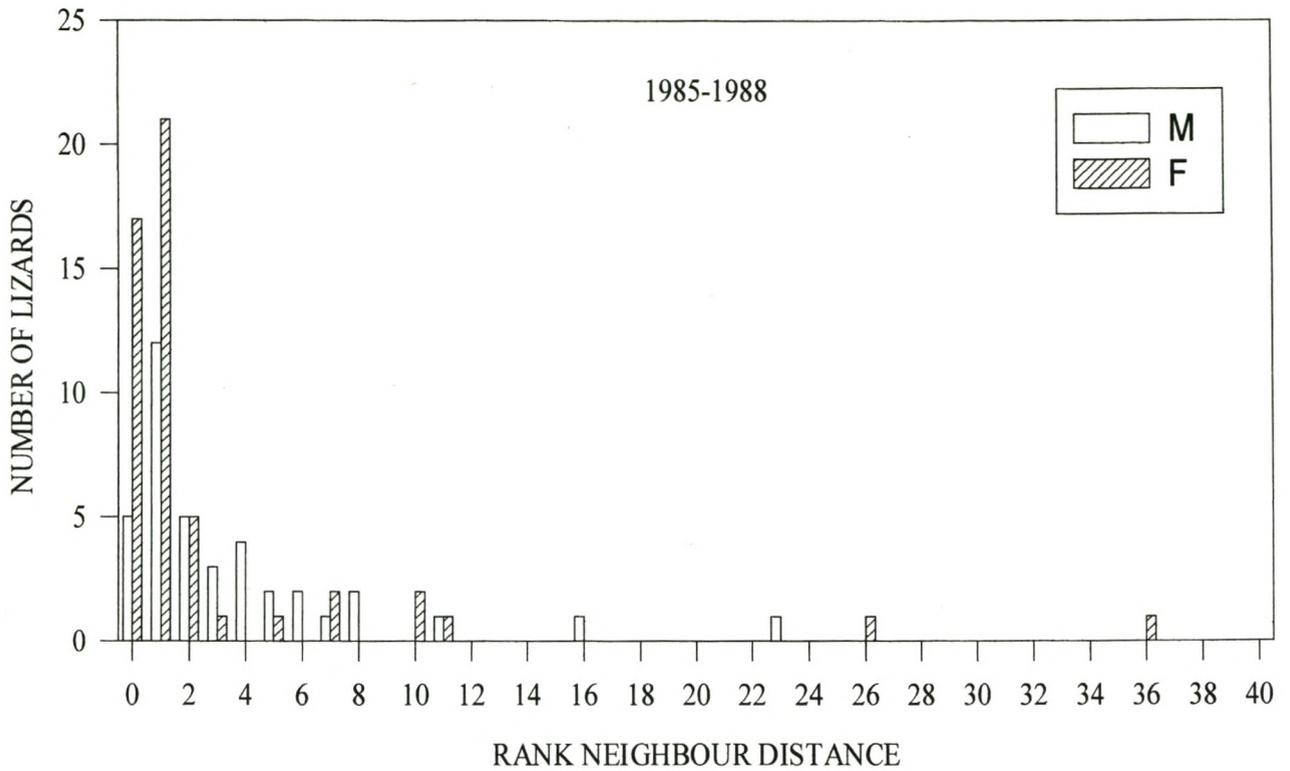


Figure 6.4. Relative dispersal distances of male and female *C. giganteus* in terms of number of lizards and furthest ranked neighbour burrow visited, over three seasons. Although a few lizards dispersed beyond nearest neighbour forty, these are not shown.

Table 6.6. Summary of the percentage use of burrows by male and female *C. giganteus* during the respective seasons.  $\chi^2$  and p values are given for comparisons between 1) percentage use of burrows, and 2) percentage use between males and females.

		NO.		ORDER OF USE		$\chi^2$	p	M vs. F	
		BURR	N	1	2			$\chi^2$	p
1985	Males	1	12	100.0				0.04	0.833
		2	14	68.9	31.1	12.04	0.001		
- 1986	Females	1	20	100.0				0.66	0.419
		2	13	71.3	28.7	14.13	0.000		
1986	TOTALS	1	32	100.0				0.14	0.906
		2	27	70.1	29.9	26.08	0.000		
1986	Males	1	4	100.0				0.14	0.906
		2	11	68.3	31.7	8.87	0.003		
- 1987	Females	1	15	100.0				0.14	0.906
		2	13	75.1	24.9	19.70	0.000		
1987	TOTALS	1	19	100.0				-	
		2	24	72.0	28.0	27.91	-		
1987	Males	1	9	100.0				0.14	0.906
		2	8	67.7	32.3	6.02	0.014		
- 1988	Females	1	18	100.0				0.14	0.906
		2	9	70.0	30.0	8.64	0.003		
1988	TOTALS	1	27	100.0				0.14	0.906
		2	17	68.9	31.1	14.61	0.000		

Table 6.7. Summary of the percentage use of burrows by male and female *C. giganteus* over three seasons.  $\chi^2$  and p values are given for comparisons between 1) percentage use of burrows, and 2) percentage use between males and females.

	NO. BURR	n	ORDER OF USE					$\chi^2$	p	M vs. F	
			1	2	3	4	5			$\chi^2$	p
Males	1	4	100.0								
	2	20	75.0	25.0				56.4	0.000	0.07	0.792
	3	8	54.5	30.4	15.2			28.2	0.000	2.54	0.281
	4	6	42.9	32.0	13.7	11.4		24.5	0.000		
	5	3	50.0	21.8	9.4	9.4	9.4	27.9	0.000		
1985	1	17	100.0								
- Females	2	28	76.1	24.0				110.1	0.000	0.07	0.792
1988	3	9	64.8	24.0	11.6			63.0	0.000	2.54	0.281
TOTAL	1	21	100.0								
	2	48	75.7	24.3				166.4	0.000		
	3	17	59.9	26.8	13.3			88.1	0.000		
	4	8	44.6	31.5	13.7	10.2		36.9	0.000		
	5	4	50.0	23.5	8.8	8.8	8.8	38.6	0.000		

are only properly measurable over more than one season. Such "core areas" within a home range have been described in other species (Christian *et al.*, 1986), where there is more intensive use of resources in that area. However, with *C. giganteus*, the core area is determined solely by burrow positions, since activity is concentrated around burrow entrances. In *C. giganteus*, the resources that determine "home range" movements are 1) the area around burrow entrances, and 2) the identity of burrow occupants. Resources directly associated with burrows are refuge site, basking sites and food, since refuging, basking and feeding constitute the majority of the daily time budget (see chapter seven). It seems unlikely that potential mates are a defended resource due to the low levels of natural interactions (chapter seven) and limited spatial overlap (this study).

Burrows occupied by *Cordylus giganteus* were distributed in a non-random pattern, which seems to be strongly related to sex. This spatial distribution probably largely reflects the social system of *C. giganteus*, since the habitat is highly homogeneous. In addition, since *C. giganteus* individuals are mostly sedentary and highly site-specific, burrow spacing becomes very important in ensuring that mating partners are in close proximity. This study highlights the importance of using spatial distribution (in terms of deviations from random spacing) rather than only home range analyses in species that occupy fixed refuges. Random spacing of lizards in relation to individuals of the same sex is probably a result of the clumping of male and female *C. giganteus* burrows. Since individuals of the opposite sex determine the spacing of one another, the result is that lizards of the same sex are randomly spaced. This also makes sense in view of the fact that interactions between lizards of the same sex are almost non-existent (chapter seven), since higher frequencies of interactions would tend to result in a more uniform spacing of individuals (Eifler, 1996).

Movements around the burrow entrance were characterised mainly by position changes to optimise thermoregulation during the day, and these movements were restricted to distances not exceeding a 1m radius around burrow entrances. Movements between burrows were quick and lizards knew the spatial positioning of destination burrows. It is unclear, however, what factors aid *C. giganteus* in orientating with respect to other burrows, since burrow entrances are not visible from surrounding burrows due to the high grass. Although visual cues or landmarks could be used to aid in orientation to refuges (Zuri and Bull, 1999), this would be very difficult in a homogenous environment such as that which *C. giganteus* inhabits. However, high site fidelity together with use of a small number of burrows and limited dispersal (most lizards moved only as far as second nearest neighbour), could enhance familiarity with burrow surroundings, especially if learning occurs in the time span of about

nine days reported by Zuri and Bull (1999). *Cordylus giganteus* also make intensive use of tongue-flicking for investigative behaviour around the burrow entrance (see chapter five), a behaviour that suggests constant confirmation of familiarity with a site or presence of other lizards. However, chemoreception may only play a limited role in between-burrow movements, since lizards displayed little tongue-flicking between burrows, and movement was too brief to allow sufficient chemosensory investigation. Mechanisms of burrow orientation require further attention in *C. giganteus*.

It seems unclear why male *C. giganteus* maintained a greater distance from burrow entrances than female *C. giganteus*, although the difference was very small (ca 6cm). Active defence a larger area surrounding the burrow entrance is unlikely, since lizards cannot observe each other due to the nature of the habitat. A possible option is the presence of juveniles at burrows of adults. Amongst the observation lizards, four male *C. giganteus* had juveniles as co-occupants, while only one female had a juvenile as co-occupant. Two lizards at a burrow entrance could probably enhance vigilance, and therefore allow either lizard to move further away from the burrow entrance than if there is only one lizard. This phenomenon of enhanced vigilance has also been shown in monogamous pairs of the lizard, *Tiliqua rugosa* (Bull and Pamula, 1998). However, whether this is a real relationship in *C. giganteus* is still speculative, and would require further testing.

Males and females showed significant differences in most of the burrow movement parameters, with males moving more often, occupying more burrows and generally dispersing further than females. Van Wyk (1994a) reported the following reproductive classes among female *C. giganteus* during the annual reproductive cycle: vitellogenic, gravid and non-reproductive. *C. giganteus* females exhibit biennial reproduction (Van Wyk, 1991), i.e. the proportion of reproductive females in a season does not differ significantly from 50%. The proportion of females that moved seemed to fluctuate around 50% during each season, and probably represent that part of the female population that are reproductively active during the mating season, when most movements between burrows occur (Van Wyk, 1992). Observational data also confirmed that females as well as males moved between burrows during mating events; as such, male and female mating partners actually swapped their burrows. However, these females would probably move less during pregnancy, as gravidity can impair movement and increase predation risk (Cooper *et al.*, 1990). Male *C. giganteus*, on the other hand, do not exhibit biennial reproductive activity (Van Wyk, 1995), and generally more than 50% of the male population moved during each season, and in two out of the three seasons a significantly greater proportion of males moved than females. During

observations in October 1998, it was also noted that females that were not involved in any reproductive activity did not move between burrows. It is therefore very likely that less movement by female *C. giganteus* may be brought about by current physiological or reproductive status. Energetic status could probably play a role in allowing more movements in reproductive females, since these females usually possess larger fat bodies than non-reproductive females (Van Wyk, 1994). In contrast, males do not exhibit more than one reproductive class and energy requirements therefore show less variation than in females. If males have to distinguish between reproductively active and non-active females, the result would be more movements by males due to searching for receptive females, since the operational sex ratio (OSR) is then actually male-biased. This could also influence distances moved by males, since the spatial position of reproductively active females determines how far males will search during the mating season.

The intensive use of the immediate area around burrow entrances and high burrow fidelity, even over a few seasons, suggests a highly site-specific lizard. The fact that male and female *C. giganteus* display extreme aggression towards intruding conspecifics of the same sex (see chapter seven), and remain at a distance that is much less than half the mean distance between nearest neighbour burrows, provides sufficient evidence that *C. giganteus* exhibits specific site defence, as defined by Stamps (1977). *Cordylus giganteus* is a sit-and-wait forager (Cooper *et al.*, 1997), with morphology that is not suited to fast locomotion in relation to active foragers, i.e. large body with short, stocky limbs. High site fidelity would therefore be advantageous to *C. giganteus*, because it increases the chances of predator avoidance when considering the constraints of a sit-and-wait foraging strategy coupled with the associated morphology. Predator avoidance behaviour has not been studied per se in this study, but adaptations related to predator avoidance certainly put constraints on other aspects of a species' biology, such as its social system, hence the high site fidelity and brief movements between burrows. This would also explain the extremely low frequency of natural interactions between lizards (see chapter seven). Lizards of the genus *Cordylus* are rupicolous and often inhabit specific refuges and have similar body forms with thick epidermal protection (Branch, 1988), suggesting that predator avoidance adaptations are commonplace in this genus. Sit-and-wait foraging, lack of prey chemical discrimination and a rupicolous lifestyle probably co-evolved in the ancestor of the Cordylidae (Mouton and Van Wyk, 1997), resulting in the intensive use of refuges to compensate for prolonged exposure to predators during basking and feeding. Therefore, predator-avoidance mechanisms seemed to

have taken preference over social interactions in the evolutionary history of *Cordylus*, resulting in a constrained social system.

An interesting result of this study was the differences in burrow movement parameters between seasons. Although in two out of the three seasons studied differences in male and female *C. giganteus* movements were maintained, there were no significant differences in movements in the 1985/1986 season, and there were no differences with respect to *all* the parameters in this season. The most likely explanation is the occurrence of a veld fire in the study area during this season (Van Wyk, pers. comm.), that could have drastically affected visibility and movements of lizards. An analysis of the annual rainfall and temperature data for this season (Van Wyk, 1992) shows that the 1985 spring season began with less monthly rainfall and continued with higher mean monthly maximum temperatures in the following months, than the other seasons. It may be that the weather regime in a particular season could affect the amount of movements made by lizards and possibly affect males more than females. Another possibility is the lower survivorship of males during 1986 (Van Wyk, 1992), so that many males that had moved were probably not recaptured. However, why movements of males would be more affected than that of females remains unclear.

Home range studies have shown a relationship between body size and home range size in lizards (Turner *et al.*, 1969; Christian and Waldschmidt, 1984), with larger lizards requiring larger home ranges. *Cordylus giganteus* showed no correlation between body size and number of burrows occupied within or over gender classes. This lends support to Christian and Waldschmidt's (1984) finding that no significant relationship between body size and home range size exists within a foraging group, such as within insectivores. Why would there be no relationship between these variables in a species where physiological condition seems to play an important role in determining reproductive events, with the associated movements? Stated otherwise, one would expect reproductive female *C. giganteus* to have larger bodies to sustain more movements during the mating period. It may be that fat body mass alone would be associated with amount of movement, but this would not be obvious when whole body mass is taken into account, since fat body mass variation accounts for only between 0.4 and 2.4% of the whole body mass (calculated from Van Wyk, 1994b). Therefore, larger fat body reserves could provide the energy required for more frequent movements. However, the nature of movements between burrows could negate this, since these movements are so brief, and constitute a negligible amount of time in relation to total activity time, that it requires less energy than would be expected, thus resulting in no relationship between body size and number of burrows occupied.

*Cordylus giganteus* showed high levels of refuge fidelity during and over three seasons, with a single burrow being used more often than other burrows. When lizards used more than one burrow, other burrows were always those of the mating partner, which were shared between them and offspring. However, as was the case with other movement parameters, there was no difference in degree of fidelity between male and female *C. giganteus*. Adult males and females defended burrows aggressively against intruding conspecifics of the same sex (see chapter seven), and used the immediate area around burrows very intensively (this study). This pattern, and the fact that *C. giganteus* is a large-bodied, long-lived viviparous lizard, closely resembles that of the Australian skink, *Tiliqua rugosa*, which is also a large-bodied, long-lived lizard that maintain stable home ranges (Bull, 1995) and monogamous pairing during breeding seasons (Bull *et al.*, 1998). This skink also exhibits mother-offspring recognition (Main and Bull, 1996), and home ranges of mothers and offspring tend to overlap considerably (Bull and Baghurst, 1998). Although kin recognition still needs to be investigated in *C. giganteus*, juveniles tend to remain at the burrows of parents for up to four years before dispersing away from home burrows, based on size of juvenile co-occupants (Van Wyk, 1992). High burrow fidelity would then certainly be advantageous for proper growth and maturation of lizards that are long-lived and take longer than most smaller lizards to reach maturity, thereby creating a stable, familiar environment in which young are less exposed to predation and other environmental factors that cause mortality.

Analysis of long-term movements of animals can provide insight into factors that affect dispersal over a few generations, especially in long-lived species like *C. giganteus*. Although *C. giganteus* is very site-specific with limited dispersal within seasons, the dynamics of burrow movements becomes apparent in the long-term. During a single season, most movements occur during the mating period when males and females exchange burrows and mating take place; thereafter, occasional movements take place between these burrows outside the breeding months. This pattern will repeat itself the following season, except that males will probably visit a different female, and over a few seasons lizards generally would have extended their movements much further than first or second nearest neighbour mating partners. Therefore, male and female lizards increase their range of movements over time, moving further and visiting more burrows. However, only a small percentage dispersed over distances further than the 15<sup>th</sup> nearest neighbour. Which factors determine dispersal is unclear, but could include incest avoidance, burrow displacement by more dominant individuals, or dispersal of older juveniles. Incest avoidance is a very likely option, because if

offspring did not disperse further than immediate neighbours, the chances would be very good for closely related individuals to mate. The only way to avoid incest in a highly site-specific species would therefore be for kin to disperse further than mating partners, which usually are the first or second nearest neighbours.

Although male *C. giganteus* dispersed further than females only during one season, by the end of all three seasons, males had dispersed much further than females. Males probably disperse further due to mate searching, especially during the mating season, when there are greater frequencies of burrow changes than other months of the year (Van Wyk, 1992). Greater dispersal of males could explain their higher mortality and smaller body size (Van Wyk, 1992), since they are more exposed to predation. Alternatively, the costs of reproduction in female *C. giganteus* (fat body depletion in gravid females, carrying of young and stress associated with birth), could simply be constraining their ability to disperse as far as male *C. giganteus*. Therefore, one might find that the female dispersers (those females that moved further than the average distance away from home burrows) represent the non-reproductive proportion of the population, while male dispersers represent those males that could not obtain successful matings. This phenomenon has been reported in the sand lizard (*Lacerta agilis*), where females with low reproductive output disperse further than more successfully breeding females (Olsson *et al.*, 1997). However, in the case of *C. giganteus*, non-reproductivity in females is probably related to energetics, and these female dispersers may even be searching for better resources to improve energy reserves.

Sex ratios reported by Van Wyk (1992) and Jacobsen *et al.* (1990) and this study, indicate a slightly female-biased ratio. This, together with the fact that males generally occupied more burrows per season than females, suggests a polygynous mating system (Emlen and Oring, 1977). However, data from the October 1998 observations suggest that males mate only with a single mating partner during a season, and then with a different female in the next season. Therefore, males are monogamous over one season, but polygynous over more than one season. This would make the apparent female-biased sex ratio seem functionally necessary, since without an excess of females the net reproduction rate would probably be too low to sustain the population, since females tend to skip reproduction in alternative years. Therefore, in one year males will mate with the reproductive proportion of females, and in the next year with that proportion that was non-reproductive in the previous season. The clumping and high degree of association of male and female *C. giganteus* burrows also suggests that lizards are forming groupings consisting of male and female mating partners. Furthermore, there were several cases where two females were grouped

around a single male (Figure 6.1), suggesting that these groupings consist of females clustered around males. It would be important in such a mating system for males to be spatially associated, since acquisition of females, especially in a relatively sedentary animal, depends largely on the temporal and spatial distribution of females (Emlen and Oring, 1977; Stamps, 1983).

A question that arises from this study is what factors determine where dispersing lizards position themselves in old burrows, or in making new burrows, in relation to existing burrows? Two possibilities emerge: 1) lizards are searching for resources, in which case spacing will be random, and 2) lizards are searching for mating partners, which will result in male-female aggregations. The clumped spatial distribution found in this study supports the second option. However, excavation of burrows by *C. giganteus* has rarely been noted in the field (Van Wyk, 1992, this study), and it seems that existing burrows that are deserted serve largely as a reservoir for dispersing lizards (Van Wyk, 1992). As mentioned in chapter seven, this population of *C. giganteus* may be at a density too low to allow any interactions to occur. It could be possible that the spacing pattern differs in populations with higher densities, and possibly also where the habitat is not limiting. This aspect requires further attention in *C. giganteus*.

In summary, burrow movements of *C. giganteus* are dictated seasonally by mating events, and to a limited extent by dispersal events. Differences in movements between males and females could be ascribed to differential reproductive effort. High refuge fidelity seems to be coupled with a strong predator avoidance strategy, which has probably put constraints on the social system. Spatial distribution of *C. giganteus* allows male and female mating partners to be in close proximity, and clumping of female burrows around male burrows, together with more movements of males, suggests a polygynous mating system over seasons. The burrow movement dynamics of this species seem to be closely associated with the fact that *C. giganteus* is a large-bodied, long-lived viviparous lizard.

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## CHAPTER SEVEN

### BEHAVIOURAL RESPONSES OF RESIDENTS TO INTRUDERS

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#### 7.1. INTRODUCTION

Social behaviour forms an integral part of an animal's mating system, and functions to maintain territories, dominance hierarchies and communication between individuals (Ferguson, 1977; Martins, 1994). At the most basic level, social behaviour is comprised of discrete behavioural acts, which result from a particular set of muscular actions or motor sequences (Carpenter and Ferguson, 1977). Animal communication has evolved so that individuals can make decisions based upon the behaviour, physiology or morphology of others through the use of signals, and functions through the transfer of information from one individual (the emitter) to another individual (the receiver) (Endler, 1993). In lizards, many social behavioural acts have been identified and described, and are used in the context of aggression, courtship and mating, and defence of resources (Carpenter and Ferguson, 1977). These behavioural acts also vary according to the spatial distributions of individuals in a population, which may vary from free-ranging, to defence of a home range, territory, specific site or personal space (Stamps, 1977). Thus, social behaviour in lizards, in terms of the type, diversity and frequencies of behaviours, is strongly linked to the mating system. Consequently, a significant relationship often exists between the social system, morphology and habitat of lizards. For example, sexual dimorphism is greatest in highly territorial species, and species where individuals defend large areas have higher frequencies of display behaviour than those defending a site (Stamps, 1977, 1983).

Aggressive encounters between lizards are well documented, and usually occur as a result of territorial encounters and resource competition between conspecifics (Martins, 1994). Aggressive behaviour is also graded in intensity. Display behaviour is less intense than combat behaviour and simply conveys information regarding dominance, mating and territorial or site ownership to other conspecifics, while combat behaviour ensues when conspecifics intrude on another individual's resource (Martins, 1994). Aggressive behaviour therefore ultimately serves for defence of resources, which is mediated by dominance hierarchies related to size (e.g. Tokarz, 1985; Ruby and Baird, 1993), or the resource holding power (RHP) of contestants (Parker, 1974). In many cases lizards also display differential aggression towards familiar and unfamiliar intruders, providing evidence of individual

recognition (e.g. Qualls and Jaeger, 1991; Whiting, 1999). The recognition of contestants in aggressive encounters may reduce the costs associated with fighting behaviour, and is known as the dear enemy phenomenon (Fisher, 1954). The asymmetric war of attrition model predicts that the degree of escalation in agonistic encounters depends on the degree of familiarity of the contestants with each other, such that encounters between neighbours will be less intense than encounters between non-neighbours (Ydenberg *et al.*, 1988).

Social studies on cordylids are lacking. Whiting (1999) investigated the dear enemy phenomenon in *Platysaurus broadleyi*, and the only *Cordylus* species for which there is behavioural data is *Cordylus cordylus*, which appears to be territorial with a high degree of site defence (Ruddock *et al.*, in press; Burrage, 1974; Wirminghaus, 1990; Cooper *et al.* 1996, 1999a). Two of the four genera (*Cordylus* and *Chamaesaura*) of the family Cordylidae exhibit very little or no sexual dimorphism (Mouton and Van Wyk, 1992). The eventual aim of behavioural studies on cordylid lizards is to explore further the relationship between sexual dimorphism and social system in lizards, by investigating a family of lizards with differing degrees of sexual dimorphism. *Cordylus giganteus* exhibits no colour dimorphism, but slight female-plus size dimorphism, and they live in large colonies in approximately evenly spaced burrows that adults occupy singly for long periods of time (chapter six; Van Wyk, 1992). Furthermore, the habitat of *C. giganteus* may be a limiting factor for social display behaviour. In view of the above-mentioned associations between use of space, morphology, habitat and social system, does *C. giganteus* show aggression towards conspecifics, and if they do, is it related to sex and familiarity of rivals?

The purpose of this behavioural study was to test the hypothesis that 1) residents defend a specific site (burrow in this case) and 2) that residents can distinguish neighbours from non-neighbours by sex (dear enemy recognition) in agonistic encounters. Data collected during this study were also used to construct the behavioural repertoire of *C. giganteus*.

## **7.2. MATERIALS AND METHODS**

### **7.2.1. Observations: behavioural time budget**

#### ***General***

Observations of marked lizards were made during October 1998, which falls in the mating season of *C. giganteus* (September to November) (Van Wyk, 1995), to determine the frequency and nature of natural behavioural interactions. Procedures for observations and marking are discussed in chapter six. During scan sampling, any natural behavioural interactions at lizard burrows were recorded. This included number and type of behavioural

acts, length of interaction, burrows where interactions occurred, and identities of lizards involved in interaction. To determine if residents defended a particular area in relation to nearest neighbours, distance of lizards from their burrow entrances was also recorded at each scan sample.

### ***Data analysis***

Observation data were used to calculate the behavioural budget of lizards in terms of number of scans, and converted to percentage time spent on a particular behaviour. The proportions of time spent per activity were then compared with a Chi-square test between males and females. Distance data were converted to mean distance from burrow entrance, and compared between sexes with the Mann-Whitney test. Mean distance from burrow entrance was also compared to mean nearest neighbour distance to determine use of space between burrows with the Mann-Whitney test.

## **7.2.2. Behavioural experiment: neighbour recognition and agonistic behaviour**

### ***General***

The aim of this experiment was to determine 1) if residents show a differential agonistic response towards neighbours compared to non-neighbours (dear enemy recognition) and 2) if residents defend their burrows from intruders (specific site defence). Staged introductions of "intruder" lizards (i.e. a lizard other than the resident of a burrow) to residents were performed during November 1999, which falls within the mating season (September to November) of *C. giganteus* (Van Wyk, 1995).

Focal animal sampling (Altmann, 1968) of the staged introductions were made from behind a hide. Hides were constructed from light-turquoise shade-cloth (1.5 × 0.5 m), which was suspended between two upright tent poles. An observation hole, about the size of a human eye, was cut to allow an observer to see the burrow. The hide was placed 3 m away from and facing the burrow, so that lizards could not detect the observer from the burrow. Hides were set up at the relevant burrow at least three days prior to a trial at that burrow.

Prior to an introduction, the resident and intruder (neighbour or non-neighbour) were caught (see chapter 1) and kept in separate cloth bags until the trial, during which they were left undisturbed by the observer. The cloth bags simulated the closed environment of *C. giganteus* burrows, and therefore decreased the chance of stress factors influencing results. At the beginning of a trial, the resident lizard was placed at its burrow entrance and the intruder tethered by an anchored rope nearby (within 30 cm) the resident, and both covered by

a cloth bag. The observer then retreated to the hide and slowly removed the cloth bag using a nylon line attached to the bag. All ensuing behavioural acts and the total duration of the interaction were then recorded on a tape recorder. A trial was terminated when behavioural acts ceased. Each of six male and six female residents were given two trials: neighbour-intruder and non-neighbour-intruder of the same sex. For each lizard, trials were separated by at least one day for the same lizard and arranged in counter-balanced order to control for order effects. Neighbours were the nearest lizard of the same sex, whereas non-neighbours were any other lizard of the same sex, further than 100 m from the resident's burrow.

### ***Data analysis***

To assess whether residents defend their burrows from intruders, their response to either neighbour or non-neighbour intruder during the behavioural experiment was scored as agonistic or non-agonistic. To determine if resident show differential response between neighbours and non-neighbours, the under-mentioned behavioural parameters were compared between the two. Therefore, both of these questions were addressed with the same behavioural experiment.

Behavioural acts and their level of aggression were recorded for the first time during these staged introductions. Therefore, levels of aggression could only be assigned after behavioural trials were completed. The behavioural repertoire of *Cordylus cordylus* was used as a framework for determining aggression levels (Ruddock *et al.*, 2001, *J. Herpetol.*, in press; Wirminghaus, 1990). Each behavioural act was then assigned a numerical score, increasing with levels of aggressiveness (Table 7.1.). During trials, duration and frequency of behavioural acts were recorded, as well as the number of bouts of aggression towards intruders. A bout is defined as discrete series of behavioural acts following in close succession (Martin and Bateson, 1988).

All data were converted to frequency of behavioural acts per minute. To assess the degree of aggressiveness of residents towards intruders, behavioural frequencies were used to calculate an index of aggressiveness,

$$IA = \sum f(AS) \quad (1)$$

where

IA = Index of aggressiveness

*f* = frequency of behavioural act

AS = aggression score for behavioural act (Table 7.2.)

An index of aggressiveness based on presence or absence of behavioural acts was also calculated,

$$IA = \sum p(AS) \quad (2)$$

where  $p = 1$  (present) or 0 (absent)

The first index takes into account both the level of aggressiveness reached by a lizard, and the intensity of each behavioural act, whereas the second index reflects aggression based on the presence or absence of behavioural acts. Level of aggressiveness and scores assigned to behavioural acts are shown in Table 7.2. For comparison, the level of aggression reached was also assigned to each behavioural trial.

To assess whether there was a difference between display frequency and combat frequency between neighbours and non-neighbours, all display behaviours were included in total display behaviour frequency, and all combat behaviours included in total combat display frequency, and these compared (see Table 7.2 for classification of display and combat behaviours).

To assess whether males and females differed in their response towards intruders, responses of males towards intruders, and females towards intruders, were also compared. If there was no difference in response to neighbour or non-neighbour intruder, these data were pooled for males and females, i.e. response to male neighbour and response to male non-neighbour were included in “response to male intruders”, and response to female neighbour and response to female non-neighbour were included in “response to female intruder”.

Two-tailed Wilcoxon signed-rank (matched pairs) tests were used to assess significance of differences between neighbours and non-neighbours with aggression indices, while other data were tested with two-tailed paired *t*-test where the data did not violate parametric assumptions. Two-tailed Mann-Whitney and *t*-tests were used respectively to test the same behavioural parameters when comparing males and females in their response to intruders.

## 7.3. RESULTS

### 7.3.1. Observations: behavioural time budget

Results of observational data are summarised in Table 7.1. Other than spatial proximity between male and female mating partners, no other behavioural interactions were recorded. When all age classes were pooled, lizards spent most of their time in refuge in their

burrows, while only 7.22% of their time was spent visiting burrows other than their own (Table 7.1.). The rest of the time was spent basking, with very rare feeding events.

A comparison of the time budgets of males and females revealed a significant difference in allocation to the various behaviours ( $\chi^2_2 = 10.67$ ,  $p = 0.005$ ). Males spent relatively more time visiting female burrows and refuging in their burrows, while females spent relatively more time basking (Table 7.1). Due to the low sample sizes for male and female juveniles, they were not included in this analysis, but are shown in Table 7.1 for comparison.

Males maintained a mean ( $\pm$  SD) distance of  $0.47 \pm 0.23$  m from the burrow entrance, which was significantly further than the mean distance of  $0.41 \pm 0.17$  m maintained by females ( $T = 167818.50$ ,  $p < 0.0001$ ). Overall, lizards also maintained a mean distance ( $0.43 \pm 0.20$  m) that was significantly smaller than half the mean distance ( $7.78 \pm 3.49$  m) between nearest neighbours in the study site ( $T = 13960.0$ ,  $p < 0.0001$ ).

### **7.3.2. Behavioural experiment: neighbour recognition and agonistic behaviour**

#### ***General***

All male and female resident lizards reacted aggressively towards intruders, whether they were neighbours or strangers. Behavioural acts performed by lizards during intruder experiments are described in Table 7.2. Behavioural acts could be categorised into investigative, display, encounter and combat behaviour, in order of increasing aggression towards an intruding lizard.

During investigative behaviour, which was used initially by residents, lizards used tongue-flicking and probably visual cues to investigate other lizards. Tongue-flicking was directed at most parts of the intruder's body, but particularly at the tail, hind- and forelegs, and neck area.

Display behaviour involved the use of various aggressive displays directed towards the other lizard, but with no physical contact between them. Displays were always accompanied by jerky movements of the body, where the body would be rocked quickly to and fro. Displays seemed to have the purpose of making the resident look larger, such as engorging the throat, arching the back or raising the body off the ground with all four legs. Wavy movements of the tail were also used and directed towards the intruder; a sweeping motion of the tail by intruders was used in a submissive context — unaccompanied by any aggressive behaviour.

Table 7.1. Behavioural time budget (% of total scans) by age and sex class of *C. giganteus* observed in the study area during the mating season. “Visiting” refers to time spent by lizards at the burrows of mating partners. The observations represent a total of 63 scan animal observation hours (127 scans). Percentages sum to values greater than 100% because overlap in behaviour often occurred (e.g. visiting while basking).

SEX-AGE CLASS	n	BASKING	FEEDING	VISITING	REFUGING
Males	7	38.50	0.33	7.70	61.27
Females	9	44.44	0.43	5.64	55.12
Male juveniles	3	46.61	0.52	15.63	52.86
Female juveniles	1	60.94	3.13	0.00	36.72
Juveniles (unsexed)	1	24.22	0.00	0.00	76.56
Totals	21	42.60	0.52	7.22	56.99

During encounters there was physical contact, but no fighting between lizards. The resident lizard would usually circle the intruder and walk over its tail or back while moving very jerkily.

Combat occurred when the resident used physical contact that could possibly hurt or injure the other lizard. Biting was used in most cases, and usually either a limb or the tail would be gripped in the resident's mouth, after which the resident would maintain the grip while moving jerkily. If the intruder struggled, the residents would either shake violently or flick at the intruder with its tail.

Investigative behaviour was usually used initially, after which display behaviour ensued which in most cases culminated in fighting behaviour by residents. Behavioural acts did not differ much in structure between trials, with each behaviour being performed in much the same way by different lizards. Jerky movements of the body were performed in conjunction with most other behavioural acts, and lizards constantly used tongue-flicking. The "raised on all fours, arched back and engorged throat" acts were more often used in combination than separately.

There was no difference in the behavioural acts used by males or females, and both sexes exhibited the same behavioural repertoire.

### ***Neighbour recognition***

Results of the behavioural experiments for male and female *C. giganteus* are shown in Table 7.3. (a) and (b) respectively. Both aggressiveness indices were highly correlated (Pearson Product  $r = 0.763$ ,  $p < 0.0001$ ), so only the first aggressiveness index was used, since it accounts for behavioural intensity; furthermore, since behavioural acts seemed to be conservative over most trials, intensity of behavioural acts would indicate more accurately if there was a difference in agonism between treatments. With respect to males (Table 7.3. (a)), there were no significant differences between responses to neighbour or non-neighbour males in any of the behavioural parameters, i.e. resident males were just as aggressive towards neighbour intruders as towards non-neighbour intruders. This pattern was also for females (Table 7.3. (b)).

Since there were no significant differences between response to neighbours and non-neighbours by male and female residents, these data were pooled for each sex, and response of male residents to male intruders compared to response of female residents to female intruders. Females were slightly more aggressive towards female intruders than males were towards male intruders (Table 7.4.). Females reached a higher level of aggression, and had a

Table 7.2. Behavioural acts (agonistic and non-agonistic) performed by *C. giganteus* during behavioural experiments. Also given are the numerical values assigned to each of the behavioural acts (aggression score), which were used to calculate indices of aggressiveness of each resident towards intruders. Level of aggression represents the position of a behavioural act in the succession from less aggressive to more aggressive behaviour. \*Sub. = subordinate; aggr. = aggressive.

Behaviour type	Behavioural act	Aggression level	Aggression score	Description
Display	Tail-wagging (sub.)*	0	-1	Tail is wagged from side to side in sweeping manner
Investigative	Tongue-flicking	1	+0	Lizard extends tongue beyond mouth, usually touching femoral region of hindlegs, forelegs, tail, flanks, neck area and face of intruder
Display	Jerky movements	2	+1	All movements made by lizard with a jerky motion
Display	Tail-wagging (aggr.)*	2	+1	Tail is wagged in wave-like manner, towards intruder
Display	Raised on all fours	3	+2	Lizard raises itself off the ground by extending legs
Display	Engorged throat	3	+2	Skin under throat is expanded slightly, making neck area look larger
Display	Arched back	3	+2	Back is arched upwards, i.e. convex with respect to the ground, usually in conjunction with engorged throat
Encounter	Circling	4	+3	Lizard walks round or over back of intruder, usually with arched back and engorged throat.
Encounter	Walk over back	5	+4	Lizard walks over back or tail of intruder.
Combat	Tail-lashing/flicking	6	+5	Tail is swung very quickly, often in quick succession, towards intruder, usually hitting face area
Combat	Biting	7	+6	Lizard bites hindleg, foreleg, tail or head of intruder, usually holding on while moving jerkily

Table 7.3. (a). Summary of frequencies of behavioural acts (acts per min  $\pm$  1SE) performed by resident male *C. giganteus*, and aggression score/level reached, towards neighbour and non-neighbour intruders during the behavioural experiment. P-levels (last column) indicate significance of paired *t*-tests (t) or Wilcoxon matched pairs tests (T).

	MALE		t (df)	T	p
	NEIGHBOUR	NON-NEIGHBOUR			
Duration of trial	14.24 $\pm$ 2.59	18.09 $\pm$ 1.75	-0.92 (5)		0.401
Number of bouts	0.46 $\pm$ 0.09	0.29 $\pm$ 0.06	1.16 (5)		0.298
Tongue-flicks	1.34 $\pm$ 0.31	1.46 $\pm$ 0.64	-0.13 (5)		0.900
Display frequency	0.98 $\pm$ 0.17	0.91 $\pm$ 0.09	-0.15 (5)		0.887
Combat frequency	0.14 $\pm$ 0.07	0.13 $\pm$ 0.13		35.5	0.366
Aggressiveness level	4.57 $\pm$ 0.75	3.67 $\pm$ 0.67		-1.0	0.750
Aggressiveness score	2.05 $\pm$ 0.55	1.78 $\pm$ 0.59		-1.0	1.000

(b). Summary of frequencies of behavioural acts (acts per min  $\pm$  1SE) performed by resident female *C. giganteus*, and aggression score/level reached, towards neighbour and non-neighbour intruders during the behavioural experiment. P-levels (last column) indicate significance of paired *t*-tests (t) or Wilcoxon matched pairs tests (W).

	FEMALE		t (df)	T	p
	NEIGHBOUR	NON-NEIGHBOUR			
Duration of trial	18.57 $\pm$ 4.11	18.54 $\pm$ 1.73		2.0	0.875
Number of bouts	0.22 $\pm$ 0.06	0.41 $\pm$ 0.06	-2.62 (5)		0.079
Tongue-flicks	0.22 $\pm$ 0.08	1.27 $\pm$ 0.24		0.0	0.125
Display frequency	1.04 $\pm$ 0.31	0.80 $\pm$ 0.14	0.43 (5)		0.697
Combat frequency	0.22 $\pm$ 0.15	0.26 $\pm$ 0.05		2.0	0.855
Aggressiveness level	5.00 $\pm$ 0.84	6.57 $\pm$ 0.42		6.0	0.250
Aggressiveness score	2.38 $\pm$ 1.11	3.28 $\pm$ 1.24		2.0	0.875

Table 7.4. Summary of frequencies of behavioural acts (acts per min  $\pm$  1SE) performed by resident male *C. giganteus* towards all male intruders, and by resident female *C. giganteus* towards all intruder females during behavioural experiments. P-levels (last column) indicate significance of *t*-tests (t) or Mann-Whitney U tests (U).

	MALE vs	FEMALE vs	t (df)	U	p
	MALE INTRUDER	FEMALE INTRUDER			
Duration of trial	16.01 $\pm$ 1.65	18.55 $\pm$ 1.87	-1.02 (22)		0.319
Number of bouts	0.38 $\pm$ 0.06	0.33 $\pm$ 0.05	0.65 (22)		0.521
Tongue-flicks	1.40 $\pm$ 0.32	0.84 $\pm$ 0.21		129	0.149
Display frequency	0.95 $\pm$ 0.10	0.90 $\pm$ 0.15	0.29 (22)		0.77
Combat frequency	0.14 $\pm$ 0.07	0.25 $\pm$ 0.07		191.5	0.057
Aggressiveness level	4.15 $\pm$ 0.50	5.92 $\pm$ 0.47		78	<0.001
Aggressiveness score	1.92 $\pm$ 0.39	2.91 $\pm$ 0.83		176	0.289

higher aggressiveness score than males. Although non-significant, females exhibited a higher frequency of combat behaviour towards female intruders.

#### 7.4. DISCUSSION

These data indicate that 1) residents react aggressively towards intruders, 2) they react just as aggressively towards neighbours as towards non-neighbours, and 3) females seemed to be slightly more aggressive towards female intruders than males were towards male intruders. The results from this study clearly show that male and female *C. giganteus* show aggression towards conspecifics of the same sex, if intruders approach the burrows of resident lizards. Aggressive responses often escalated to fighting, indicating that resident lizards show little toleration towards intruding conspecifics.

The behavioural repertoire reported here for *C. giganteus* is not much unlike that of male *Cordylus cordylus* (Ruddock *et al.*, 2001, *J. Herpetol.*, in press; Wirminghaus, 1990). All the behaviours used by residents are the same as that used by *C. cordylus*, except that *C. giganteus* used tail lashing when highly aggressive. *Cordylus giganteus* possess very spinous tails, used as defence when retreating into a burrow, which also makes it an effective deterrent to intruders. The tail was also used by intruders in a submissive display, which differed from the aggressive tail display used by residents (see Table 7.2.). It seems therefore that the spiny tail of *C. giganteus* has two functions: predator defence, and social signalling.

A jerky body movement during aggressive displays and biting seems to be the most common aggressive display used by *C. giganteus*, as well as by *C. cordylus*. Almost all the behaviours used by *C. giganteus* have been reported in other lizards as well (Carpenter and Ferguson, 1977), which involves 1) display actions to make the body look larger (engorged throat, arched back, body raised by all fours), and 2) biting and tail-lashing to inflict injury.

Evidence for specific site defence by animals includes 1) exclusive occupancy of the site, and 2) active defence of the site, although often the former evidence is used only, and site defence is inferred indirectly (Stamps, 1977). Most *C. giganteus* individuals observed in the study site occupied the same burrow during the whole study period (see chapter 6), and the response of resident *C. giganteus* to intruding conspecifics suggest that they do not tolerate other adult lizards near their burrows. These data clearly indicate that *C. giganteus* show specific site defence. Furthermore, observational data did not provide any evidence for defence of a territory or home range, although this was not investigated experimentally. Therefore, following Martins (1994), *C. giganteus* display aggressive types IV to VI, showing combat, threat and avoidance behaviour in defence of a specific site. The only other lizard

families, for which there are sufficient evidence, demonstrating specific site defence are skinks and geckos (Stamps, 1977).

Although resident lizards showed high levels of aggression in the behavioural experiment, this was not reflected in the frequency of natural behaviour (also noted in Van Wyk, 1992). Resident lizards remained close to their burrows throughout the entire day, and movements around the entrance were related mostly to shifts in basking position, and some movements for feeding; movements away from burrows have also been attributed to defecation (Van Wyk, pers. comm.). This apparent contradiction raises the question: why do residents show aggression towards intruders, but natural interactions are so rare they almost do not exist? It may be that *C. giganteus* individuals in the population studied are distributed in densities that are too low to allow any interactions to occur. Consequently, each lizard occupies their own burrow in the absence of competition from neighbouring lizards, which means less chance of interactions between neighbouring lizards. Various studies (e.g. Bustard, 1970; Stamps, 1973; Ruibal and Philibosian, 1974; Philibosian, 1975) have indicated the role that population density plays in the frequencies of display and combat behaviour between neighbouring lizards; frequencies of interactions increase with population density. If aggressive behaviour is as important as shown by the results of this study, it may be that population densities today are much lower than in historical times. A study investigating if natural frequencies of behaviour increase with an increase in population density would be a valuable addition to the knowledge gained in this study.

Another limiting factor that may play a role in reducing the frequency of interactions is the nature of the habitat. The dominant vegetation, *Themeda triandra*, even during the dry season (March to October), prevents lizards from observing one another at their burrows. Visibility is an important factor in determining the defence style (Stamps, 1977), and habitats with poor visibility will tend to favour a defence style that does not require defence of a large area. The distance between neighbouring burrows and the dense vegetation makes display behaviour and defence of a territory futile in *C. giganteus*. This aspect also deserves further attention in *C. giganteus*, and behavioural studies could also be done on populations where the habitat is not a limiting factor.

The results also indicate that *C. giganteus* males and females show no differential response towards neighbour and stranger intruders of the same sex. Although lizards occupy the same burrow for several seasons (Van Wyk, 1992), and therefore one might expect neighbours to be more familiar than non-neighbours, the extremely low level of interaction between neighbouring lizards (this study), negates this. Low levels of interactions between

lizards, as a result of low population density, together with limited movements around burrows would therefore make the dear enemy phenomenon (Fisher, 1954) unlikely in *C. giganteus*. Spatial association between lizards was only between mating partners and parent-offspring pairs, which suggests that residents will only tolerate potential mates and kin. Mate recognition and kin recognition may therefore be more likely forms of individual recognition in *C. giganteus*, and requires further investigation.

Although there was no significant difference in response towards neighbour or stranger intruders, females seemed to be slightly more aggressive towards female intruders than males were towards male intruders. To determine if this was a general response of females during the breeding season would require larger sample sizes, but it could also be a real effect. In many lizard species males tend to be the more aggressive sex in agonistic encounters with other males (e.g. Ruby, 1978; Deslippe *et al.*, 1990; Torr and Shine, 1996), and therefore have been the main focus of behavioural studies on lizards (Stamps, 1977). However, females in some groups are territorial and will defend areas as aggressively as males (Mahrt, 1998).

In summary, these results suggest that *C. giganteus* display high levels of site-defence, but probably do not defend a territory. Frequencies of social behaviour suggest that lizards are spaced too far apart to cause aggressive encounters, but this may also be due to the nature of the habitat. The behavioural acts exhibited by *C. giganteus* do not differ much from those reported for many other lizards, but seem to be dominated by jerky movements. It seems that resident lizards cannot distinguish between neighbour and non-neighbour intruders, but females are marginally more aggressive in agonistic encounters than males. Several further studies are needed to clarify certain aspects of the social system.

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## CHAPTER EIGHT

### GENERAL DISCUSSION AND CONCLUSIONS

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#### 8.1. SOCIAL STRUCTURE IN *CORDYLUS GIGANTEUS*

Although the social structure of an animal encompasses much more than the scope of this study, the results of this study have provided some interesting insights into the social structure of *C. giganteus*. Aspects of communication, movements, spatial distribution, social behaviour and mating system have been covered. *Cordylus giganteus* can be classified as highly site-specific, exhibiting site defence, and displaying aggressive behaviour towards intruding conspecifics of the same sex. The presence of specialised epidermal glands, variable femoral gland secretion composition and dependence on tongue-flicking behaviour, suggests a well-developed chemical communication system. Burrow movements suggest long-term occupancy with very limited movements, and tentatively a polygynous mating system over seasons, but monogamy within seasons, is suggested.

From the results obtained in this study, a basic framework of the social structure of *C. giganteus* can be created. Individuals occupy burrows for extended periods of time, which they will defend from intruding conspecifics. Social interactions are very rare due to the nature of the habitat, limited movements from burrows, and/or population densities that are too low to allow any interactions to occur. Instead, chemical signals could be the main means by which individuals communicate, based on variable lipid and protein composition of femoral gland secretions, and to a limited extent the response to these secretions by resident female lizards. The most probable function of femoral glands is to aid in chemical marking of burrows and burrow entrances, since these glands are situated on the underside of the hind legs, facilitating deposition; glands could also advertise reproductive or social status during mating events. Single occupancy by adults also suggests that conspecific co-occupants are not tolerated, and therefore that the refuge is a protected resource, together with basking spots and possibly food. The only interactions that occur in such populations are during the mating season, when male and female mating partners visit one another's burrows; even these interactions are short-lived and restricted to burrows and/or burrow entrances. Males possibly mate with one female during a mating season, and then with another during the next mating season, since the chances are good that at least 50% of reproductively mature females will not breed during a season (Van Wyk, 1991); however, the possibility is not excluded that some

males may mate with the same female in consecutive years, since some females do not skip years for reproduction (Van Wyk, 1991). This is also dependent on, where male-occupied burrows are surrounded by two or more female-occupied burrows, whether these females' reproductive cycles are synchronised. If their cycles alternate, seasonal monogamy is implicated, whereas coinciding cycles may result in seasonal polygyny. Males move further than females from home burrows, probably in search of reproductively active females during the mating season, and change burrow occupancy more often than females. Furthermore, male and female occupied burrows are spatially aggregated, with several cases where male burrows seem to be adjoined by two female burrows. These data all suggest that *C. giganteus* is polygynous over seasons, but monogamous within seasons.

Social structure in lizards has been classified according to spatial patterns, defence style and mating system (Stamps, 1977; Martins, 1994). According to these schemes, most lizards can be categorised in terms of their social structure, although there are often exceptions or modifications. Generally, it seems that the social system is phylogenetically determined (Martins, 1994), and co-varies with many other aspects of life history (see chapter two). Martins' (1994) scheme classifies lizards according to their defence style and defence area, which takes both use of space and type of defence into account. Three types of defence styles are recognised: 1) combat behaviour: aggressive acts involving physical contact that may result in injury; 2) threat behaviour: aggressive communicative display in response to another lizard, but without physical contact; 3) avoidance behaviour: use of indirect displays like chemical signals or broadcast displays (Martins, 1994). According to this scheme, 10 different types of social systems emerge (Table 8.1), of which more than one type can occur in a population. *Cordylus giganteus* defends a specific site, makes use of all three defence styles during agonistic encounters, and probably signals burrow occupancy with chemical signals. This would classify *C. giganteus* in Types IV, V and VI. Based on the phylogenies of Estes *et al.* (1988) and Frost and Etheridge (1989), defence area seems to be neatly divided according to major taxa (Martins, 1994). Iguanians defend all or part of a home range, anguids and varanids defend no specific area, teiids and lacertids defend no specific area, xantusids defend specific sites, gekkonids exhibit both, while skinks defend a specific site (Stamps, 1977; Martins, 1994). At this stage, indications are that some cordylids exhibit site defence (as is the case in *C. giganteus*), although information for all genera are still lacking. The only other *Cordylus* species for which there is sufficient data is *Cordylus cordylus*, which seems to be territorial, but with a high degree of site defence (Burrage, 1974; Wirminghaus, 1990; Ruddock *et al.*, 2001, *J. Herpetol.*, in press). Site defence seems to be a likely defence

Table 8.1. Classification scheme of aggressive defence behaviour and area defended in lizards, taken from Martins (1994). See text for descriptions of behaviour.

Defence style	Defence area		
	All or part of home range	Specific site (basking, shelter)	No area (self)
Combat	Type I	Type IV	Type VII
Threat	Type II	Type V	Type VIII
Avoidance	Type III	Type VI	Type IX
Type X = affiliative aggregations or random distribution of animals			

style in the genus *Cordylus*, since most species are rupicolous and inhabit refuges, although, as is the case with *C. cordylus*, a territory may be defended. Chemical communication also seems to be highly developed in this genus (Van Wyk and Mouton, 1992; Cooper *et al.*, 1996, 1999). Furthermore, some genera (*Platysaurus*, *Pseudocordylus*) exhibit sexual and size colour dimorphism (Mouton and Van Wyk, 1992, 1993), suggesting that different social systems may be operating in these species (e.g. Whiting, 1999; Whiting and Bateman, 1999). The caution taken by Martins (1994) in inferring phylogenetic states in the immediate ancestors of cordylids and scincids is necessary, making any conclusions at this stage tenable. However, it seems that home range defence is the primitive condition in lizards, with defence of no specific area the apomorphic state (Martins, 1994). If so, *C. giganteus* exhibits a relatively advanced social system in terms of lizard phylogeny.

Biological correlates of social structure for *C. giganteus* are summarised in Table 8.2, together with the social structure as inferred from the simple model presented in chapter two. Although several of the social systems may not be applicable to *C. giganteus*, quite a few of the factors were good predictors of site defence in *C. giganteus*. As mentioned in chapter two, the interrelationships between these factors and social system are complex, but by analysing how such a model fits to lizard species can aid in understanding evolutionary origins of social systems. It is also obvious that not *all* the factors were accurate predictors of the social structure of *C. giganteus*.

Sexual dimorphism in lizards is usually indicative of territoriality or a dominance hierarchy, where males are constantly involved in agonistic interactions, thereby resulting in sexual selection for bright colours and/or larger body size (Fitch, 1981; Stamps, 1983; Baird *et al.*, 1997). Indirectly, it can also be inferred that little sexual dimorphism is indicative of non-territoriality or site defence (Stamps, 1983). However, lack of sexual dimorphism may also be as a result of both sexes being territorial and therefore involved in agonistic encounters (Mahrt, 1998). In so doing, larger body size or display colouration may be selected for in both sexes, resulting in lack of major sexual dimorphism. This option may be applicable to *C. cordylus*, which also exhibits virtually no sexual dimorphism (Cordes *et al.*, 1995), yet both sexes seem to be territorial (Burrage, 1974). On the other hand, sexual selection is not the only explanation for sexual dimorphism in animals, which can also result from differential energy allocation or resource partitioning in males and females (Schoener, 1977). Both *C. giganteus* and *C. cordylus* exhibit slight sexual dimorphism in head size (Van Wyk, 1992; Cordes *et al.*, 1995), which could be as a result of differential reproductive effort by males and females (Cooper and Vitt, 1989). However, results from this study on *C.*

Table 8.2. Biological correlates of social structure in *C. giganteus*. The social system as inferred from chapter two is given in the last column.

FACTORS	<i>Cordylus giganteus</i>	SOCIAL SYSTEM
Foraging mode	Ambush	Territorial/site defence
Reproductive mode	Viviparous	Territorial/site defence
Communication mode	Chemical	Site defence
Habitat	Closed	Non-territorial/site defence
	Food uniformly distributed	Territorial
Morphology	Sexual dimorphism absent	Non-territorial/both sexes territorial
	Dull (non-colourful)	Non-territorial/site defence
	Short, stocky limbs	Site defence
	No male colour morphs	Non-territorial/site defence
Use of space	Home range overlap?	Non-territorial/site defence
	Clumped distribution	Dominance hierarchy
Refuge	Inhabits refuge (site fidelity)	Site defence

*giganteus* and Ruddock *et al.* (in press) on *C. cordylus*, have shown that biting is a common aggressive behavioural act used in agonistic encounters in these species, so the possibility that head size, which is related to gape size (Vitt and Cooper, 1985), could be under sexual selection, should not be excluded. Then again, although aggressive interactions are frequent in *C. cordylus* (Burrage, 1974), the low frequency of aggressive interactions in *C. giganteus* casts doubt on this possibility.

These observations on *Cordylus* species are in contrast to the situation that is found in some members of the closely related genus *Pseudocordylus*. Two species, *P. melanotus* and *P. microlepidotus* exhibit sexual dichromatism as well as sexual size dimorphism (FitzSimons, 1943; Loveridge, 1944; Mouton and Van Wyk, 1993). Indications are that these lizards are territorial, and polygynous in the case of *P. melanotus*, and slightly polygynous in the case of *P. microlepidotus* (Van Wyk, pers. comm.). Levels of sexual dimorphism seem to be associated with the degree of polygyny in these species, with *P. melanotus* exhibiting the higher level of sexual dimorphism (Mouton and Van Wyk, 1993). Both these species inhabit rocky terrain with good visibility (Branch, 1998). These associations lend very good support for the correlation of habitat and morphology with social system, also suggesting that sexual selection is operating in some species of the Cordylidae. Whether a sharp dichotomy in social system exists between the sexually dichromatic genera (*Platysaurus* and *Pseudocordylus*) and sexually monomorphic genera (*Cordylus* and *Chamaesaura*) is still speculative, because at this stage even within *Cordylus*, there seems to be variation in social system (this study; Ruddock *et al.*, in press). The preponderance of refuge use in this genus suggests that site defence may be the plesiomorphic state of this clade, which is well suited to the origin of sit-and-wait foraging and viviparity later on, in the ancestor of the Cordylidae (Mouton and Van Wyk, 1997). Furthermore, the possibility that site defence originated even earlier cannot be excluded, since the sister group to the Cordylidae, the Scincidae, also exhibit site defence (Stamps, 1977). If the above-mentioned holds, the social systems in some of the cordylid genera may represent evolutionary reversals, if territory/home range defence is considered the primitive condition (Martins, 1994).

Viviparity, a sit-and-wait foraging strategy, large body size, thermoregulatory-dominated activity, a high degree of predator-avoidance mechanisms, and a high degree of site fidelity are a selectively advantageous combination in *C. giganteus*. Viviparity requires intensive energy allocation by females (Guillette, 1993), especially in a large-bodied lizard with slow growth rates in comparison to other lizards (Van Wyk, 1992); it is not surprising that *C. giganteus* females exhibit biennial reproduction (Van Wyk, 1991). Embryonic

development is facilitated by an increase in basking time (Guillette, 1993), and a sit-and-wait feeding strategy results in less metabolic costs associated with active foraging (Bennett and Nagy, 1977; Bennett and Gleeson, 1979). Furthermore, the morphology of *C. giganteus* is not well suited to fleeing from predators. Therefore, long-term occupancy and restricted activity around burrows is the most viable option for *C. giganteus*. The result of the above-mentioned is a social system with site defence, but very low frequencies of interactions. This makes the spatial distribution of individuals very important, so that males and females are in close proximity to decrease time spent between burrows, and therefore exposure to predators. It is not surprising that the spatial distribution reflects a high degree of association between males and females, and that movements are restricted mainly to the closest nearest neighbours (chapter six). Since there is no variation in colour between individuals or between sexes, chemical recognition of conspecifics becomes the only alternative; chemical recognition of self (chapter five) is important for confirmation of burrow identity. It seems that predator-avoidance, or the origin of viviparity coupled with large body size (Mouton and Van Wyk, 1997), were more important selective forces in the evolutionary history of *C. giganteus*, and probably other cordylids as well, than sexual selection.

## 8.2. CONSERVATION IMPLICATIONS

*Cordylus giganteus* has been listed as a vulnerable species in the South African Red Data Book since 1988, mainly due to habitat threat from agricultural activities and mining, and to a limited extent from pet trade and pollution. Since most populations seem to occur on arable land and private farming properties, destruction of burrows in suitable grassland is the biggest concern. To date, the most promising solution has been the relocation of populations to protected areas (Jacobsen *et al.*, 1990), and is possibly the only viable option if farming activity continues to usurp suitable habitat. Although farmer education is also an option, this method has met with opposition, and also depends largely on the demand for increase in crop production, which usurps *C. giganteus* habitat.

Unfortunately in the first attempted relocations, the effect of relocating individuals to an alien environment was not taken into account, which may account for up to 30% mortality rates (Van Wyk, pers. comm.). Studies like this one are required to further our understanding of the biology of *C. giganteus*, which in turn can promote relocation attempts with possibly higher success rates. This study has indicated that spatial distribution and chemical communication seem to very important components in the social structure of *C. giganteus*, so these factors should be taken into account when creating new habitat for relocated

populations. It would probably be necessary to relocate them in a similar spacing (clumped according to sex), with the same individuals situated relative to one another. Burrow co-occupants (mostly adults and juveniles) should be relocated into the same burrow again. Furthermore, since chemical detection of burrow identity seems to be very important, new burrows should somehow contain an individual's own secretion odour, which would assure lizards of burrow identity and reduce stress associated with an unfamiliar environment. In addition, relocations should not be attempted during the mating season, as this is when lizards are the most active (Van Wyk, 1992; this study), and relocations would be most disruptive. If the area of relocation contains pre-existing burrows, care should be taken to ensure lizards are not released into occupied burrows; this can result in many relocated lizards being "evicted" by residents (chapter seven), exposing these lizards to predation and the elements. Although the above-mentioned factors are important in relocation attempts, social structure is not the only variable under consideration, and other variables like prevailing weather patterns, soil characteristics, vegetation cover and surrounding land use should all be taken into consideration.

The eventual aim of these studies is to contribute towards compiling an informed management and conservation strategy for *C. giganteus*. Cooperation from all stakeholders, especially landowners like farmers and mining companies, is of course also essential towards conserving a unique and threatened lizard species.

### **8.3. FUTURE DIRECTIONS**

As mentioned in the objectives of this study (chapter one), the main purpose was to provide baseline information regarding the social structure of *C. giganteus*. However, not only has this study only just touched on the multitude of aspects of social structure, but also it has indicated several further directions of study to broaden our knowledge on *C. giganteus*.

Basic variation of chemical composition of femoral gland secretions was investigated in chapters three and four. This can also include generation glands, which are currently being analysed. The relationship between reproductive status and gland composition/activity needs further attention, while more behavioural experiments are needed to elucidate the functions of femoral and generation glands. However, behavioural testing requires more refining, since captive experiments do not suit these lizards, and field experiments are tedious and time-consuming. Although movements of lizards was well covered in chapter six, a question remaining is population dynamics over the long-term, and how far lizards disperse from their home burrows over their lifetime. Mechanisms underlying orientation with respect to

burrows still remain unclear and could be investigated with innovative experiments. This question can be extended to include population genetics, since farming activity has fragmented *C. giganteus* populations. Minisatellite fingerprinting analysis is currently under way to determine paternity of young, distribution of related individuals, and whether gland secretion similarity is correlated with genetic similarity. More behavioural experiments are necessary to determine the response of residents to mating partners and related individuals. A study that is long overdue is investigating the effects of relocation on population and individuals, which will contribute enormously to conservation of this species. Finally, indications are that a primitive form of parental care is operating in *C. giganteus*, and requires further hypothesis testing.

The dynamics of grassland habitat seems to be unique in comparison to other habitats (Van Wyk, 1992). Although studies on a single species like *C. giganteus* are valuable, they should be included in a larger project investigating the dynamics of grassland ecosystems. The effects of environmental contaminants are becoming a contentious issue in present conservation issues, and the effects of agricultural chemicals should also be investigated.

#### 8.4. REFERENCES

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**APPENDIX 1****BRIEF CV OF STUDY PERIOD**

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**• Papers accepted for publication**

- Ruddock, L., J.H. van Wyk and M.I. Cherry 2001. Territoriality in male *Cordylus cordylus* (Reptilia: Cordylidae). *J. Herpetol.*, in press.
- Van Wyk, J.H. and L. Ruddock 2001. The male reproductive cycle of the lizard, *Agama atra* (Reptilia: Agamidae). *Amphibia-Reptilia*, in press.

**• Papers in preparation**

- Van Wyk, J.H. and L. Ruddock. The male and female reproductive cycles of the lizard, *Gerrhosaurus flavigularis* (Reptilia: Gerrhosauridae).
- Van Wyk, J.H. and L. Ruddock. The male and female reproductive cycles of the lizard, *Cordylus warreni* (Reptilia: Cordylidae).
- Van Wyk, J.H. and L. Ruddock. Thermoregulation paper.

**• Symposia attended**

- Zoological Society of Southern Africa, Symposium (attended)  
6 - 10 July 1998  
Durban, South Africa
- Herpetological Association of Africa, Fifth Symposium (poster presented)  
14 - 16 September 1998  
Stellenbosch, South Africa
- Zoological Society of Southern Africa, Symposium (paper presented)  
18 - 21 July 1999  
Pietersberg, South Africa

**• Research assistance**

- Reproductive cycles of southern African lizards
- Thermoregulation in southern African lizards
- Endocrine disruptor project

**• Techniques mastered**

- Histology of lizard (various *Cordylus* spp.) and frog (*Xenopus laevis*) gonads
  - Dissection of frogs (*Xenopus laevis*) and lizards (various *Cordylus* spp.)
  - DNA extraction, Southern Blotting, minisatellite probing
  - Protein gel electrophoresis (SDS-Page)
  - Behavioural field observations
  - Mark/recapture of lizards
- 
- **Miscellaneous**
    - Demonstrator for practical sessions for first years as part of Medical course (1998).
    - Presented lectures on Evolution for first years as part of Biology course (May 2000).
    - Radio-tracking of Gordon's Wildcat near Sharjah in the United Arab Emirates (Breeding Centre for Arabian Endangered Wildlife) (June/July 2000).

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**APPENDIX 2**

**PAPERS, ABSTRACTS AND SYMPOSIA**

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## Herpetological Association of Africa, Fifth Symposium

(Poster abstract)

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**TERRITORIALITY AND MICROHABITAT SELECTION IN THE CAPE GIRDLED LIZARD, *CORDYLUS CORDYLUS* (REPTILIA: CORDYLIDAE)**

L. Ruddock

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Few studies have looked into the social behaviour and mating systems of cordylid (Reptilia: Cordylidae) lizards, which can contribute towards a better understanding of the adaptive radiation of the family. *Cordylus cordylus* is a cordylid lizard that inhabits crevices and occurs in dense aggregations along rocky coastlines and inland rocky outcrops of the southwestern and eastern Cape, South Africa. Other than a descriptive field study and observations on captive *C. cordylus*, no studies have investigated experimentally the social structure of this lizard. A small population of *C. cordylus* selected for a short-term study on their spacing, crevice occupancy and aggressive behaviour related to site defense, to give indications of territorial behaviour and reasons for the observed spacing and crevice occupancy. Distances between crevices were measured, characteristics of occupied crevices recorded and male resident lizards were tested for behavioural responses to models of larger and smaller "intruders". Lizards generally had a nonrandom spacing, with females being further from each other than males from each other, crevice characteristics were biased in terms of lizard occupancy and male residents responded more aggressively to the larger model, with little or no response to the smaller model. The results suggest that *C. cordylus* 1) selects crevices for predator avoidance and microhabitat advantages, and 2) is territorial, defending at least a refuge.

Zoological Society of Southern Africa, Symposium  
(Paper abstract)

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**PROTEIN VARIATION IN THE FEMORAL GLAND SECRETIONS OF THE LIZARD, *CORDYLUS GIGANTEUS* (SAURIA: CORDYLIDAE)**

L. Ruddock and J.H. van Wyk

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Lizard femoral glands have long been implicated in chemical communication, but only a few studies have reported on the chemical composition of their secretions. The chemical communication hypothesis predicts that if chemicals are to be used in communication, there should be variation between individuals in the composition of the chemical secretions. Lizards of the genus *Cordylus* possess well-developed epidermal glands on the postero-ventral margin of their hindlegs, and therefore are useful subjects of research in this regard. *Cordylus giganteus* is a large terrestrial lizard inhabiting the highveld grasslands of the Free State, and is presently considered vulnerable in the SA Red Data Book. Due to the nature of its habitat, visual communication is limited, so chemical communication is a viable alternative. Femoral gland secretions of 15 adult male and 16 adult female *C. giganteus* individuals were analysed with SDS polyacrylamide protein gel electrophoresis, and the banding profiles of individuals and sexes compared. No two lizards, excepting two, had identical banding patterns, and according to similarity indices calculated for all pairs of individuals, there was greater inter- than intrasexual variation in their protein composition. Differences in proteins were found in both high and low molecular weight proteins. Our data therefore supports the chemical communication hypothesis. Possible functions of femoral glands in *C. giganteus* implicated in this study include individual recognition, sex recognition and kin recognition.

Final manuscript submitted before acceptance

Journal of Herpetology

July 2000

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JOURNAL OF HERPETOLOGY

LRH: L. RUDDOCK ET AL.

RRH: TERRITORIALITY IN CORDYLUS CORDYLUS

Territoriality in male Cordylus cordylus (Sauria: Cordylidae) during the autumn, at the time  
of testicular recrudescence

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Key words: Aggressive behavior, Cordylidae, Cordylus cordylus, Sexual dimorphism, Site  
defense, Site fidelity, Social behavior, Territoriality

A territory can be defined as an area of an animal's home range that is 1) defended with specific behavioral acts designed to evoke escape or avoidance in rival conspecifics; and 2) is mediated by aggressive interactions or display behavior, resulting in exclusive use of such areas (Brown and Orians, 1970). Territoriality may result in regulation of population density (Wynne-Edwards, 1962) or conservation of food resources (Lack, 1966), and the spacing structure of territorial species is closely associated with the mating system of that species (Hixon, 1987). Lizards display a variety of territorial patterns, the extent of territory defense varying from the whole home range to a small area around an individual (Stamps, 1977). Data available for many territorial lizard species can be used to infer the evolution of lizard territorial behavior, but for many lizard families these data are lacking (Martins, 1983).

C. cordylus belongs to the family Cordylidae, which includes some 60 species divided into four genera (Cooper, Whiting & van Wyk, 1997), and is restricted in distribution to southern Africa. Lizards of this family are characterized by short stocky limbs and scales arranged in "girdles" around the body (Branch, 1988). All members excepting one genus (Platysaurus, which are oviparous) are viviparous, and habitat use ranges from rupicolous to terrestrial (Cooper, Whiting & van Wyk, 1997; Mouton and van Wyk, 1997). Many species of the family Cordylidae possess specialized epidermal holocrine glands, in the mid-dorsal region, ventral aspects of the hindleg and pre-cloacal regions (Van Wyk and Mouton, 1992). Two main categories of epidermal glands can be distinguished: tubulo-follicular femoral glands and intra-epidermal generation glands. Femoral glands secrete a waxy exudate in the form of secretion plugs through a gland tube, while generation glands are multilayered glandular masses exposed on scale surfaces as part of the normal epidermal generation (Van Wyk and Mouton, 1992). Although males and females may possess femoral and generation glands, glands may be more numerous and better developed in males compared to females.

Studies on territoriality, and social behavior in general, are especially lacking for cordylid lizards. Pronounced sexual dimorphism is restricted to only two genera, Pseudocordylus and Platysaurus, whereas Chamaesaura and Cordylus show little or no sexual dimorphism in size or color (Mouton and van Wyk, 1993; Cordes et al., 1995). Since Cordylus species are often restricted to refuges in dense colonies, they provide an excellent opportunity to study social behavior in lizard species with the absence of pronounced sexual dimorphism.

Cordylus cordylus occurs in colonies (Burrage, 1974) in the southwestern, southern and eastern parts of the Western Cape, South Africa (FitzSimons, 1943). They are rupicolous lizards inhabiting narrow crevices in rocks on the coast and further inland (Branch, 1997), and display only very slight sexual dimorphism in head size, with males having larger heads

(Cordes *et al.*, 1995). Male *C. cordylus* exhibit a prenuptial spermatogenic cycle with the onset of testicular recrudescence in autumn. Spermiogenesis is completed in winter and continues through spring and early summer followed by a short testicular regression period before the onset of the next spermatogenic cycle (Jacobs and Van Wyk, unpublished data). Vitellogenic activity in females starts in late autumn and continues through winter until ovulation in early summer. Females are viviparous and two – three young are born in autumn. Although no data are available for time of year when mating occurs, it is assumed that mating takes place around the time of ovulation in spring and early summer. Burrage (1974) reported on population structure and various behavioral aspects of *C. cordylus*, mainly describing social organization and suggesting that this species is territorial. Wirminghaus (1990) documented the behavioral repertoire of *C. cordylus* in captivity, and reported on various displays and behavioral postures also found in other species, while Cordes (1995) performed staged encounters between lizards and reported on aggression between individuals. These studies suggest that *C. cordylus* is territorial. However Burrage (1974) did not record all the postures reported by Wirminghaus (1990), and there is no empirical evidence indicating what specific territorial pattern (Stamps, 1977) occurs in *C. cordylus*. Furthermore, these studies do not address the existence of a dominance hierarchy, or a description of the mating system in *C. cordylus*.

The aim of this study was to document the specific territorial pattern of male *C. cordylus* in the non-mating season, but during testicular recrudescence, as a baseline study for further studies. Although most behavioral studies of lizards are conducted in the mating season, we specifically investigated whether a territorial social structure is maintained outside the expected mating season as well, since males show increased testicular activity during this time, whereas vitellogenesis only started in females. We used the behavior reported by Burrage (1974) during summer and Wirminghaus (1990) as a comparison for our results, although the first was mostly a descriptive study, and the second a study conducted in captivity. To address the question of territoriality, we investigated: 1) the response of residents to intruding lizards; 2) spacing of individuals; 3) occupancy of crevices; and 4) the area defended by residents.

The study area is situated along the south coast of the Western Cape province of South Africa (34°33'S; 19°21'E). The study was conducted during April and May 1998, during the onset of the male spermatogenic cycle. During April 1998, the study site was searched for crevices, which were marked and numbered with rock beacons, and lizards were caught by extracting them from their crevices with a noose-stick. On capture each lizard was sexed

according to the relative abundance of generation glands on the postero-ventral margins of their hindlegs (males have proportionally more: van Wyk & Mouton, 1992) and the presence of hemipenal bulges in males. Snout-vent length was measured to the nearest 0.5 mm using a ruler. Non-toxic paint was used to paint unique color codes on the tails of lizards to allow easy identification during observations. All individuals were then returned to their point of capture.

For the spacing analysis, we used a tape measure and compass to measure distances (nearest m) and directions (nearest degree) between crevices containing lizards, and compiled a scale map of the study area, indicating crevice positions. From the scale map, nearest neighbor distances were determined. Statistical tests for deviation of spatial distribution of lizards from randomness followed Donnelly's modification of Clarke and Evans' (1954) test. An index of aggregation,

$$R = \frac{r_c}{r_A}$$

where  $R$  = index of aggregation

$r_c$  = expected distance to nearest neighbor corrected for lack of boundary strip

$r_A$  = mean distance to nearest neighbor was calculated for nearest neighbor distances, and tested for significant deviation from a random pattern ( $R = 1$ ) with a z-statistic:

$$z = \frac{(r_A - r_c)}{sr}$$

where  $z$  = standard normal deviate

$s_r$  = standard error of expected distance to nearest neighbor corrected for lack of boundary strip

With a clumped pattern,  $R$  approaches zero, and with a regular pattern  $R$  approaches an upper limit of 2.15. This test was done to determine the nature of male-female, male-male, and female-female spatial distribution. To compare spatial association between the same sex and between opposite sexes, frequencies of male-male, male-female, and female-female nearest neighbors were analyzed in a contingency table with the Chi-square test (Krebs, 1978).

To measure crevice occupancy, we censused the study site every week for four weeks and noted whether marked lizards were present at or absent from the crevices in which they were originally found. We also recorded the age group (juvenile or adult) and number of crevices occupied by more than one lizard.

For behavioral experiments an oblique rocky terrace site (facing towards the observation point) of 2500 m<sup>2</sup> was chosen. Observations were done from an observation point out of sight of the lizards, using a 30× telescope. Prior to all observational trials, the test lizard was chased into its crevice, and a painted model placed on the same contour as the crevice in a randomly chosen direction (yet allowing easy detection of the model by the lizard) at the relevant spot by the observer. Models were made using a mold and copper-plating technique described by Bakken and Gates (1975), and then painted to resemble the coloration of a *C. cordylus* male. The observer then retreated to the observation point and a trial commenced when the resident emerged from its crevice. Each behavioral act (following Table 1) performed by a resident lizard was then recorded for a period of ten minutes per trial. All different treatments for the same lizard were separated by at least one day. We verified the use of models in behavioral experiments by introducing a live, tethered lizard nearby the crevice entrances of male resident lizards; these residents showed similar responses to the model introductions. Two behavioral experiments were performed, and were separated in time by one week.

Firstly, to test whether resident male lizards defend a territory or just a refuge (crevice), the lizard model was arbitrarily placed at 1.0 m, 0.5 m, and 0.1 m from the crevice entrance of a resident male ( $n = 5$ ) in partially counterbalanced order, and the behavior recorded (Table 1) over ten minutes. With this experiment, behavior at each distance for each lizard was scored as a positive response or no response for a particular behavioral act, i.e. the resident either responded or did not respond with a particular behavior towards the model at a given distance. The data was then converted to percentage of lizards that responded with the given behavior at a given distance.

Secondly, to compare the response of resident males to “intruders” of different sizes, we presented two models of different sizes to the same residents ( $n = 6$ ; plus one more resident) in random sequence, and recorded the resident’s behavior. The mean SVL of the male test residents was  $78.8 \pm 3.4$  mm. The small model (“SVL” = 67 mm) was smaller than all residents, but larger than all juveniles (mostly hatchlings) found in the study site, and the large model (“SVL” = 83 mm) the same size or only slightly larger than all residents (size difference not easily discernible to the naked eye). We scored the behavioral responses of lizards in this behavioral experiment in terms of the scores shown in Table 1. The responses of lizards were then used to calculate an additive aggression index (Table 1, after Baird *et al.*, 1997), according to the presence or absence of displays. If a display was present (once or more than once in a trial), corresponding scores were assigned (from Table 1) and summed to

yield the final aggressive index for a resident lizard in a trial of ten minutes. This second experiment was performed a week after the first experiment.

All behaviors performed by the test lizards during the two behavioral experiments were also compared to the behaviors reported by Wirminghaus (1990), and their frequency of occurrence recorded as a percentage of the total focal animal observations in which they occurred.

All data were first tested for normality with the Kolmogorov-Smirnov test for normality, and where these data violated the assumptions of normality and homogeneity of variances, non-parametric tests were used. All behavioral data were analyzed with non-parametric statistical tests. Statistical procedures followed Zar (1984), and analyses were done with SigmaStat™ for Windows (Jandel Corporation). Results were designated significant when  $p < 0.05$ .

Seventy-five percent of lizards censused over four weeks remained in the same crevice they were originally caught in, indicating a high level of crevice loyalty, at least during the non-mating season. One adult lizard per crevice occurred in 97% of crevices censused, and only one crevice had a male and female together. Twenty-nine percent of juveniles censused were found in crevices occupied by adults, and significantly more (82% of these juveniles) were found with an adult lizard than alone (18%;  $\chi^2 = 4.45$ ,  $p < 0.03$ ). Of these, significantly more juveniles were found with females (78% of juveniles with females) than with males (11% of juveniles with males;  $\chi^2 = 26.7$ ,  $p < 0.01$ ).

All nearest neighbor distance distributions deviated significantly from a random distribution towards a clumped pattern (Table 2(a)). There was a higher frequency of intersexual nearest neighbors than intrasexual nearest neighbors (Table 2(b);  $\chi^2 = 6.86$ ,  $df = 1$ ,  $p < 0.01$ ). These results suggest aggregation of lizards, but with males and females occurring closer to one another than males are to one another.

There was a graded behavioral response by resident males depending on the distance of the model from the crevice entrance, with the greatest response when the model was within 0.1 m from the crevice entrance (Table 3). All residents showed at least one aggressive behavior towards the model at 0.1 m, while less did so at 0.5 m. Most residents (80%) showed interest in the model at 1.0 m, although there were no aggressive responses at this distance. Resident males were significantly more aggressive towards the large model than towards the small model (Mann-Whitney U Test:  $T = 57.0$ ,  $p = 0.002$ ; Fig. 1). However, there were no significant correlations between SVL of the resident male and aggressiveness index in response to either the large model ( $r = -0.58$ ,  $p = 0.24$ ) or the small model ( $r = 0.41$ ;  $p = 0.42$ ).

Table 4 summarizes the behavioral acts displayed by C. cordylus during behavioral experiments. These include two (arched back, engorged throat) that were not described by Wirninghaus (1990). Both displays were most often used in conjunction than separately and usually preceded physical aggression towards an intruder (as observed from the live lizard focal observations). During the engorged throat display, the lizard's skin of the throat was flexed such that the size of the throat increased considerably, giving the impression of a slightly larger neck, and therefore making the lizard look slightly larger and more aggressive. During the arched back display, the body between the fore- and hind-legs was arched upwards and the body compressed slightly laterally, increasing the body depth size. The most aggressive display by residents always included both these displays as well as jerky movements of the body and the head. Head rubs were often performed during natural territorial displays between adjacent male residents.

We believe our data on C. cordylus conform to the common definition of territoriality in animals, i.e. defense of an area, loyalty to a particular refuge, single occupancy of a refuge, and aggression towards intruding conspecifics (Martins, 1994). It seems in the case of C. cordylus that a defined area around the crevice is defended with aggressive behavioral acts, but the refuge itself is defended with greater aggression. Although there were no aggressive responses at a distance of one meter from the crevice entrance, one must remember that these distances were chosen arbitrarily, so one might not expect an appreciable response at the furthest distance. However, there were some lizards that showed aggressive response at half a meter, indicating that at least a small area is defended with display behavior. It may be that the size of this area is increased during the mating season, and this would require further investigation. According to this study, C. cordylus does not fit into the categories of aggressive behavior suggested by Stamps (1977), as an area is defended, but a specific site (crevice in this case) is inhabited and defended more aggressively. Furthermore, C. cordylus may also make extensive use of chemical cues (Cooper et al., 1996), which would place males of this species somewhere between type 3 or type 4 (Martins, 1994; after Stamps, 1977). Type 3 behavior involves the use of indirect displays such as chemical cues involves (avoidance behavior, defense of part of home range), while type 4 behavior involves the use of physical aggressive behavior (combat behavior, defense of refuge) towards intruders. This probably indicates an "intermediate" territorial condition, where territory defense has evolved from the ancestral condition (Martins, 1994), and site defense has become more important. Territoriality with a high degree of site defense would be well suited to a rupicolous lifestyle

and a sit-and-wait foraging strategy (Mouton and van Wyk, 1997; Cooper *et al.*, 1997), as it allows for visual detection of intruding conspecifics while basking.

Two hypotheses have been proposed to explain the evolution of sexual dimorphism in animals: intraspecific competition avoidance and intrasexual selection (Stamps, 1983). Although *C. cordylus* males have slightly greater head length and width than females, this does not seem to be related to the social system, but rather to differential allocation of energy by males and females (Cordes *et al.*, 1995). This does not conform to the polygyny model of Stamps (1983), which predicts that sexual dimorphism should be greatest in territorial species. However, females might also defend their crevices aggressively, which would place both males and females under a similar selection pressure for larger size, and decrease dimorphism; female lizards have been shown to exhibit territorial defense as well (Mahrt, 1998). Alternatively, as *C. cordylus* exhibits greater site than area defense, it may be that shelters or refuges have played a greater role in the evolution of head size dimorphism in *C. cordylus*. A sit-and-wait feeding strategy coupled with well-developed body armor suggests a social system that has responded more to natural selection than sexual selection, since these characteristics are predators escape mechanisms.

Behavioral responses to models by resident male *C. cordylus* were based on visual cues, as the models had no odor, and lizards could also distinguish the size of the intruder visually. Larger lizards probably pose a greater threat in territorial encounters than smaller lizards, and if this is manifested in a dominance hierarchy related to size, it would reduce costs associated with intruder encounters (Martins, 1994). The high level of tolerance of juveniles in adult crevices supports this. Body size of lizards seems to be important in aggressive encounters of territorial lizards, e.g. *Anolis sagrei* (Tokarz, 1985) and *Sceloporus jarrovi* (Ruby and Baird, 1993), where larger individuals tend to dominate smaller individuals in aggressive encounters. However, in the case of the larger model only, resident male lizards displayed extreme levels of aggression, irrespective of their body size relative to the larger model, although they all showed less aggression towards the smaller model. This indicates that residency of a refuge probably takes precedence over body size in determining outcomes of territorial encounters in nature, at least in adult males that are similar in size.

Tongue-flicking also occurred in all the intrusion experiments (i.e. all residents displayed tongue-flicking behavior), indicating that chemical cues are also important in mediation of territorial encounters, a prediction that Cooper *et al.* (1996) made after observing tongue-flicking in captive *C. cordylus*. These lizards, and others of the same family, possess well developed femoral and generation glands (van Wyk and Mouton, 1992) on the postero-ventral

margin of their hindlegs, which allows for constant deposition of this exudate around and in the immediate vicinity of their crevices. Territories can therefore potentially be advertised by visual and chemical cues. Further field studies of chemoreception by C. cordylus would be valuable.

Although this study was conducted in the non-mating season of C. cordylus (Jacobs and van Wyk, unpublished data), we believe that high levels of aggression and single crevice occupancy were observed. Seasonal differences in social behavior are well known in lizards where reproductive and social behavior is controlled by elevated hormone levels (Stamps, 1990). It is not surprising that male C. cordylus displayed aggressive behavior during the non-mating season, since testicular recrudescence was observed during autumn (March, April, May) (Jacobs and van Wyk, unpublished data).

Nearest neighbor analysis suggests both that lizards are distributed non-randomly, and that lizards of the opposite sex tend to live closer to one another than do members of the same sex. The high levels of aggregation of occupied crevices is probably the result of habitat patchiness, which forces closer than would be the case in an homogenous environment. Therefore, these spacing results may not reflect the true spacing of C. cordylus. Stamps (1988, 1990) found that juvenile Anolis aeneus were aggregated, when habitat patchiness was controlled for; unfortunately we had no measure of habitat patchiness, so this was not taken into account in our analysis. This spacing is probably maintained very conservatively over seasons, as younger lizards could be selecting crevices with relation to previous occupancy. Burrage (1974) reported that new C. cordylus individuals took over territories of experimentally removed lizards, and Stamps (1987, 1991) has shown in Anolis aeneus that lizards may preferentially select previously occupied refuges, as they are an indication of territory quality. As male and female C. cordylus live in closer proximity, male territories may overlap with those of females, and males maintain greater distances between themselves. This is also supported by the greater frequency of male-female nearest neighbors (Fig. 1). Home range analysis data is required during the mating season of C. cordylus.

Although a captive study allows an observer to classify and describe behavioral acts, it does not take into consideration the context in which the behavior would be used in nature. This field study on C. cordylus confirmed the behavioral repertoire of C. cordylus that was reported by Wirminghaus (1990) based on observations of captive lizards. In addition, we found that male lizards used an engorged throat and raised arched-back display. We observed the "shuffle-walk", as described by Wirminghaus (1990), being enacted with all four legs

raising the body well off the ground. The jerky head movements displayed by C. cordylus males could possibly be classified as head-bobs, as described by Wirringhaus.

Field studies on lizard behavior are generally lacking in the literature, yet such studies can provide greater insights into natural behavior, since animals are not under captivity stress, and the influence of environmental factors can also be taken into account. Furthermore, behaviors identified in captivity may be used in a totally different context in the natural environment.

In conclusion, we feel our results provide sufficient evidence that C. cordylus is a territorial lizard, but with a greater level of site (crevice) defense than territory defense. As this study was conducted during the fall, it seems this social system is maintained even outside the mating season (spring), in comparison to the summer study of Burrage (1974), who reported high levels of aggression amongst male lizards. More studies are necessary on cordylid lizards to determine the variety of territorial patterns within this clade. Such studies can provide interesting insights into the evolution of territoriality in lizards with little or no sexual dimorphism.

*Acknowledgments.*—This study was funded by grants awarded to MIC and JHVW from the National Research Foundation of South Africa.

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Table 1. List of behaviors and their descriptions used by *C. cordylus* during agonistic encounters, and the associated scores in terms of level of aggressiveness. Scores were used to calculate the aggressiveness index for each lizard.

Behavior/ posture	Description	Additive Score
Tail-wag	Tail wagged to and fro in sweeping motion	-1
Gape	Mouth opened wide and held open for a few seconds	-1
Movements	Movements between basking spots around crevice entrance	0
Semi-elevated	Anterior part of body is lifted off substrate by forelegs, while posterior part of body remains touching the substrate	0
Tongue-flicking	Investigative behavior where tongue is extruded, touches the object of interest and is then retracted	0
Head-rub	Assertive display where side of head is rubbed on substrate	+1
Looking	Lizard focuses on an object of interest	+1
Jerky-walk	Lizard walks jerkily in slow, stuttered movements	+2
Jerky head-bobs	Head is jerked up and down at regular intervals	+2
Flat-walk	Lizard moves with whole ventral part of body touching substrate, usually with head slightly raised off the ground	+3
High-walk	Body is raised off substrate by all four legs, while moving jerkily	+3
Arched back	Body between the fore- and hindlegs is arched upwards, while moving jerkily	+3
Engorged throat	Throat is enlarged in size slightly by extension of throat skin, associated with jerky movements	+3
Face-off	Two lizards circle one another (head of one to tail of other) during aggressive encounter	+4
Chase	Lizard runs towards intruder	+4
Bite-attack	Lizard bites tail, legs or head of intruder and holds on while moving jerkily or shakes violently by twisting its whole body	+4

Table 2(a). Nearest-neighbor spacing analysis: comparison of deviation of nearest neighbor distances from a random distribution in *C. cordylus*, in terms of an index of aggregation (R) (see text for details). Deviation is significant if  $|z| > 1.96$ .

Nearest neighbor	R	z	Spacing
All	0.62	-5.10	Clumped
Male-male	0.14	-25.0	Clumped
Male-female	0.50	-8.05	Clumped
Female-female	0.07	-47.0	Clumped

(b). Comparison of frequencies (observed numbers) of inter- and intrasexual nearest neighbors in *C. cordylus*.

	M	F	$\chi^2$	p
	7	11	6.86	0.01
F	9	1		

Table 3. Percentage of male resident *C. cordylus* (n = 5) that showed the listed behaviors (once or more than once) in response to a large model lizard placed at different distances from the resident's crevice, during a trial of ten minutes per distance.

Behavior	Additive Score	Model distance from crevice entrance		
		0.1m	0.5m	1.0m
Looks at model	0	100	40	80
Tongue-flicks	0	80	20	0
Semi-elevated	0	100	40	0
Jerky-walk	+2	100	20	0
Jerky head-bobs	+2	40	20	0
Engorged throat	+3	0	20	0
High walk	+3	0	20	0
Chase	+4	20	20	0

Table 4. Summary of various behavioral postures exhibited by *C. cordylus* during the focal observations (n = 33 focal observations) of the two behavioral experiments. Frequencies of behaviors are given as percentage of total focals (n = 33) in which the specific behavior occurred.

Aggressive/Submissive	%
Tongue-flick	58
Head-rub	8
Tail wag	4
Jerky walk	54
Flat walk	15
High walk	12
Arched back	19
Engorged throat	19
Face-off	4
Chase	4
Bite	8
Other behavior	%
Tongue-flick	50
Gape	20

Fig. 1. Comparison of the additive aggressiveness indices of male resident *C. cordylus* towards large and small model intruders. Numbers below the bars indicate the lizard individuals tested. Lizard Number 5 had an aggression index of 0.00 in response to the small model.

