# HABITAT UTILIZATION OF CAPE CLAWLESS OTTERS *AONYX CAPENSIS*

by

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## DECLARATION

I, the undersigned, hereby declare that the work contained in this dissertation 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.

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M.J. Somers

## SUMMARY

This study tested several hypotheses regarding various aspects of habitat use by Cape clawless otters *Aonyx capensis,* in various habitats. The hypotheses, namely that *A. capensis* do not select any prey types, prey sizes or habitat type were tested. Habitat type was investigated at a scale that enabled separating the effects of types of riparian vegetation, geomorphology and anthropogenic influences. Aspects of the resource dispersion hypothesis (RDH) and optimal foraging theory were tested. This was done in both the marine and freshwater environments.

The annual and seasonal diets of *A. capensis* in the Olifants and Eerste Rivers, Western Cape Province, are described. Crabs were found to be the main prey and fish the second most important prey of *A. capensis* in both the rivers during all seasons. The percentage occurrence of prey of *A. capensis* in both rivers, showed an increase in the amount of crab in summer and a corresponding decrease in the number of fish eaten. The seasonal fluctuation in crabs and fish found in the spraints (faeces), corresponded with the expected frequencies as determined from trapping.

Seven *A. capensis* were caught in the two rivers and radio-tracked between 1993 and 1995. Total home range length varied from 4.9 to 54.1 km and core home range length from 0.2 to 9.8 km. Total area of water used ranged from 4.9 to 1062.5 ha and core area used from 1.1 to 138.9 ha. As predicted using the RDH total home range length was correlated to mean reed bed nearest neighbour distance. The otters were typically active from dawn for 2.6 h and moved a mean of 0.9 km. They were also typically active

from sunset for a mean of 2.3 h moving a mean of 1.3 km. They were found to select for areas with boulders and/or reed beds.

*Aonyx capensis* were found to be mainly solitary in all the habitats. The pattern of female home ranges was suggestive of territoriality. The males, however, had overlapping home ranges, both with other males and females.

From spraint analysis and direct observations, the seasonal diet and foraging behaviour of *A. capensis* feeding in the surf zone in False Bay, Western Cape Province, were determined. The most common prey species during all seasons was Cape rock crab *Plagusia chabrus*. Diversity of prey was lowest in winter, increasing through the seasons from spring to autumn. Foraging behaviour data support the optimal breathing hypothesis, which predicts that both surface and dive times should increase for dives of greater depths. However, diving efficiency did not decrease with increasing depth, nor did percentage time at the surface increase with increasing depth. These results are contrary to the optimal breathing hypothesis.

How *A. capensis* use their habitat in the presence of potential competitors spotted-necked otters *Lutra maculicollis* and water mongooses *Atilax paludinosus* was also determined by investigating their trophic overlap during enforced cohabitation in a relatively small range during drought conditions.

The analysis of trophic overlap showed that even during enforced cohabitation in a relatively small range during drought conditions, there was separation of diets of *A. capensis, L. maculicollis* and *A. paludinosus*.

These results and their implications for conservation management are discussed.

## OPSOMMING

Hierdie studie het 'n aantal hipoteses oor verskeie aspekte van habitat gebruik deur die Groototter *Aonyx capensis,* in verskillende habitatte, getoets. Die nul hipotese, nl. dat *A. capensis* nie vir enige prooitipe, prooigrootte of habitat-tipe selekteer nie, is getoets. Habitat tipe is ondersoek teen 'n skaalgrootte wat dit moontlik gemaak het om die effekte van tipes oewer plantegroei, geomorfologie en antropogeniese invloede van mekaar te skei. Aspekte van die hulpbron verspreiding hipotese (HVH) en optimale kossoek gedrag, is in beide die varswater en seewater omgewing getoets.

Die jaarlikse en seiseonale diëte van *A. capensis* in die Olifants and Eerste Riviere in die Wes-Kaap Provinsie, word beskryf. Daar is gevind dat krappe die hoof prooi en vis die tweede mees belangrike prooi van *A. capensis* in beide riviere, gedurende al die seisoene, was. Die persentasie *A. capensis* prooi teenwoordig in beide riviere het 'n toename in krap getalle in die somer en 'n ooreenstemmende afname in die hoeveelheid vis wat geeet word getoon. Die seisoenale verandering van krap en vis wat in die keutels (mis) voorkom, het ooreengestem met die verwagte frekwensies soos bepaal deur fangste in fuike.

Sewe *A. capensis* is in die twee riviere gevang en tussen 1993 en 1995 d.m.v. radiosenders gevolg. Die totale tuisgebied lengte het van 4.9 tot 54.1 km, en die kern tuisgebied lengte van 0.2 tot 9.8 km, gewissel. Die totale area water wat gebruik is het van 4.9 tot 1062.5 ha, en kerngebiede van 1.1 tot 138.9 ha gewissel. Soos voorspel deur gebruik van die HVH, was die totale tuisgebied lengte gekorreleer met die gemiddelde rietbedding naaste-buurman analise afstand.

Die otters was tipies aktief vanaf sonsopkoms vir 2.6 ure en het dan 'n gemiddeld van 0.9 km beweeg. Hulle was ook tipies aktief vanaf sonsondergang vir 'n gemiddeld van 2.3 ure en het dan gemiddeld 1.3 km beweeg. Daar is gevind dat hulle selekteer vir areas met rotse en areas met rietbeddings. Dit is ook gevind dat

*A. capensis* in alle habitatte hoofsaaklik alleenlopend is. Die wyfies se tuisgebied-patroon het op territorialiteit gedui, terwyl die manlike diere se tuisgebiede oorvleuel het met beide dié van wyfies, en met dié van ander mannetjies.

Die seisoenale dieet en kossoekgedrag van *A. capensis* wat in die brander sone van Valsbaai, Wes-Kaap Provinsie, voed, is deur keutel analise en direkte waarneming bepaal. Die mees algemene prooi spesie gedurende al die seisoene was die Kaapse rotskrap *Plagusia chabrus*. Prooi diversiteit was die laagste in winter en het toegeneem vanaf lente tot herfs. Kossoekgedrag gegewens ondersteun die optimale asemhalings hipotese, wat voorspel dat beide oppervlak- en duik tye toeneem met dieper duike. Duik effektiwiteit het egter nie afgeneem met toenemende diepte nie, en persentasie tyd op die oppervlakte het ook nie toegeneem met toenemende diepte nie. Dit is dus in teenstelling met die optimale asemhalings hipotese.

Hoe *A. capensis* hul habitat in die teenwoordigheid van potesieele kompiteerders nl. Klein otters *Lutra maculicollis*, en Water muishonde *Atilax paludinosus* gebruik, is ook bepaal. Dit is gedoen deur hul trofiese oorvleueling gedurende noodgedwonge saamleef, veroorsaak deur droogte kondisies in 'n relatiewe klein tuisgebied, te ondersoek.

Die resultate van die trofiese oorvleueling analise het getoon dat selfs gedurende noodgedwonge saamleef gedurende droogte toestande in 'n relatiewe klein gebied, daar 'n verskil was in die diëte van *A. capensis, L. maculicollis* and *A. paludinosus*.

Hierdie resultate en hul implikasies vir bewaringsbestuur word bespreek.

# ACKNOWLEDGEMENTS

# CONTENTS

Chapter 4 : Habitat selection by Cape clawless (*Aonyx capensis*) otters in rivers

Chapter 5 : Seasonal variation in the diet of Cape clawless otters (*Aonyx capensis*) in a marine habitat.

Chapter 6 : Foraging behaviour of Cape clawless otters (*Aonyx capensis*) in a marine habitat.

Chapter 7 : Trophic overlap between three syntopic semi-aquatic carnivores: Cape clawless otter (*Aonyx capensis*), spotted-necked otter (*Lutra maculicollis*), and water mongoose (*Atilax paludinosus*).

Chapter 8 : Conclusion and conservation management considerations

## List of Tables

## List of Figures

"The rivers are our brothers. They quench our thirst. They carry our canoes and feed our children. So you must give the rivers the kindness you would give any brother"

Chief Seattle, 1852

# CHAPTER 1

# INTRODUCTION

## BACKGROUND

When an animal harvests food, it has to make decisions. For example where to hunt for food, which kinds of prey to eat, when to move and how far to move (Crawley & Krebs 1992). The optimal foraging theory (OFT), first proposed by Emlen (1966) and MacArthur & Pianka (1966), states that foraging strategies may involve decisions that optimise food intake per unit effort or of some other measure of foraging efficiency (Emlen 1966; MacArthur & Pianka 1966; Schoener 1971; Krebs & Kacelnik 1991; Perry & Pianka 1997).

Optimality models have three main components: the currency, the constraints, and the decision variable (Krebs & Kacelnik 1991). In the case of diving organisms, the currencies could include maximising the rate of energy intake, maximising the rate of oxygen intake, minimising the risk of predation, or a combination of these. Constraints and variables could be: travel time (duration of time taken to get to the bottom), bottom or search time (duration of time searching on the bottom), unsuccessful dive time (travel and bottom time of an unsuccessful dive), successful dive time (travel and bottom time of a successful dive), recovery time (duration of time after surfacing from an unsuccessful dive to the start of the next dive), processing time (duration of time after surfacing from an successful dive to the start of the next dive), hunting success (HS: % of dives yielding prey), % time at surface, time preceding each catch, success or failure (capturing or not capturing prey) and whether to eat or reject a small prey. Owing to loss of energy in the water (Kruuk et al. 1997) it would be expected that otters would always maximise the net rate of energy gain.

Cape clawless otters *Aonyx capensis* exploit a variety of aquatic habitats, including marine, estuarine, riparian, mangrove and lacustrine (see below for a discussion on their distribution) and are primarily crab eaters (Rowe-Rowe & Somers 1998). To understand how *A. capensis* use their habitats and in order to make conservation management decisions regarding the otters, it is necessary to have baseline information on the feeding ecology of the species. Diet of *A. capensis* using spraints analysis has been determined (*freshwater habitats*: Turnbull-Kemp (1960); Rowe-Rowe (1975, 1977a, 1978); Donnelly & Grobler (1976); Kruuk & Goudswaard (1990); Butler (1994); Butler & du Toit (1994); Ligthart *et al.* (1994); Purves *et al.* (1994); Carugati (1995); Somers (1996); Perrin & Carugati (2000a); *marine habitats*: van der Zee (1979, 1981); Arden-Clarke (1983, 1986) and Verwoerd (1987)), but no-one has attempted to relate it to relative prey abundance. As food availability has a powerful influence on animals in both the determination of habitable areas and the numbers of individuals which these areas can support (Krebs 1985), the relative densities of the otters' main prey were determined in the present study. Also as only Rowe-Rowe (1977a) and Purves *et al.* (1994) provide some seasonal data, this study provides more detailed seasonal data for *A. capensis*, living in both marine and freshwater environments. The above studies on the diet of *A. capensis* have shown *A. capensis* to eat a variety of prey both in terms of size and type. Optimal foraging theory can be used to account for the types and sizes of prey items taken by predators (Krebs & Kacelnik 1991). One possible hypothesis to explain why several types of prey are eaten is that the times taken to search for the most profitable sizes influence the choice. If it takes a long time to find a profitable fish, the otter might be able to obtain a higher overall rate of intake by eating some of the less profitable crabs. The same applies to sizes of prey eaten.

An extension of the OFT is the marginal value theorem (MVT) (Charnov 1976), which, in brief, states that an animal foraging for food in patches spends much of its time travelling between patches, or searching for and handling food within patches. As a

forager depletes the available food within a patch over time, the benefit of staying in the patch decreases. In order to forage optimally in a particular patch, the animal should therefore leave the patch when the expected net gain from staying drops to that expected from travelling to and searching in a new patch. The optimal breathing hypothesis (Kramer 1988), which originates from the MVT, suggests that oxygen stores of diving animals are replenished according to a curve of diminishing returns. The hypothesis predicts that for diving animals such as *A. capensis* both surface and dive time will increase with dives of greater depths, as will the percentage time spent at the surface. These predictions are tested for *A. capensis* in the present study. Optimal breathing strategies (Kramer 1988) are affected by such factors as body size, physiological abilities, feeding requirements, and whether a species is a single-prey or multi-prey loader (Kruuk 1993). As otters hunt for prey under water but feed on the surface, they can be regarded as central place foragers as well as single prey loaders (Houston & McNamara 1985). Otters do not return to a fixed central place, for example a den, but do need to return to the surface.

As habitat selection by animals provides a theoretical basis for habitat management decisions (Kopp *et al.* 1998) it is a common and important aspect of wildlife science (Alldredge & Ratti 1986). Habitat selection is determined by identifying the disproportionate use of habitats (Johnson 1980). Common aims of habitat use studies are to determine whether a species uses habitats available at random, to rank habitats in order of relative use, to compare use by different groups of animals, to relate use to variables such as food abundance, or to examine the effects of habitat on movement and home range size (Aebischer *et al.* 1993). Animal movements and habitat use are related to both the acquisition of primary resources (e.g. food, shelter, mate, and host) and the avoidance of sources of stress (e.g. predators, thermal extremes, dehydration) (Barbaresi *et al.* 1997).

Our understanding of otter habitat selection comes mainly from studies on the distribution and abundance of otter spraints

and resting places (reviewed by Mason & Macdonald 1986).
However, Green *et al.* (1984); Kruuk *et al.* (1986) and Conroy &
French (1987) show that for European otters *Lutra lutra* the
position of spraints is an unreliable indication of where otters
spend their time. They are, however, an indication of how the
otters use land, which is important for semi-aquatic otters. Data
from radiotelemetry would therefore compliment these data, giving
a better understanding of how the otters use their habitat.
Radiotelemetry, as used in the present study, is one of the most
powerful tools available to wildlife biologists (Aebischer *et al.*
1993), particularly to get insight into the ecology of elusive
species such as otters. In environments intensively used by
humans, thorough and reliable data on habitat use by otters can
be obtained only by radiotelemetry, and this information is
critical not only to understanding the ecology of these species,
but also to planning effectively for their conservation.

There have been numerous radiotelemetry habitat selection
studies done on otters such as *L. lutra* (e.g. Green *et al.* 1984;
Durbin 1993, 1996a, 1996b, 1998; Kruuk 1995), North American
river otters *Lutra canadensis* (Melquist & Hornocker 1983),
spotted-necked otters *Lutra maculicollis* (Perrin & D'Inzillo
Carranza 2000; Perrin *et al.* 2000), sea otter *Enhydra lutris*
(Ralls *et al.* 1995) and smooth coated otters *Lutra perspicillata*
(Hussain & Choudhury 1995). Up to now only Arden-Clarke (1983,
1986) provided data on *A. capensis* using radiotelemetry. Although
he did not look at habitat variables (Arden-Clarke 1986), he did
show differential use of the home range of *A. capensis* along the
Tsitsikama coast.

Solitary and group-living individuals provide a dichotomy in
carnivore spacing patterns (Sandell 1989). These two modes of
living involve a trade-off between the advantages of cooperation
[e.g. predator detection (Rasa 1986); shared parental care
(Clutton-Brock *et al.* 1998); cooperative hunting (Stander 1992)
and the disadvantages of competition (Ranta *et al.* 1993)].
Predictions regarding social structure and movement parameters of
*A. capensis* can be made using the resource dispersion hypothesis

(RDH) (Macdonald 1983). The RDH (Macdonald 1983; Kruuk & Macdonald 1985; Carr & Macdonald 1986) tries to explain, within the limits of all constraints, interspecific and intraspecific variation in territories and group sizes in ecological terms. The RDH predicts that spatial organisation will be determined by dispersion of resources (particularly food) and that group size will be determined by the richness of these patches when animals occupy the smallest economically defendable area (Macdonald 1983; Kruuk & Macdonald 1985; Carr & Macdonald 1986). In addition to the dispersion and richness of resources, the rate of resource renewal after depletion may also influence sociality, with high recovery rates favouring group-living (Waser 1981). There is a distinction between social groups (Gittleman 1989) and "spatial groups", where there is no cooperation, but the cost of evicting additional animals, outweighs that of tolerating them (Macdonald & Carr 1989). The data of Arden-Clarke (1983, 1986) indicates that *A. capensis* do not conform to the standard mustelid spacing patterns (Powell 1979), which is to have intrasexual territories where males are territorial against males, females against females (perhaps including most recent offspring), but where there is extensive overlap between sexes with male territories being larger than those of females (Powell 1979). It appears that *A. capensis* mostly forage alone but occur in groups of up to five (Rowe-Rowe 1978; Arden Clarke 1983). This was further investigated in the present study, which for the first time radio-tracked female *A. capensis*. It was also the first time that *A. capensis* in freshwater habitats were radio-tracked. The RDH was used to generate predictions regarding the otters' home range size and social structure.

Although intraspecific competition is common (Connell 1983), there is a paucity of studies concerning ecological separation and competition among smaller sympatric carnivores. Previous to this study only Rowe-Rowe (1977a) had given data on the diet of *A. capensis* living syntopically with *L. maculicollis* and water mongoose Atilax *paludinosus*. As competition may affect the way *A.*

*capensis* forages these data are important in a discussion on how *A. capensis* exploits resources.

Many of the 13 otter species occurring worldwide are rapidly disappearing along with the clean wetlands they inhabit (Foster-Turley *et al.* 1990). This may apply to otters in South Africa as well, but little is known about their biology. Against this background, this project on habitat use by *A. capensis* in South Africa was undertaken.

## TAXONOMY AND PHYLOGENY OF *AONYX CAPENSIS*

The classification of the species is as follows (Meester *et al.* 1986; Skinner & Smithers 1990):

| | |
|---|---|
| Class: | Mammalia |
| Order: | Carnivora |
| Family: | Mustelidae |
| Subfamily: | Lutrinae |
| Genus: | *Aonyx* (Lesson, 1827) |
| Species: | *capensis* (Schinz, 1821) |

The common English names for *A. capensis* are African clawless otter and Cape clawless otter (used here). The original scientific application was *Lutra capensis* (Schinz, 1821).

The phylogeny and taxonomy of the Lutrinae have been reviewed by Harris (1968); van Zyll de Jong (1987); Koepfli & Wayne (1998) and Bininda-Emonds *et al.* (1999). The only congeneric to *A. capensis* is the Congo otter *Aonyx congica* with a time of divergence estimated to be 2.6 MYBP (Bininda-Emonds *et al.* 1999). The small-clawed otter *Amblonyx cinerea* is estimated to have diverged from *Aonyx* 4.2 MYBP (Bininda-Emonds *et al.* 1999).

Only two extant genera of otters occur in Africa – *Aonyx* and *Lutra* – with four species recognised: *A. capensis*, *A. congica*, *L. maculicollis* and *L. lutra*.

## DISTRIBUTION AND STATUS OF *AONYX CAPENSIS*

*Aonyx capensis* occur over most of sub-Saharan Africa (Rowe-Rowe 1990, 1991; Rowe-Rowe & Somers 1998; Nel & Somers in press) in diverse habitats, for example the mangrove forests of KwaZulu-Natal Province (personal observation), the southern and eastern coast (Rowe-Rowe 1992; van der Zee 1979; Arden-Clarke 1983, 1986; Verwoerd 1987; Somers & Nel 1996; van Niekerk *et al*. 1998; personal observation), salt water lakes (Lake St Lucia, KwaZulu-Natal) (Kröger & Forrest 1978), estuaries (Kosi Bay, KwaZulu-Natal) (Kyle 1981), freshwater lakes (Lake Sibaya, KwaZulu-Natal) (Tinley 1958) and the desert conditions surrounding the upper Doring River and Fish River in southern Namibia (Nel unpublished data). They are also the only otters occurring on offshore islands, e.g. the Bijago archipelago of Guinea-Bissau (Nel & Somers in press). They occur in extremely arid areas (<: 30 mm rainfall/annum) as long as pools of freshwater persists (Nel & Somers in press). They have been found in towns (e.g. Stellenbosch) and cities (e.g. Port Elizabeth, Cape Town) (personal observations). They sometimes occur in rivers with high pollution and eutrophication levels (Heath & Claassen 1999; Nel & Somers unpublished data).

The occurrence of otters in specific African countries has been reviewed by Nel & Somers (in press). *Aonyx capensis* is the most widely distributed otter species in Africa, occurring in 35 countries. It is common or fairly common in 19 (but could be rare in parts of a country), and rare to very rare in 12 countries (Nel & Somers in press). The distributional range and/or population size appears stable in 29 countries and declining in six (Nel & Somers in press). For most African countries the geographical distribution and population status of otter species occurring are poorly known (Nel & Somers in press).

*Aonyx capensis* are listed in Appendix II of the "Convention on International Trade in Endangered Species of Wild Fauna and Flora" (CITES). Appendix II lists species that are not necessarily currently threatened with extinction but that may

become so unless trade is closely controlled. It also includes so-called "look-alike species", i.e. species of which the specimens in trade look like those of species listed for conservation reasons. International trade in specimens of Appendix II species may be authorized by the granting of an export permit or re-export certificate while no import permit is necessary. Permits or certificates should only be granted if the relevant authorities are satisfied that certain conditions are met, and above all, that trade will not be detrimental to the survival of the species in the wild.

## PREVIOUSLY PUBLISHED WORK ON *AONYX CAPENSIS*

General descriptions of *A. capensis* and their natural history have been given by Tayler (1970); Kingdon (1977); Chanin (1985) and Foster-Turley *et al.* (1995), with reviews on our knowledge of the species given by Rowe-Rowe (1990); Skinner & Smithers (1990); Somers (1997) and Larivière (2001).

The feeding behaviour of *A. capensis* has been described by Rowe-Rowe (1977b, 1977c) and Verwoerd (1987), while aspect of the diet of *A. capensis* in freshwater habitats have been given by Turnbull-Kemp (1960); Rowe-Rowe (1975, 1977a, 1978); Kruuk & Goudswaard (1990); Butler (1994); Butler & du Toit (1994); Ligthart *et al.* (1994); Purves *et al.* (1994); Carugati (1995); Butler & Marshall (1996); Somers (1996) and Perrin & Carugati (2000a), and in marine habitats by van der Zee (1979, 1981); Arden-Clarke (1983, 1986); Verwoerd (1987) and van Niekerk *et al.* (1998). In these studies crustaceans were shown to be their most important prey, but fish, frogs, insects, birds, reptiles, molluscs, dung (ungulate) and mammals are also taken. Boshoff (1978) speculated on there being commensalism with regards to finding food between pied kingfishers *Ceryle rudis* and *A. capensis*. Donnelly & Grobler (1976) speculated on them using an anvil to break open freshwater mussels *Aspatharia wahlbergi*.

Arden-Clarke (1983, 1986) used radio-tracking and radionuclide recovery from spraints to determine density and

range utilization in the Tsitsikama Coastal National Park. Density estimates in Tsitsikama Coastal National Park have been given as one otter per 1.9 - 2 km of coast (van der Zee 1979, 1982; Arden-Clarke 1983, 1986). Verwoerd (1987) estimated one otter per 2 km of coast at Betty's Bay. As the otters rarely ventured further than 100 m from shore (Arden-Clarke 1983, 1986) these densities are equivalent to one per 20, 19 and 20 ha of water for the three studies respectively. Estimates of density in freshwater habitats are one otter per 1.25-2.5 km (Carugati 1995; Perrin & Carugati 2000b), one otter per 3-4 km (Rowe-Rowe 1992) and one otter per 8-10 km of river (Butler & du Toit 1994).

Perrin & Carugati (2000b) analysed habitat selection by *A. capensis* in a freshwater environment by comparing sites of otter activity on land with environmental variables. They found the otters select, for time spent on land, undisturbed areas with rock cover and natural dense vegetation. Rowe-Rowe (1992) and Butler & du Toit (1994) give densities of spraints and resting places but do not relate these to habitat variables. Rowe-Rowe (1992) discussed his findings on the distribution of otter sign for use in surveying otter populations in South Africa. He suggested that sign of otters could possibly be used to estimate relative abundance in different areas, provided that limitations of the method are taken into account.

Along the coast there is evidence that *A. capensis* select places of activity on land to be near thick vegetation, an abundant food resource and fresh water (van der Zee 1982; Arden-Clarke 1986; van Niekerk *et al.* 1998).

There is a paucity of studies on factors regarding and promoting ecological separation among the smaller sympatric carnivores. Prior to this study only Rowe-Rowe (1977a) had provided data on the trophic overlap of *A. capensis, L. maculicollis* and *A. paludinosus* living syntopically. Purves *et al.* (1994) provides trophic overlap data on *A. capensis* and *A. paludinosus* living in the Olifants River, and Kruuk & Goudswaard (1990) provide data on the diet of *A. capensis* and *L. maculicollis* living in Lake Victoria. Butler & Marshall (1996)

include *A. capensis* in a crab-eating guild with African mottled eels *Anguilla bengalensi* and rainbow trout *Oncorhynchus mykiss*. These studies show some overlap with regards to prey species eaten but there appears to be resource partitioning with regards size and diversity of prey eaten.

Recent distribution and status data have been provided by Somers (1997); Rowe-Rowe & Somers (1998); Larivière (2001); Nel & Somers (in press) and Nel *et al.* (in press) (see above for details). *Aonyx capensis* are often killed for their skins, or because they kill domestic waterfowl and fish, or are caught and drowned in fish traps or fishnets (Rowe-Rowe 1990, 1991, 1995; Butler 1994; Baranga 1995; Nel & Somers unpublished data).

Mason & Rowe-Rowe (1992) found levels of organochlorine pesticide residues and polychlorinated biphenyls (PCBs) in otter spraints from KwaZulu-Natal to be low and unlikely to pose a threat to otter populations at the localities studied.

*Aonyx capensis* have been shown to make friendly yet unpredictable pets (Maxwell 1960, 1963, 1968; Eyre 1963).

The results of these various works and their implications for the present study are discussed in the introductions and discussions of the relevant chapters.

Much has been published on other species of otters particularly *L. lutra* (for review see Chanin (1985); Mason & Macdonald (1986) and Kruuk (1995)).

## OBJECTIVES AND LAYOUT OF THE STUDY

The main aim of this study was to establish relationships among the food, home range parameters, spatial organisation, habitat variables and competitors of *A. capensis*. It was aimed to make a significant contribution to our knowledge and understanding of *A. capensis* and the way in which they use the environment. These aims are addressed in six chapters, each with more specific objectives. Each chapter is designed to stand alone, giving specific introductions, descriptions of study sites, materials and methods, discussions and references.

**Chapter 2** gives the annual and seasonal diet of *A. capensis*, as estimated from spraint analysis, in relation to the presence of their main prey (crabs and fish) in two rivers. The main questions asked were 1) What is the species composition of the diet of the otters? 2) How does diet vary with season? 3) How does the variation of crabs and fish in the diet of the otters relate to availability of crabs and fish in the two rivers?

**Chapter 3** provides data, from radio telemetry, on movement parameters of individual *A. capensis* in two rivers. The main objectives of this chapter were 1) To determine, for the first time, home range sizes and movement parameters of *A. capensis* in freshwater habitats. 2) To determine spatial organisation, density and group sizes of *A. capensis* in freshwater habitats 3) To test the hypothesis that *A. capensis* in freshwater habitats do not conform to the typical mustelid spacing pattern (Powell 1979), and 4) To test predictions based on a hypothesis (RDH of Macdonald 1983) relating otter dispersion to the distribution of resources.

**Chapter 4** reports on the habitat selection by individual *A. capensis*, determined by radio-tracking in the Olifants and Eerste Rivers. The hypothesis tested was that active otters do not select for any particular habitat.

**Chapter 5** presents data on the seasonal diet of *A. capensis* in a marine habitat, as determined by spraint analysis. Chapter 5 quantifies sizes of marine crustaceans eaten by *A. capensis*, using length of eyestalks found in spraints. The sizes of the fish eaten are also determined, using the diameter of otoliths in the spraints.

The main aim of this chapter was to determine the diet of *A. capensis* in a marine habitat and, for the first time, relate this to prey availability and season.

Chapter 5 has been published as Somers (2000a). Ms. B. Elliot, Dr. D.T. Rowe-Rowe and two anonymous referees provided useful comments which have been incorporated into the thesis.

**Chapter 6** provides the first detailed quantitative data on foraging by free swimming *A. capensis* in a marine habitat. It was

hypothesised that *A. capensis* maximise their diving success rate and that they dive at depths where they get most prey for least effort.

Chapter 6 has been published as Somers (2000b). Dr. D.T. Rowe-Rowe, Dr. P. Chanin and an anonymous referee provided useful comments on the manuscript prior to publication.

**Chapter 7** determines how *A. capensis* uses its prey source in relation to other syntopic semi-aquatic carnivores: *L. maculicollis* and *A. paludinosus,* under conditions of enforced competition.

Chapter 7 has been published as Somers & Purves (1996). Mr. M. Purves accompanied me on the field trip and helped collect the data. He was also responsible for the analysis of the *A. paludinosus* scats, while Ms. T. Mudge analysed the *L. maculicollis* spraints. Mr. M. Purves also critically read the manuscript prior to submission for publication. As the manuscript was accepted, with no changes, as submitted, no referees' comments were included.

## REFERENCES

AEBISCHER, N.J., ROBERTSON, P.A. & KENWARD, R.E. 1993. Composition analysis of habitat use from animal radio-tracking data. *Ecology* **74:** 1313-1325.

ALLDREDGE, J.R. & RATTI, J.T. 1986. Comparison of some statistical techniques for analysis of resource selection. *Journal of Wildlife Management* **50:** 157-165.

ARDEN-CLARKE, C.H.G. 1983. Population density and social organisation of the Cape clawless otter, *Aonyx capensis* Schinz, in the Tsitsikama Coastal National Park. M.Sc. thesis, University of Pretoria, Pretoria, South Africa.

ARDEN-CLARKE, C.H.G. 1986. Population density, home range size and spatial organization of the Cape clawless otter, *Aonyx capensis*, in a marine habitat. *Journal of Zoology, London* **209:** 201-211.

BARANGA, J. 1995. The distribution and conservation status of

otters in Uganda. *Habitat* **11**: 29-32.

BARBARESI, S., GHERARDI, F. & VANNINI, M. 1997. Movement patterns of river crabs (Decapoda, Potamoidea) in the field: predictable and unpredictable components. *Journal of Zoology, London* **242**: 247-259.

BININDA-EMONDS, O.R.P., Gittleman, J.L. & PURVIS, A. 1999. Building large trees by combining phylogenetic information: a complete phylogeny of the extant Carnivora (Mammalia). *Biological Review* **74**: 143-175

BOSHOFF, A.F. 1978. Possible pied kingfisher-clawless otter commensalism. *Ostrich* **4**: 89.

BUTLER, J.R.A. 1994. Cape clawless otter conservation and a trout river in Zimbabwe: a case study. *Oryx* **28**: 276-282.

BUTLER, J.R.A. & DU TOIT, J.T. 1994. Diet and conservation of Cape clawless otters in eastern Zimbabwe. *South African Journal of Wildlife Research* **24**: 41-47.

BUTLER, J.R.A. & MARSHALL, B.E. 1996. Resource use within the crab-eating guild of the upper Kairezi River, Zimbabwe. *Journal of Tropical Ecology* **12**: 475-490.

CARR, R.J. & MACDONALD, D.W. 1986. The sociality of solitary foragers: a model based on resource dispersion. *Animal Behaviour* **34**: 1540-1549.

CARUGATI, C. 1995. Habitat, prey, and area requirements of otters (*Aonyx capensis* and *Lutra maculicollis*) in the Natal Drakensberg. M.Sc. thesis, University of Natal. Pietermaritzburg, South Africa.

CHANIN, P. 1985. *The natural history of otters.* Facts on File Publications, New York.

CHARNOV, E.L. 1976. Optimal foraging: the marginal value theorem. *Theoretical Population Biology* **9**: 129-136.

CLUTTON-BROCK, T.H., GAYNOR, D., KANSKY, R., MACCOLL, A.D.C., MCLLRATH, G., CHADWICK, P., BROTHERTON, P.N.M., O'RIAIN, J.M., MANSER, M. & SKINNER, J.D. 1998. Costs of cooperative behaviour in suricates (*Suricata suricatta*). *Proceedings of the Royal Society of London B* **265**: 185-191.

CONNELL, J.H. 1983. On the prevalence and relative importance of

interspecific competition: evidence from field experiments. *American Naturalist* **122**: 661-696.

CONROY, J.W.H. & FRENCH, D.D. 1987. The use of spraints to monitor populations of otters (*Lutra lutra* L.). *Symposia of the Zoological Society of London* No. 58: 247-262.

CRAWLEY, M.J. & KREBS, J.R. 1992. Foraging theory. In: *Natural enemies: The population biology of predators, parasites and diseases,* (ed) M.J. Crawley, Blackwell Scientific publications, Oxford.

DONNELLY, B.G. & GROBLER, J.H. 1976. Notes on food and anvil using behaviour by Cape clawless otter, *Aonyx capensis* in the Rhodes Matopos National Park, Rhodesia. *Arnoldia Rhod.* **7**: 1-8.

DURBIN, L.S. 1993. Food and Habitat Utilization of Otters (*Lutra Lutra L.)* in a Riparian Habitat. D. Phil. thesis, University of Aberdeen, Aberdeen, Scotland.

DURBIN, L.S. 1996a. Some changes in the habitat use of free-ranging female otter *Lutra lutra* during breeding. *Journal of Zoology, London* **240**: 761-764.

DURBIN, L.S. 1996b. Individual differences in spatial utilization of a river-system by otters *Lutra lutra*. *Acta Theriologica* **41**: 137-147.

DURBIN, L.S. 1998. Habitat selection by five otters *Lutra lutra* in rivers of northern Scotland. *Journal of Zoology, London* **245**: 85-92.

EMLEN, J.M. 1966. The role of time and energy in food preference. *American Naturalist* **100**: 611-617.

EYRE, M. 1963. *Otter in our parlour.* Tafelberg, Cape Town.

FOSTER-TURLEY, P., MACDONALD, S. & MASON, C. 1990. *Otters: an action plan for their conservation.* IUCN/SSC Otter Specialist Group, Gland.

GITTLEMAN, J.L. 1989. Carnivore group living: comparative trends. In: *Carnivore behaviour, ecology and evolution,* (ed) G.L. Gittleman, Chapman and Hall, London.

GREEN, J., GREEN, R. & JEFFERIES, D.J. 1984. A radio-tracking survey of otters *Lutra lutra* on a Perthshire river system. *Lutra* **27**: 85-145.

HARRIS, C. J. 1968. Otters: a study of the Recent Lutrinae. Weidenfeld and Nicolson, London.

HEATH, R.G.M. & CLAASSEN, M. 1999. *An overview of the pesticide and metal levels present in populations of the larger indigenous fish species of selected South African rivers*. WRC Report No 428/1/99, Water Research Commission, Pretoria.

HOUSTON, A.I. & MCNAMARA. J.M. 1985. A general theory of central place foraging for single-prey loaders. *Theoretical Population Biology* **28**: 233-262.

HUSSAIN, S.A. & CHOUDHURY, B.C. 1995. Seasonal movement, home range, and habitat use in smooth coated otters in National Chambal Sanctuary, India. *Habitat* **11**: 45-55.

JOHNSON, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* **61**: 65-71.

KINGDON, J. 1977. *East African mammals : an atlas of evolution in Africa. Volume III A (Carnivores)*. Academic Press, London.

KOEPFLI, K.-P. & WAYNE, R.K. 1998. Phylogenetic relationships of otters (Carnivora: Mustelidae) based on mitochondrial cytochrome *b* sequences. *Journal of Zoology, London* **246**: 401-416.

KOPP, S.D., GUTHERY, F.S., FORRESTER, N.D. & COLE, L.C. 1998. Habitat selection modeling for northern bobwhites on subtropical rangeland. *Journal of Wildlife Management* **62**: 884-895.

KRAMER, D.L. 1988. The behavioral ecology of air breathing by aquatic animals. *Canadian Journal of Zoology* **66**: 89-94.

KREBS, C.J. 1985. *Ecology: The experimental analysis of distribution and abundance*. Harper and Row, New York.

KREBS, J.R. & KACELNIK, A. 1991. Decision making. In: *Behavioural ecology an evolutionary approach*, (eds) J.R. Krebs, & N.B. Davies, Blackwell Scientific Publications, Oxford.

KRÖGER, Z. & FORREST, G.W. 1978. First record of clawless otter from Lake St Lucia. *Lammergeyer* **26**: 64.

KRUUK, H. 1993. The diving behaviour of the platypus (*Ornithorhynchus anatinus*) in waters with different trophic status. *Journal of applied Ecology* **30**: 592-598.

KRUUK, H. 1995. *Wild otters: Predation and populations.* Oxford University Press, Oxford.

KRUUK, H. & MACDONALD, D.W. 1985. Group territories of carnivores: empires and enclaves. In: *Behavioural ecology: ecological consequences of adaptive behaviour*, (eds) R.M. Sibly & R.H. Smith, Blackwell Scientific Publications, Oxford.

KRUUK, H. & GOUDSWAARD, P.C. 1990. Effects of changes in fish populations in Lake Victoria on the food of otters (*Lutra maculicollis* Schinz and *Aonyx capensis* Lichtenstein). *African Journal of Ecology* **28**: 322-329.

KRUUK, H., CONROY, J.W.H., GLIMMERVEEN, U. & OUWERKERK, E.J. 1986. The use spraints to survey populations of otter *Lutra lutra*. *Biological Conservation* **35**: 187-194.

KRUUK, H., TAYLOR, P.T. & MOM, G.A.T. 1997. Body temperature and foraging behaviour of the Eurasian otter (*Lutra lutra*), in relation to water temperature. *Journal of Zoology, London* **241**: 689-697.

KYLE, R. 1981. The clawless otter-extension of known range in Natal. *Lammergeyer* **31**: 44.

LARIVIÈRE, S. 2001. *Aonyx capensis. Mammalian Species* **671**:

LIGTHART, M.F., NEL, J.A.J. & AVENANT, N.L. 1994. Diet of Cape clawless otters in part of the Breede River system. *South African Journal of Wildlife Research* **24**: 38-39.

MACARTHUR, R.H. & PIANKA, E.R. 1966. On optimal use of a patchy environment. *American Naturalist* **100**: 603-609.

MACDONALD, D.W. 1983. The ecology of carnivore social behaviour. *Nature, London* **301**: 379-384.

MACDONALD, D.W. & CARR, G.M. 1989. Food security and the rewards of tolerance. In: *Comparative socioecology: The behavioural*

*ecology of humans and animals*, (eds) V. Standen & R.A. Foley, Blackwell Scientific, Oxford.

MASON, C.F. & MACDONALD, S.M. 1986. *Otters: ecology and conservation*. Cambridge University Press, Cambridge.

MASON, C.F. & ROWE-ROWE, D.T. 1992. Organochlorine pesticide residues and PCBs in otter scats from Natal. *South African Journal of Wildlife Research* **22**: 29-31.

MAXWELL, G. 1960. *Ring of bright water*. Longmans Green, London.

MAXWELL, G. 1963. *The rocks remain*. Longmans Green, London.

MAXWELL, G. 1968. *Raven seek thy brother*. Longmans Green, London.

MEESTER, J.A.J., RAUTENBACH, I.L., DIPPENAAR, N.J. & BAKER, C.M. 1986. Classification of Southern African mammals. *Transvaal Museum Monographs* No. 5: 1-359.

MELQUIST, W.E. & HORNOCKER, M.G. 1983. Ecology of river otters in west central Idaho. *Wildlife Monographs* **83**: 1-60.

NEL, J.A.J. & SOMERS, M.J. In press. The status of otters in Africa: an assessment. *Habitat* **13**:

NEL, J.A.J., SOMERS, M.J. & ROWE-ROWE, D.T. In press. Conservation of sub-Saharan otters. In: Otter Action Plan 2000. IUCN.

PERRIN, M.R. & CARUGATI, C. 2000a. Food habits of coexisting Cape clawless otter and spotted-necked otter in the KwaZulu-Natal Drakensberg, South Africa. *South African Journal of Wildlife Research* **30**: 85-92.

PERRIN, M.R. & CARUGATI, C. 2000b. Habitat use by the Cape clawless otter and the spotted-necked otter in the KwaZulu-Natal Drakensberg, South Africa. *South African Journal of Wildlife Research* **30**: 103-113.

PERRIN, M.R. & D'INZILLO CARRANZA, I. 2000. Habitat use by spotted-necked otters in the KwaZulu-Natal Drakensberg, South Africa. *South African Journal of Wildlife Research* **30**: 8-14.

PERRIN, M.R., D'INZILLO CARRANZA, I. & LINN, I.J. 2000. Use of space by the spotted-necked otter in the Natal Drakensberg, South Africa. *South African Journal of Wildlife Research* **30**: 15-21.

PERRY, G. & PIANKA, E.R. 1997. Animal foraging: past, present and future. *Trends in Ecology and Evolution* **12**: 360-364.

POWELL, R.A. 1979. Mustelid spacing patterns: variations on a theme by *Mustela*. *Zeitschrift für Tierpsychologie* **50**: 153-163.

PURVES, M.G., KRUUK, H. & NEL, J.A.J. 1994. Crabs *Potamonautes perlatus* in the diet of the otter *Aonyx capensis* and water mongoose *Atilax paludinosus* in a freshwater habitat in South Africa. *Zeitschrift für Säugetierkunde* **59**: 332-341.

RALLS, K., HATFIELD, B.B. & SINIFF, D.B. 1995. Foraging patterns of California sea otters as indicated by telemetry. *Canadian Journal of Zoology* **73**: 523-531.

RANTA, E., RITA, H. & LINDSTRÖM, K. 1993. Competition versus cooperation: success of individuals foraging alone and in groups. *American Naturalist* **142**: 42-58.

RASA, O.A.E. 1986. Ecological factors and their relationships to group size, mortality and behaviour in the dwarf mongoose *Helogale undulata* (Peters, 1852). *Cimbebasia* **8**: 15-21.

ROWE-ROWE, D.T. 1975. Biology of Natal mustelids. M.Sc. thesis, University of Natal, Durban, South Africa.

ROWE-ROWE, D.T. 1977a. Food ecology of otters in Natal, South Africa. *Oikos* **28**: 210-219.

ROWE-ROWE, D.T. 1977b. Prey capture and feeding behaviour of South African otters. *Lammergeyer* **23**: 13-21.

ROWE-ROWE, D.T. 1977c. Variation in the predatory behaviour of the clawless otter. *Lammergeyer* **23**: 22-27.

ROWE-ROWE, D.T. 1978. The small carnivores of Natal. *Lammergeyer* **25**: 1-48.

ROWE-ROWE, D.T. 1990. Otter distribution and protection in South Africa. *IUCN Otter Specialist Group Bulletin* No. 5: 17-23

ROWE-ROWE, D.T. 1991. Status of otters in Africa. *Habitat* **6**: 15-20.

ROWE-ROWE, D.T. 1992. *The carnivores of Natal*. Natal Parks Board, Pietermaritzburg.

ROWE-ROWE, D.T. 1995. Distribution and status of African otters. *Habitat* **11**: 8-10

ROWE-ROWE, D.T. & SOMERS, M.J. 1998. Diet, foraging behaviour and coexistence of African otters and the water mongoose. *Symposia of the Zoological Society of London* No. 71: 215-227.

SANDELL, M. 1989. The mating tactics and spacing patterns of solitary carnivores. In: *Carnivore Behaviour, Ecology, and Evolution,* (ed) Gittleman, J.L. Chapman and Hall, London.

SCHOENER, T.W. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics* **2**: 369-404.

SKINNER, J.D. & SMITHERS, R.H.N. 1990. *The mammals of the Southern African subregion.* University of Pretoria, Pretoria.

SOMERS, M.J. 1996. Cape clawless otters associated with the Riviersonderend and Breede Rivers. In: *The Riviersonderend: Situation assessment, with specific reference to the effects of Tweewaterskloof Dam on the riverine ecosystem,* (eds) Ractliffe, G., Snaddon, K. & Brown, C. Department of Water Affairs and Forestry, Cape Town.

SOMERS, M.J. 1997. *Aonyx capensis.* In: *The Complete Book of Southern African Mammals,* (eds) Mills, M.G.L. & Hess, L. Struik Winchester, Cape Town.

SOMERS, M.J. 2000a. Foraging behaviour of Cape clawless otters (*Aonyx capensis*) in a marine habitat. *Journal of Zoology, London* **252**: 473-480.

SOMERS, M.J. 2000b. Seasonal variation in the diet of Cape clawless otters (*Aonyx capensis*) in a marine habitat. *African Zoology* **35**: 261-268.

SOMERS, M.J. & NEL, J.A.J. 1996. Otters in the Eastern Cape. *Pelea* **15**: 56-62.

SOMERS, M.J. & PURVES, M.G. 1996. Trophic overlap between three syntopic semi-aquatic carnivores: Cape clawless otter, spotted-necked otter, and water mongoose. *African Journal of Ecology* **34**: 158-166.

STANDER, P.E. 1992. Cooperative hunting in lions: the role of the individual. *Behavioral Ecology and Sociobiology* **29**: 445-454.

TAYLER, C. 1970. The elusive otter. *The Eastern Cape Naturalist* **39**: 20-23.

TINLEY, K.L. 1958. *A preliminary report on the ecology of Lake Sibaya with special reference to the hippopotamus.* Natal Parks Board Unpublished Report, Pietermaritzburg.

TURNBULL-KEMP, P.ST.J. 1960. Quantitative estimations of populations of river crab, *Potamon (Potamonautes) perlatus* (M. Edw.), in Rhodesian trout streams. *Nature, London* **185:** 481.

VAN DER ZEE, D. 1979. Food and status of the Cape clawless otter (*Aonyx capensis* Schinz 1821) in the Tsitsikama Coastal National Park. M.Sc. thesis, University of Pretoria, Pretoria, South Africa.

VAN DER ZEE, D. 1981. Prey of the Cape clawless otter (*Aonyx capensis*) in the Tsitsikama National Park, South Africa. *Journal of Zoology, London* **194:** 467-483.

VAN DER ZEE, D. 1982. Density of Cape clawless otters *Aonyx capensis* (Schinz, 1821) in the Tsitsikama Coastal National Park. *South African Journal of Wildlife Research* **12:** 8-12.

VAN NIEKERK, C.H., SOMERS, M.J. & NEL, J.A.J. 1998. Freshwater availability and distribution of Cape clawless otter spraints and resting places along the south-west coast of South Africa. *South African Journal of Wildlife Research* **28:** 68-72.

VAN ZYLL DE JONG, C.G. 1987. A phylogenetic study of the Lutrinae (Carnivora; Mustelidae) using morphological data. *Canadian Journal of Zoology* **65:** 2536-2544.

VERWOERD, D.J. 1987. Observations on the food and status of the Cape clawless otter *Aonyx capensis* at Betty's Bay, South Africa. *South African Journal of Zoology* **22:** 33-39.

WASER, P.M. 1981. Sociality or territorial defence? The influence of resource renewal. *Behavioral Ecology and Sociobiology* **8:** 231-237.

# CHAPTER 2

# DIET AND PREY AVAILABILITY OF CAPE CLAWLESS OTTERS (*AONYX CAPENSIS*) IN TWO SOUTH AFRICAN RIVERS

## INTRODUCTION

When an animal harvests food, it has to make decisions. One of these decisions is which kinds of prey to eat (Crawley & Krebs 1992). The optimal foraging theory (OFT), first proposed by Emlen (1966) and MacArthur & Pianka (1966), states that foraging strategies may involve decisions that optimise food intake per unit effort or of some other measure of foraging efficiency (Emlen 1966; MacArthur & Pianka 1966; Schoener 1971; Krebs & Kacelnik 1991; Perry & Pianka 1997). Optimality models have three main components: the currency, the constraints, and the decision variable (Krebs & Kacelnik 1991). In the case of diving organisms such as Cape clawless otters *Aonyx capensis*, the currencies could include maximising the rate of energy or oxygen intake, minimising the risk of predation, or a combination of these. Constraints and variables could be: amongst others (see Chapter 1), whether to eat or reject a small prey or certain types of prey. In this chapter these two variables are considered for *A. capensis* in two freshwater habitats. As there is increased loss of energy in water (Kruuk *et al.* 1997), it would be expected that otters would always maximise the net rate of energy gain.

*Aonyx capensis* are semi-aquatic predators, which occur over most of sub-Saharan Africa (Rowe-Rowe & Somers 1998; Nel & Somers in press). *Aonyx capensis* exploit a variety of aquatic habitats, including marine, estuarine, riparian, mangrove and lacustrine (see Chapter 1 for a discussion on their distribution), and are primarily crab eaters (Rowe-Rowe & Somers 1998). To understand how *A. capensis* use their habitats it is necessary to have baseline

information on the feeding ecology of the species. Diet of *A. capensis* using spraints has been determined (*freshwater habitats*: Turnbull-Kemp (1960); Rowe-Rowe (1975, 1977a, 1978); Donnelly & Grobler (1976); Kruuk & Goudswaard (1990); Butler (1994); Butler & du Toit (1994); Ligthart *et al.* (1994); Purves *et al.* (1994); Carugati (1995); Somers (1996); Perrin & Carugati (2000); *marine habitats*: van der Zee (1979, 1981); Arden-Clarke (1983, 1986); Verwoerd (1987) and Somers (2000a, 2000b (Chapters 5 & 6)) but none of these studies have attempted to relate it to relative prey abundance. These studies show that in most areas crustaceans are the most important prey type, but fish, frogs, insects, birds, reptiles, molluscs, dung (ungulate) and mammals are also eaten. This is in contrast to most other otters, which are mainly piscivorous (Estes 1989). Asian small-clawed otters *Amblonyx cinerea,* however, also feed mostly on crabs (Kruuk *et al.* 1994). Only Rowe-Rowe (1977a) and Purves *et al.* (1994) show seasonal variation in the diet of *A. capensis* but like the other studies do not give any data on prey availability. Data on availability are important for understanding the effects of food on otter populations and behaviour (Kruuk & Moorhouse 1990). For example, in European otters *Lutra lutra* prey availability can affect otter numbers, timing of reproduction, breeding success and mortality (Kruuk & Conroy 1991; Kruuk *et al.* 1987, 1991, 1993; Heggberget & Christensen 1994; Beja 1996).

As the relationship between behaviour and the availability of resources is a central part of behavioral ecology (Pulliam 1989), and food availability has a powerful influence on animals in both the determination of habitable areas and the numbers of individuals which these areas can support (Krebs 1985), the relative density of the otters' main prey are determined in the present study. As only Rowe-Rowe (1977a) and Purves *et al.* (1994) provide some seasonal data on diet this study provides more detailed seasonal data for *A. capensis*, living in freshwater environments. The above studies on the diet of *A. capensis* have shown *A. capensis* to eat a variety of prey, both in terms of size and type. Optimal foraging theory can be used to account for the types and sizes of prey items taken by

predators (Krebs & Kacelnik 1991). One possible hypothesis to explain why several types of prey are eaten is that the times taken to search for the most profitable prey types influences choice. If it takes a long time to find a profitable fish, the otter might be able to obtain a higher overall rate of intake by eating some of the less profitable crabs. The same applies to sizes of prey eaten.

Despite freshwater crabs of the genus *Potamonautes* (the main prey of *A. capensis*) being locally abundant (up to 36 crabs m$^{-2}$) in southern African freshwater systems (Turnbull-Kemp 1960; Arkell 1978; King 1983; Raübenheimer 1986; Hill & O'Keeffe 1992; Somers & Nel 1998), and forming a major part of the diet of many other species, little information is available about their biology (Somers & Nel 1998). The crabs, besides being eaten by *A. capensis,* are eaten by many species of fish (Skelton 1993), birds (Maclean 1985), and other mammals such as spotted-necked otter *Lutra maculicollis*, and water mongoose *Atilax paludinosus* (Rowe-Rowe 1977a; Somers & Purves 1996 (Chapter 7)). Somers & Nel (1998) predict they may be important enough in freshwater systems to be termed dominant or even keystone species (Power *et al.* 1996), but more data are needed (Somers & Nel 1998).

In this chapter I report on the annual and seasonal diet of *A. capensis*, as estimated from spraint (faecal) analysis, in relation to the presence of their main prey (crabs and fish) in two South African rivers. The main questions asked were:

1. What is the species composition of the diet of the otters?
2. How does diet vary with season?
3. Are variations in crab and fish abundance in the environment reflected in the diet of otters?

## MATERIALS & METHODS

Spraints were collected in the Eerste River (near Stellenbosch (33° 56' S, 18° 52' E)) and Olifants River (near Clanwilliam (32° 11' S, 18° 23' E)) in the Western Cape Province, South Africa.

The Eerste River is a rocky, narrow river, which rises in pristine conditions in the Jonkershoek Mountains, but then flows through agricultural, industrial and urban areas. The flow rate is variable depending on rainfall, which is mostly in winter. It reaches the sea about 40 km from its source. The Eerste River is disturbed for *ca* 90% of its length by agriculture, industry and the urban environment. Cattle *Bos taurinus* farming is rare along the Eerste River. The main crops (vines, fruit, and vegetables) are subject to heavy applications of fertilizers, herbicides and pesticides (Heinecken *et al.* 1983). Winery effluents are either irrigated onto pasturelands or sent to the Stellenbosch sewage works. Treated effluent from these works is discharged into a tributary of the Eerste River (Heinecken *et al.* 1983). During heavy rainfall events overflow of the sewage works occurs and untreated sewage flows into the river below Stellenbosch (personal observations). The Eerste River and a number of its tributaries flow through Stellenbosch, and these receive all the storm water run-off from the town. Pollution levels and eutrophication increases rapidly below Stellenbosch. The treated sewage from the towns of Macassar, Somerset West and Strand is also discharged into the estuary of the Eerste River (Heinecken *et al.* 1983). For a detailed classification of the Eerste River see Eekhout *et al.* (1997).

The Olifants River is 285 km long and has a catchment area of 46 220 km$^2$. The part of the Olifants River used in this study is dominated by two impoundments: the Clanwilliam and Bulshoek Dams. There are holiday camps along the edge of the impoundments and recreational boating, swimming, and fishing takes place. The length of river between the two dams is 17.6 km and bordered by cattle and crops. There is, however, little disturbance along the water edge where mostly exotic *Eucalyptus* trees grow. Just above Bulshoek Dam the river is slow flowing, has a sandy bank with reed *Phragmites australis* beds, bulrushes *Typha capensis* and occasional sedges *Cyperus* spp along the edge. The river below Bulshoek Dam is slow flowing with marshlands, oxbows, large basins, large reed beds and bulrushes and rocky pools of up to 6

m deep. Except for recreational activities on the dam (mostly during weekends and the summer holidays) there is not much disturbance. The area down to *ca* 15 km below Bulshoek Dam is not intensively farmed, except for some cattle farming, resulting in very little disturbance. Further down (out of the present study area) the river has extensive agriculture in the form of vines, fruit and vegetables along the edge. For a detailed classification of the Olifants River see Harrison (1997) and Eekhout *et al.* (1997).

## Otter diet

From February 1993 to September 1996, 362 spraints were collected along the Eerste River and, from April 1993 to September 1996, 824 spraints were collected along the Olifants River. Identification of spraints in the field was based on their characteristic odour.

Spraints were air-dried, teased apart and prey remains identified using a stereomicroscope (X 10 - 100 magnification). Prey items were sorted into the following categories: mammal, bird, frog, fish, crab, insect, plant material and non-food such as dung, soil and leaves. The presence of mammal remains in the spraints was determined from hair, crabs and insects from carapaces or exoskeletons, fishes from bones and scales, reptiles and frogs from bones, and birds from feathers.

Fishes were identified by scales, provided by Dr. P. Skelton of the J.L.B. Smith Institute of Ichthyology, Grahamstown, or by reference material in the Department of Zoology, University of Stellenbosch, which was originally produced by Ms. T. Cousin.

The minimum number of crabs and fish represented in spraints from each season and each river was estimated from the number of crab eyestalks and fish eye lenses in 10 g dry weight of spraint ($n$ = 50 randomly selected spraints for each season and each river). To determine size of crabs eaten, the regression determined for crabs in the Olifants River (Purves *et al.* 1994) was used: C = -11.48+(8.33*E), where C = carapace width (mm) and

E = eye stalk length (mm). This correlation was highly significant ($r^2$ = 0.99, $n$ = 66, $P$ < 0.001).

The presence of each prey category in each spraint was scored, and the percentage occurrence of each prey category calculated. Scores for each category were also added and expressed as a percentage of the total number of scores of all categories, yielding relative percentage occurrence. This method has been shown to closely approximate the proportions of different items actually consumed by *L. lutra* (Erlinge 1968) and *A. capensis* (Rowe-Rowe 1977a). Carss & Parkinson (1996), however, show that for *L. lutra* it should only be used to rank importance of prey in the diet. The rank of importance, based on the percentage occurrence was therefore also determined.

For each spraint the dominant prey type was also determined by volumetric analysis of prey items. The different dominant prey items were then expressed as a percentage of the total number of spraints (Kruuk *et al.* 1994; Purves *et al.* 1994; Somers & Purves 1996 (Chapter 7)).

The diet was determined for all years combined and the four seasons: winter (June-August); spring (September-November); summer (December-February) and autumn (March-May).

**Prey abundance**

To determine expected prey availability crabs and fish were caught in plastic gauze, funnel traps (550 by 250 mm, with a funnel of 100 mm, baited with *ca* 200 g of shallow-water hake *Merluccius capensis*), which were left overnight in the river. The crabs were removed the following morning and the maximum carapace widths of these crabs were measured with callipers. The number and species of fish caught were determined. The traps, anchored with string to the shore, were placed along the edges within 5 m of the shore. This distance was used, as it is where the otters usually forage in fresh water (personal observation). As the number of crabs caught varied among different parts of the river (Somers & Nel 1998), the data used to compare relative densities between the two rivers, are from traps deposited within a 50 m

stretch of similar habitat (over rocky bottomed riverbed) in each river. The use of 50 m stretches of similar habitat ensured that only seasonal and not spatial variations were shown in the results. As each season was not sampled in each year the data are combined and compared with the overall seasonal diet of the otters. Thirty trap nights for each season in each river were used. Furthermore, in the Olifants River, crabs were trapped in the following habitat types: > 5 m from the shore (open water), within 5 m from a sandy shore, within 5 m of the rocky shore, and *ca* 1 m into a reed bed. These were sampled as above but only counting numbers of crabs caught.

# RESULTS

## Annual diet and prey availability

The results of all four methods used in quantifying the diet, showed crabs were the main prey of *A. capensis* in the Olifants and Eerste Rivers during the entire study period (Tables 2.1 & 2.2). Crab remains found in the spraints from both rivers were of *Potamonautes perlatus*, the only species of crab occurring in the study area of the Eerste River (see Stewart 1997). Within the Olifants River study area *P. perlatus* occurred up to the Bulshoek Dam wall. For the remainder of the study area, below the dam wall, a hybrid between *P. perlatus* and *P. granularis* occurs (Daniels *et al.* 1999). Fish were the second most abundant prey in the spraints from both rivers. However, the species differed with only *Tilapia sparrmanii* (92.5%) and *Micropterus dolomieu* (7.5%) being found in the spraints from the Olifants River (Table 2.1), and *T. sparrmanii* (17.8%), *Oreochromis mossambicus* (16.10%), *Oreochromis mykiss* (51%), and *Sandelia capensis* (14.4%) being found in the spraints from the Eerste River (Table 2.2).

28

28

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**Table 2.1.** Prey items recorded in 824 Cape clawless otter *Aonyx capensis* spraints collected from the Olifants River from April 1993 to September 1996, as percentage occurrence, relative frequency occurrence, percentage of spraints dominated by a prey and overall rank of importance.

| Prey type | Observed | % Occur. | Rel. freq. occur. | % Dominance | Rank |
|---|---|---|---|---|---|
| Crab (*Potamonautes perlatus*) | 794 | 96.4 | 50.0 | 82.0 | 1 |
| Fish (*Tilapia sparrmanii*) (*Micropterus dolomieu*) | 412 (381) (31) | 50.0 (46.2) (3.8) | 25.9 (24.0) (2.0) | 14.6 | 2 |
| Plant | 192 | 23.3 | 12.1 | 1.5 | 3 |
| Frog | 90 | 10.9 | 5.7 | 0.5 | 4 |
| Insect | 86 | 10.4 | 5.4 | 0.0 | 5 |
| Other (soil, leaves) | 8 | 1.0 | 0.5 | 0.5 | 6 |
| Bird | 6 | 0.7 | 0.4 | 0.5 | 7 |

**Table 2.2** Prey items recorded in 362 Cape clawless otter *Aonyx capensis* spraints collected from the Eerste River from February 1993 to September 1996, as percentage occurrence, relative frequency occurrence, percentage of spraints dominated by a prey and overall rank of importance.

| Prey type | Observed | % Occur. | Rel. freq. occur. | % Dominance | Rank |
|---|---|---|---|---|---|
| Crab (*Potamonautes perlatus*) | 340 | 93.9 | 61.3 | 91.4 | 1 |
| Fish | 118 | 32.6 | 21.3 | 6.9 | 2 |
| (*Oreochromis mykiss*) | (60) | (16.6) | (10.8) | | |
| (*Tilapia sparrmanii*) | (21) | (5.8) | (3.8) | | |
| (*Oreochromis mossambicus*) | (19) | (5.2) | (3.4) | | |
| (*Sandelia capensis*) | (17) | (4.7) | (3.1) | | |
| Insect | 40 | 11.0 | 7.2 | 0.0 | 3 |
| Frog | 24 | 6.6 | 4.3 | 0.6 | 4 |
| Bird | 17 | 4.7 | 3.1 | 0.0 | 5 |
| Mammal | 9 | 2.5 | 1.6 | 0.0 | 6 |
| Plant | 5 | 1.4 | 0.9 | 1.1 | 7 |
| Other (soil, leaves) | 2 | 0.6 | 0.4 | 0.0 | 8 |

Plant material was ranked third in the diet of the otters from Olifants River but using percentage occurrence, relative frequency occurrence and ranking, it was only seventh in the Eerste River. Percentage dominance, however, showed plant material to be ranked third in the Eerste River. Other items included frogs, insects, birds and mammals (Tables 2.1 & 2.2). Insect remains represented *Coleoptera* and *Odonata*, while mammals and frogs were unidentified.

In terms of numbers of prey, crabs again dominated the diet in both rivers. There were significantly more crabs than fish represented in the spraints in both the Olifants River (Mann-Whitney $U$ = 36795, d.f. = 399, $P$ < 0.001) and Eerste River (Mann-Whitney $U$ = 36572, d.f. = 399, $P$ < 0.001) (Table 2.3).

There was no significant difference between the relative number of crabs in the spraints (represented by half the number of eye-stalks per 10 g of spraint) from the Olifants River (mean = 3.4 per 10 g spraint, S.E. = 0.2, range = 0–20) and the Eerste River (mean = 3.3 per 10 g of spraint, S.E. = 0.2, range = 0–18) (Mann-Whitney $U$ = 19939, d.f. = 399, $P$ = 0.958).

There was also no significant difference between the relative number of fish in the spraints (represented by half the number of eye lenses per 10 g of spraint) from the Olifants River (mean = 0.2 per 10 g of spraint, S.E. = 0.01, range = 0–15.5) and the Eerste River (mean = 0.2 per 10 g of spraint, S.E. = 0.05, range = 0–7.5) (Mann-Whitney $U$ = 20319, d.f. = 399, $P$ = 0.783).

The crabs found in the spraints from the Olifants River (mean = 27.2, S.E. = 0.2, range = 4.3-66.8, $n$ = 1983) were slightly but significantly smaller (Mann-Whitney $U$ = 569122, d.f. = 2612, $P$ < 0.001) than those found in the spraints from the Eerste River (mean = 28.4, S.E. = 0.3, range = 6.9-50.5, $n$ = 630) (Fig. 2.1).
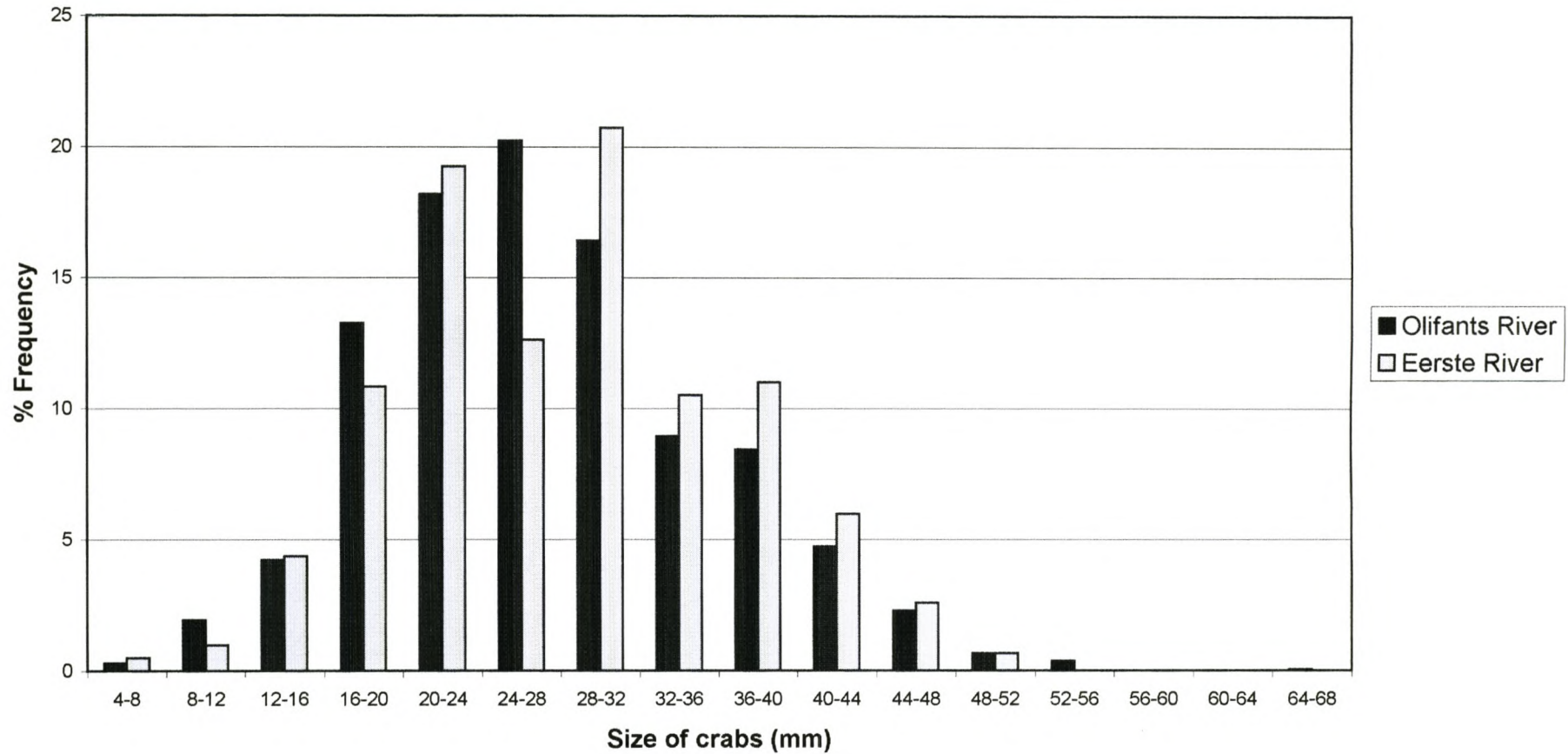
**Fig. 2.1.** The percentage frequency size distribution of crabs *Potamonautes perlatus* found in the spraints of Cape clawless otters *Aonyx capensis* in the Olifants River and Eerste River.

There were significantly different numbers of crabs caught in the open area (mean = 1.4, S.E. = 0.27, range = 0-8 crabs per trap, $n$ = 40), sandy area (mean = 2.2, S.E. = 0.35, range = 0-6 crabs per trap, $n$ = 30) rocky area ((mean = 2.6, S.E. = 0.36, range = 0-8 crabs per trap, $n$ = 42) and in the reed beds (mean = 5.9, S.E. = 0.67, range = 1-22 crabs per trap, $n$ = 35) ($H$ = 52.63, d.f. = 3, $P$ < 0.001). An all pairwise multiple comparison (Dunn's method) isolated reeds to differ from the others with regards number of crabs caught.

In the Eerste River crabs with a mean carapace width of 41.22 mm were caught, while Somers & Nel (1998) caught crabs by hand (a more accurate collection method) with a mean carapace width of 18.25 (S.E. = 0.34 mm, range = 5.05–44.0 mm).

Comparing the data from this study and Somers & Nel (1998) there was a significant difference between the size of trap and hand caught crabs (Mann-Whitney $U$ = 906, d.f. = 627, $P$ < 0.001).

## Seasonal variation in the diet

When combining the data from all the years, the annual pattern in the percentage occurrence of prey of *A. capensis* in the Olifants and Eerste Rivers showed an increase in the amount of crab in summer vs winter and a corresponding decrease in the amount of fish eaten (Fig. 2.2 & 2.3). Another noticeable pattern in the diet of *A. capensis* in the Olifants River was that frogs were seldom eaten in summer compared to other seasons (Fig. 2.2). There was a strong concordance among seasons in the relative importance of prey categories for the Olifants River ($W$ = 0.97, $\chi^2$ = 23.21, d.f. = 6, $P$ < 0.001) and the Eerste River ($W$ = 0.89, $\chi^2$ = 24.94, d.f. = 7, $P$ < 0.001). Wilcoxon matched pairs signed rank test showed no significant difference between the seasonal relative frequency occurrences of the various prey categories between the two rivers ($P$ > 0.07 for all pairs).
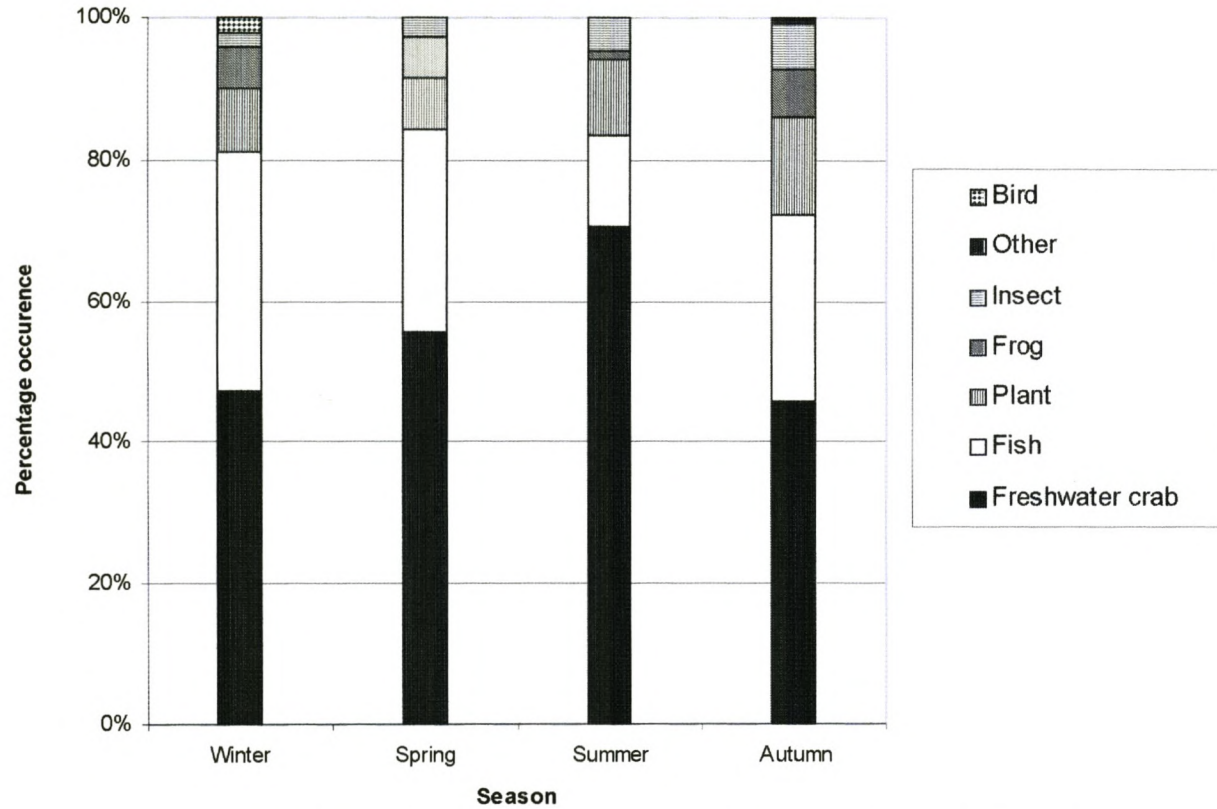
**Fig. 2.2.** The percentage occurrence of prey items found in the spraints of Cape clawless otters *Aonyx capensis* in the Olifants River, from April 1993 to September 1996 for the four seasons.
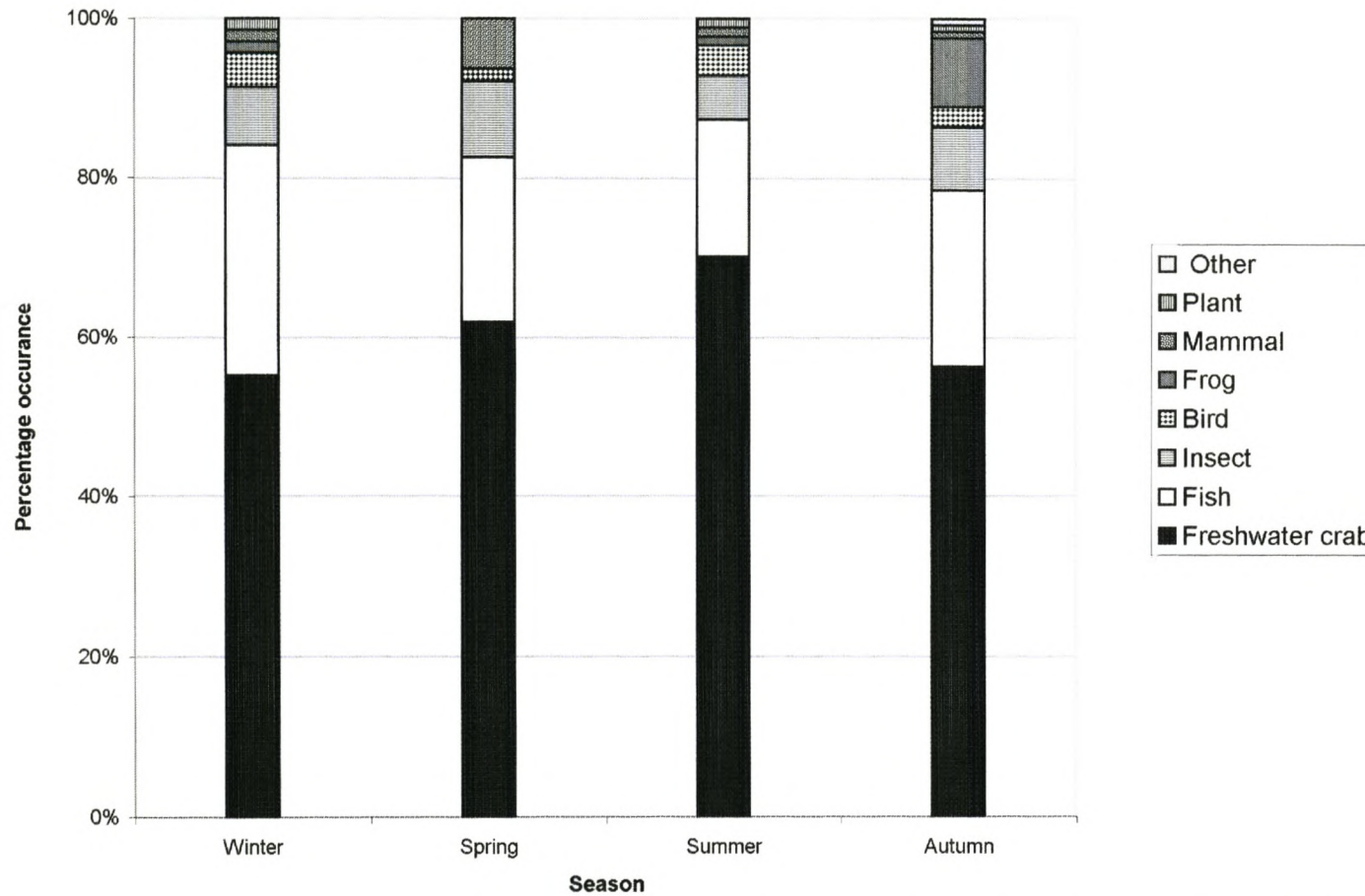
**Fig. 2.3.** The percentage occurrence of prey items found in the spraints of Cape clawless otters *Aonyx capensis* in the Eerste River, from February 1993 to September 1996 for the four seasons.

Kruskal-Wallis One Way Analysis of Variance on Ranks showed that although there is a noticeable seasonal pattern in number of crabs and fish found in the spraints of the otters (Fig. 2.4 & 2.5), only the crab numbers in the spraints collected in the Eerste River showed a significant seasonal variation ($H$ = 9.51, d.f. = 3, $P$ = 0.023). An apparent increase in the number of fish represented in the spraints during spring in the Olifants River was not significant ($H$ = 1.80, d.f. = 3, $P$ = 0.61).

There was a significant seasonal difference in the size of crabs eaten by the otters in the Olifants River ($H$ = 23.7, d.f. = 3, $P$ < 0.001) and those eaten in the Eerste River ($H$ = 134.5, d.f. = 3, $P$ < 0.001) (Tables 2.3 & 2.4).

## Diet in relation to food resources

Only *P. perlatus* and *T. sparrmanii* were caught in the baited traps in the rivers (Table 2.5). However, in both rivers, other species of fish are known to occur (Skelton 1993) and were eaten by the otters (Tables 2.1 & 2.2).

There was no significant difference between the observed numbers of crabs represented in the spraints vs the expected number during the four seasons, as determined from the traps in the Olifants River ($\chi^2$ = 4.38, d.f. = 3, $P$ = 0.22) and the Eerste River ($\chi^2$ = 0.71, d.f. = 3, $P$ = 0.87). The same applied to the number of fish represented in the spraints for the Olifants River ($\chi^2$ = 0.83, d.f. = 3, $P$ = 0.84) and the Eerste River ($\chi^2$ = 0.90, d.f. = 3, $P$ = 0.83). There was, however, a significant difference between the observed vs expected percentage occurrence of crabs in the diet from the Olifants River ($\chi^2$ = 125.38, d.f. = 3, $P$ < 0.001) and the Eerste River ($\chi^2$ = 19.98, d.f. = 3, $P$ < 0.001).
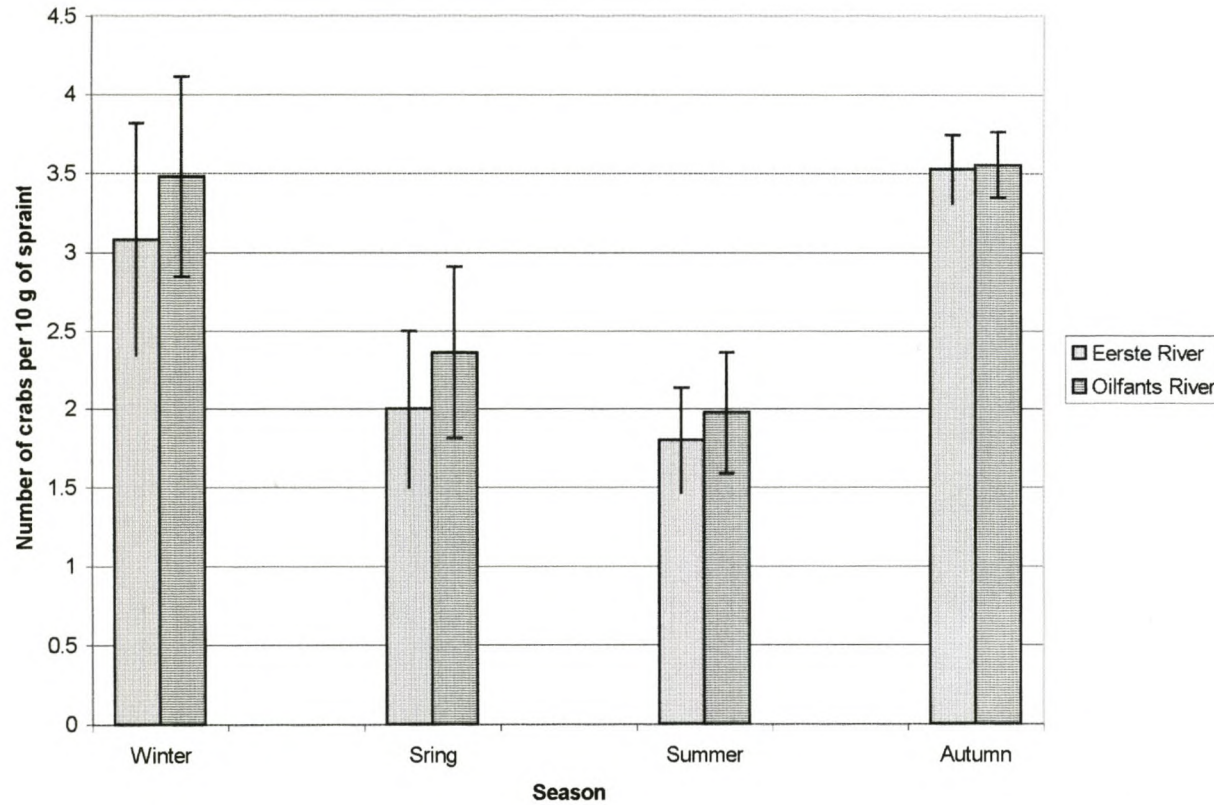
**Fig. 2.4.** The mean number (± SE) of crabs (represented by half the number of eye stalks) found per 10 g dry weight of Cape clawless otter *Aonyx capensis* spraint collected from the Eerste River (*n* = 50 per season) and Olifants River (*n* = 50 per season) during the four seasons.
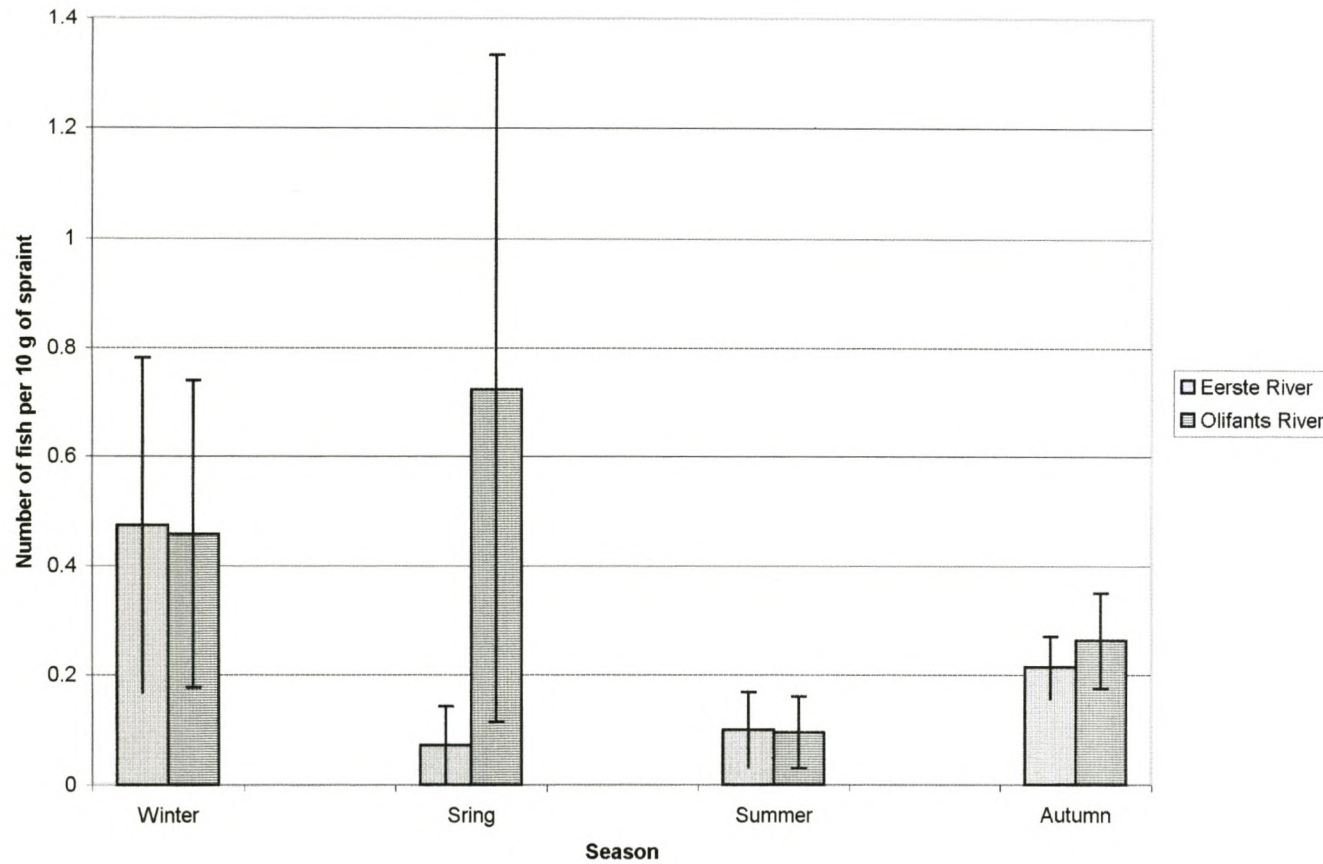
**Fig. 2.5.** The mean number (± SE) of fish (represented by half the number of eye lenses) found per 10 g dry weight of Cape clawless otter *Aonyx capensis* spraint collected from the Eerste River (*n* = 50 per season) and Olifants River (*n* = 50 per season) during the four seasons.

**Table 2.3.** The size distribution of crabs *Potamonautes perlatus* in spraints of Cape clawless otters *Aonyx capensis*, from the Olifants River, by season.

| Size of crabs (mm) | winter (%) (n = 162) | spring (%) (n = 67) | summer (%) (n = 77) | autumn (%) (n = 1676) |
|---|---|---|---|---|
| Size distribution | | | | |
| 0-4 | 0.0 | 0.0 | 0.0 | 0.1 |
| 5-9 | 0.0 | 0.0 | 0.0 | 1.0 |
| 10-14 | 3.1 | 0.0 | 0.0 | 4.9 |
| 15-19 | 6.8 | 6.0 | 5.2 | 16.0 |
| 20-24 | 22.2 | 25.4 | 23.4 | 20.9 |
| 25-29 | 25.3 | 26.9 | 20.8 | 23.6 |
| 30-34 | 15.4 | 22.4 | 27.3 | 16.0 |
| 35-39 | 13.6 | 16.4 | 10.4 | 9.7 |
| 40-44 | 7.4 | 3.0 | 11.7 | 5.3 |
| 45-49 | 3.1 | 0.0 | 2.3 | 1.9 |
| 50-54 | 2.5 | 0.0 | 0.0 | 0.4 |
| 55-59 | 0.6 | 0.0 | 0.0 | 0.1 |
| 60-65 | 0.0 | 0.0 | 0.0 | 0.0 |
| 66-70 | 0.0 | 0.0 | 0.0 | 0.1 |
| | | | | |
| Size parameters | | | | |
| Mean (mm) | 29.6 | 28.5 | 29.5 | 26.8 |
| S.E. | 0.7 | 0.8 | 0.9 | 0.2 |
| Range | 11.8-55.2 | 16.8-43.5 | 15.2-45.2 | 4.3-66.8 |

**Table 2.4.** The size distribution of crabs *Potamonautes perlatus* represented in spraints of *Aonyx capensis*, from the Eerste River, by season.

| Size of crabs (mm) | winter (%) (*n* = 63) | spring (%) (*n* = 156) | summer (%) (*n* = 228) | autumn (%) (*n* = 182) |
|---|---|---|---|---|
| 5-9 | 0.0 | 0.0 | 0.0 | 3.3 |
| 10-14 | 23.8 | 0.0 | 0.0 | 2.2 |
| 15-19 | 46.0 | 0.6 | 0.0 | 24.2 |
| 20-24 | 28.6 | 59.6 | 39.5 | 18.1 |
| 25-29 | 0.0 | 0.0 | 8.8 | 9.9 |
| 30-34 | 0.0 | 11.5 | 39.5 | 7.7 |
| 35-39 | 0.0 | 27.6 | 12.3 | 24.7 |
| 40-44 | 1.6 | 0.0 | 0.0 | 3.3 |
| 45-49 | 0.0 | 0.6 | 0.0 | 6.6 |
| | | | | |
| Size parameters | | | | |
| Mean (mm) | 18.3 | 32.9 | 28.5 | 27.7 |
| S.E. | 0.7 | 0.6 | 0.3 | 0.7 |
| Range | 12.0-43.0 | 18.0-50.5 | 21.3-38.0 | 6.9-46.3 |

**Table 2.5.** The mean number of crabs (*Potamonautes perlatus*) and fish (*Tilapia sparrmanii*) caught in traps during all seasons in the Olifants River and Eerste River, Western Cape Province, South Africa. (*n* = 30 trap nights per season per river)

| Prey type | Autumn | | Winter | | Spring | | Summer | |
|---|---|---|---|---|---|---|---|---|
| | Mean ± S.E | Range | Mean ± S.E | Range | Mean ± S.E | Range | Mean ± S.E | Range |
| **Olifants River** | | | | | | | | |
| Crabs | 7.2 ± 0.7 | 0-20 | 2.5 ± 0.5 | 0-9 | 1.2 ± 0.2 | 0-4 | 3.5 ± 0.4 | 1-10 |
| Fish | 1.5 ± 0.3 | 0-6 | 0.7 ± 0.2 | 0-5 | 2.2 ± 0.4 | 0-6 | 1.9 ± 0.3 | 0-7 |
| | | | | | | | | |
| **Eerste River** | | | | | | | | |
| Crabs | 6.2 ± 0.8 | 0-17 | 3.4 ± 0.6 | 0-10 | 3.2 ± 0.4 | 0-9 | 4.1 ± 0.4 | 1-11 |
| Fish | 0.8 ± 0.2 | 0-3 | 0.9 ± 0.2 | 0-5 | 2.0 ± 0.4 | 0-7 | 1.3 ± 0.2 | 0-4 |

The same applied to the percentage occurrence of fish in the Olifants River ($\chi^2$ = 54.46, d.f. = 3, $P$ < 0.001) and the Eerste River ($\chi^2$ = 17.47, d.f. = 3, $P$ < 0.001).

The difference between size of crabs caught in the traps and those found in the spraints was significant (Olifants River, Mann-Whitney $U$ = 54313, d.f. = 2259, $P$ < 0.001; Eerste River, Mann-Whitney $U$ = 10427, d.f. = 789, $P$ < 0.001).

There was no significant difference (Mann-Whitney $U$ = 21731, d.f. = 437, $P$ = 0.69) between the size of crabs caught in the traps in the Olifants River (mean = 40.70, S.E. = 0.3, range = 20.0-59.0, $n$ = 278) and the size of those caught in the traps in the Eerste River (mean = 41.22, S.E. = 0.4, range = 29.4-53.0, $n$ = 180).

There were significantly more crabs caught in the traps in the Olifants River than in the Eerste River (Mann-Whitney $U$ = 35885.5, d.f. = 231, $P$ < 0.001) (Table 2.5).

## DISCUSSION

### Annual Diet

This study shows freshwater crabs to be the main prey of *A. capensis* in freshwater habitats. The present results are consistent with previous studies (see Rowe-Rowe & Somers 1998 for review), except those of Rowe-Rowe (1977a) and Purves & Sachse (1998), where frogs were the second most common prey type. These two studies were, however, done at middle to high altitudes (1060-1650 m.a.s.l.) where fish faunas are poor (Rowe-Rowe & Somers 1998). No molluscs or reptiles were found in the spraints in this study whereas they have been found in low frequencies in some other areas (Rowe-Rowe & Somers 1998). Waterfowl were, as in other studies (Rowe-Rowe & Somers 1998), rarely eaten.

The importance of different secondary items found in the various studies is probably related to local prey availability (Rowe-Rowe & Somers 1998). Optimal foraging theory can be used to

account for the types and sizes of prey items taken by predators (Krebs & Kacelnik 1991). One possible hypothesis to explain why several types of prey are eaten is that the times taken to search for the most profitable type influences choice. If it takes a long time to find a profitable prey item (such as a fish), the otter might be able to obtain a higher overall rate of intake by eating some of the less profitable crabs. The same may apply to sizes of prey eaten. The size of crabs eaten here, and in other studies is relatively small compared to what is found in the environment. They may find small crabs more profitable because they are more easily found and this is what they are adapted to catching. Whereas most otter species are piscivorous (Mason & Macdonald 1986), *A. capensis*, Congo otter *Aonyx congica* and small-clawed otter *Amblonyx cinerea* are generally regarded as crab specialists in freshwater habitats (Rowe-Rowe 1977a, Kruuk *et al*. 1994), having broadened bunodont molars for crushing the exoskeletons of invertebrate prey. Their manual dexterity further enables them to feel for and capture prey such as crabs under stones and in crevices (Rowe-Rowe 1977a). The results presented here again show the importance of crabs in the diets of *A. capensis*, emphasising, for their conservation management, the need for more information about factors limiting crab numbers.

Area related differences in diet have been shown in *L. lutra* (Kemenes & Nechay 1990; Kruuk & Moorhouse 1990), southern river otter *Lutra provocax* (Medina 1998) and in *A. capensis* (Rowe-Rowe & Somers 1998). However in this study, the diets of the otters in the two study sites have been shown to be fairly similar. The notable difference was the amount of ungulate, probably cattle, dung found in the spraints collected along the Olifants River (23.3%), where cattle grazing down to the river edge is common. No record of this has been found for other species of otters and the reason remains unclear. However, one explanation is that the otters feed on dung beetles in the dung and accidentally take in some of the dung.

## Seasonal diet

As shown here for *A. capensis,* other species of otter, like *L. lutra* (Erlinge 1967; Kruuk *et al.* 1987; Weber 1990; Brzezinski *et al.* 1993; Heggberget 1993; Beja 1997), Canadian river otter *Lutra canadensis* (Tumlison & Karnes 1987; Dolloff 1993), smooth otter *L. perspicillata* (Nayerul Haque & Vijayan 1995) and Neotropical river otter *L. longicaudis* (Helder & Ker De Andrade 1997) have a seasonal variation in diet.

The seasonal pattern in the percentage occurrence of prey of *A. capensis* in the Olifants and Eerste Rivers shows an increase in the amount of crab in summer and a corresponding decrease in the amount of fish eaten. This may be a result of fish (but not crabs) being more available (perhaps more easily caught in winter, owing to them being more lethargic; Rowe-Rowe 1977b). They may also be selecting for the more energy rich fish in winter owing to the otters having higher energy demands resulting from the colder water. As water levels are lower during summer the otters may also find catching crabs easier. In winter, frequent flooding leaves isolated pools near the main stream wherein small fish are often stranded, which may also contribute towards the increased amount of fish and decreased amount of crabs eaten during winter. Purves *et al.* (1994) also showed a decrease in the percentage occurrence of crabs in the diet of the otters in winter (June) compared to summer (February). Another noticeable pattern in the diet of *A. capensis* in the Olifants River is that frogs were seldom eaten in summer compared to the other seasons (Fig. 2.2). The reason for this is unknown.

## Diet in relation to food resources

Although the crabs found in the spraints from the Olifants River were significantly smaller than those found in the Eerste River, there was no significant difference between the sizes of crabs caught in the traps from the two rivers. This suggests that the otters on the Eerste River were selecting slightly larger crabs than the otters in the Olifants River.

The traps were obviously size selective and the comparison between size of crabs eaten and the size of crabs caught in the traps, were thus meaningless. However, the relative number of crabs caught could still be used as an indication of availability. The results show the relative number of crabs caught in the traps to be represented in the diet of the otters. The percentage occurrence of crabs and fish in the diet, however, are not representative of the crabs and fish caught in the traps. This result shows that otters and traps selected differently from the available prey populations.

*Lutra lutra* have also been shown to eat prey in relation to abundance (Lanszki & Körmendi 1996) but in a marine habitat in Scotland, they ate prey not in relation to numbers of fish, but rather in relation to availability (Kruuk & Moorhouse 1990). The latter also applies to *L. canadensis* (Melquist & Hornocker 1983). Owing to this dietary plasticity between habitats, otters are regarded as opportunistic predators (Chanin 1985). This also appears to be the case here, at least with regards to number of prey being eaten by *A. capensis*.

The data supports previous findings (see Somers & Nel 1998) that smaller crabs (< 20 mm carapace width) are not sampled by traps. The reasons may be that larger crabs are more dominant (Somers & Nel 1998), or that smaller crabs are not attracted to the bait as they eat more plant material (Hill & O'Keeffe 1992). The sizes of crabs caught are, however, not representative of the population and cannot be directly compared to those caught by the otters. Sampling crabs by hand is only an option in shallow, clear water and could not be done, except in limited areas of the Eerste River. More crabs were caught in the traps placed in the reed beds than in the other habitat types sampled. This suggests that the reed beds are important habitat types for the otters. The finding that the otters select areas with reed beds (Chapter 4) further supports this.

*Oncorhynchus mykiss* breed from June through to August and prefer fast flowing water (Skelton 1993). *Sandelia capensis* and *T. sparrmanii* prefer quiet or standing waters with submerged or

emergent vegetation (Skelton 1993). All the fish species eaten, except *O. mykiss,* therefore prefer quiet or slow flowing water with submerged or emergent vegetation. These data suggest that the otters forage mostly at the edges of the rivers where the water flow is less and there is more vegetation. *Oncorhynchus mykiss*, however, are farmed in the Eerste River where otters have been seen catching them in holding tanks (personal observations). An important management problem with otters is the damage they cause to *O. mykiss* farms (Somers & Nel 1995), and the otters in the Eerste River have been a cause of concern for the local *O. mykiss* farmers and researchers. Otters are reported to be responsible for the destruction of large numbers of *O. mykiss* and domestic fowl. This supports the idea that otters are somewhat opportunistic predators (Chanin 1985) in that they select an artificial and abundant prey source (*O. mykiss*), when available. There are few *O. mykiss* in the Eerste River but it is not known if the otters are eating these or just those in the *O. mykiss* tanks.

Temporal changes in diet, owing to change in prey availability caused by otters, have been recorded in sea otters *Enhydra lutris* (Ostfeld 1982) and *L. lutra* (Lanszki & Körmendi 1996). *Enhydra lutris* has also been shown to be important in determining the structure of prey communities and can therefore be called a keystone species (Estes & Palmisano 1974; Lowry & Pearse 1974). The role of *A. capensis* in determining aquatic communities is presently unknown. Melquist & Hornocker (1983) have suggested that the river otter, *L. canadensis* do not influence its prey numbers and that the ability of vertebrate predators to regulate their prey is rare, as also stated by Erlinge *et al.* (1984) for *L. lutra*. With *P. perlatus* being very abundant (up to 36 per m$^2$) (Somers & Nel 1998), it is thought that the otters would not have much influence on the crab population, but they could have a large effect on populations of farmed fish! More data are, however, needed.

As there is a high correlation between prey density and otter recruitment (Kruuk *et al.* 1991), and evidence that otter

mortality is higher during periods of low prey availability (Kruuk & Conroy 1991) in a *L. lutra* population in Shetland, U.K., prey availability may significantly affect *L. lutra* populations. If there is a similar pattern with *A. capensis,* knowledge of crab densities or relative densities in all freshwater systems may be important to the conservation of *A. capensis*. Butler & du Toit (1994) have speculated that the low densities of *A. capensis* in Zimbabwe is probably a reflection of the poor productivity of crabs in certain water bodies. With a rapidly decreasing quality and quantity of fresh water in Africa (Davies & Day 1998) the fate of aquatic biological communities is uncertain. More detailed long-term data are needed to determine the relationships between *A. capensis* and their prey.

Much of our knowledge of the diet of otters comes from the identification of undigested prey remains in spraints (see reviews of Mason & Macdonald (1996) for all species of otters, Rowe-Rowe & Somers (1998) for African otters in freshwater habitats and Somers (2000b) (chapter 5) for *A. capensis* in marine habitats). However, frequency of occurrence data, from analysis of spraints, have certain potential shortcomings. For example, a sample with one complete specimen is counted in the same way as one having just one fish scale, fishes without scales may be missed entirely and spraints may contain remains from the gut of prey (Webb 1975). It is also not known which otter left a particular spraint, where the prey was taken, or when it was taken (Kruuk 1995). The activity level of the otter which sprainted, which is unknown, can also have a large effect on spraint composition (Carss *et al.* 1998). Confidence levels for these data, from *L. lutra* have been shown to be low and the data should therefore be interpreted with caution (Carss & Parkinson 1996). Only Somers (2000a) (chapter 6) has provided data on diet of *A. capensis* from direct observations but could not provide much detail. However, spraint analysis by frequency of occurrence can provide useful information on the prey consumed, particularly in ranking the "importance" of prey accurately (Carss & Parkinson 1996). The quantification of diet may also be improved by

assessing the relative size frequencies of the most commonly consumed prey species (Carss & Parkinson 1996), which was done here for crabs.

# REFERENCES

ARDEN-CLARKE, C.H.G. 1983. Population density and social organisation of the Cape clawless otter, *Aonyx capensis* Schinz, in the Tsitsikama Coastal National Park. M.Sc. thesis, University of Pretoria, Pretoria, South Africa.

ARDEN-CLARKE, C.H.G. 1986. Population density, home range size and spatial organization of the Cape clawless otter, *Aonyx capensis*, in a marine habitat. *Journal of Zoology, London* **209**: 201-211.

ARKELL, G.B.F. 1978. Aspects of the feeding and breeding biology of the giant kingfisher. *Ostrich* **50**: 176-181.

BEJA, P.R. 1996. Seasonal breeding and food resources of otters, *Lutra lutra* (Carnivora, Mustelidae), in south-west Portugal: a comparison between coastal and inland habitats. *Mammalia* **60**: 27-34.

BEJA, P.R. 1997. Predation by marine-feeding otters (*Lutra lutra*) in south-west Portugal in relation to fluctuating food resources. *Journal of Zoology, London* **242**: 503-518.

BRZEZIŃSKI, M., JĘDRZEJEWSKI, W. & JĘDRZEJEWSKA, B. 1993. Diet of otters (*Lutra lutra*) inhabiting small rivers in the Białowieża National Park, eastern Poland. *Journal of Zoology, London* **230**: 495-501.

BUTLER, J.R.A. 1994. Cape clawless otter conservation and a trout river in Zimbabwe: a case study. *Oryx* **28**: 276-282.

BUTLER, J.R.A. & DU TOIT, J.T. 1994. Diet and conservation of Cape clawless otters in eastern Zimbabwe. *South African Journal of Wildlife Research* **24**: 41-47.

CARSS, D.N. & PARKINSON, S.G. 1996. Errors associated with otter *Lutra lutra* faecal analysis. I. Assessing general diet from spraints. *Journal of Zoology, London* **238**: 301-317.

CARSS, D.N., ELSTON, D.A. & MORLEY, H.S. 1998. The effects of otter (*Lutra lutra*) activity on spraint production and composition: implications for models which estimate prey-size distribution. *Journal of Zoology, London* **244**: 295-302.

CARUGATI, C. 1995. Habitat, prey, and area requirements of otters (*Aonyx capensis* and *Lutra maculicollis*) in the Natal Drakensberg. M.Sc. thesis, University of Natal, Pietermaritzburg, South Africa

CHANIN, P. 1985. *The natural history of otters*. Facts on File Publications, New York.

CRAWLEY, M.J. & KREBS, J.R. 1992. Foraging theory. In: *Natural enemies: The population biology of predators, parasites and diseases,* (ed) M.J. Crawley, Blackwell Scientific publications, Oxford.

DANIELS, S.R., STEWART, B.A. & GIBBONS, M.J. 1999. Genetic structure among populations of *Potamonautes perlatus* (Decapoda: Potamonautidae) from the Olifants River system in the Western Cape, South Africa. *Journal of Zoology, London* **249**: 137-142.

DAVIES, B.R. & DAY, J.A. 1998. *Vanishing waters*. University of Cape Town Press, Cape Town.

DOLLOFF, C.A. 1993. Predation by river otters (*Lutra canadensis*) on juvenile coho salmon (*Oncorhynchus kisutch*) and Dolly Varden (*Salvelinus malma*) in southeast Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* **50**: 312-315.

EEKHOUT, S., KING, J.M. & WACKERNAGEL, A. 1997. *Classification of South African river, volume 1.* Department of Environment Affairs and Tourism, Pretoria.

EMLEN, J.M. 1966. The role of time and energy in food preference. *American Naturalist* **100**: 611-617.

ERLINGE, S. 1967. Food habits of the fish-otter, *Lutra lutra* L. in South Swedish habitats. *Viltrevy* **4**: 371-443.

ERLINGE, S. 1968. Food studies on captive otters *Lutra lutra* L.. *Oikos* **19**: 259-270.

ERLINGE, S., GÖRANSSON, G., HÖGSTEDT, G., JANSSON, G., LIBERG, G., LOMAN, L., NILSSON, I.N., VON SCHANTZ, T. & SYLVÉN, M. 1984. Can vertebrate predators regulate their prey? *American Naturalist* **123**: 125-133.

ESTES, J.A. 1989. Adaptations for aquatic living by carnivores. In: *Carnivore behavior, ecology and evolution,* (ed) J.L. Gittleman, Chapman and Hall, London.

ESTES, J.A. & PALMISANO, S.F. 1974. Sea otters: their role in structuring near shore communities. *Science* **185**: 1058-1060.

HARRISON, T.D. 1997. A preliminary survey of coastal river systems on the South African west coast, Orange River – Groot Berg, with particular reference to the fish fauna. *Transactions of the Royal Society of South Africa* **52**: 277-321.

HEGGBERGET, T.M. 1993. Marine-feeding otters (*Lutra lutra*) in Norway: seasonal variation in prey and reproductive timing. *Journal of the Marine Biological Association of the United Kingdom* **73**: 297-312.

HEGGBERGET, T.M. & Christensen, H. 1994. Reproductive timing in Eurasian otters on the coast of Norway. *Ecography* **17**: 339-348.

HEINECKEN, T.J.E., BICKERTON, I.B. & HEYDORN, A.E.F. 1983. *A Summary of Studies of the Pollution Input by Rivers and Estuaries Entering False Bay*. Council for Scientific and Industrial Research, Stellenbosch.

HELDER, J. & KER DE ANDRADE, H. 1997. Food and feeding habits of the neotropical river otter *Lontra longicaudis* (Carnivora, Mustelidae). *Mammalia* **61**: 193-203.

HILL, M.P. & O'KEEFFE, J.H. 1992. Some aspects of the ecology of the freshwater crab (*Potamonautes perlatus* Milne Edwards) in the upper reaches of the Buffalo River, eastern Cape Province, South Africa. *South African Journal of Aquatic Science* **18**: 42-50.

KEMENES, I. & NECHAY, G. 1990. The food of otters *Lutra lutra* in different habitats in Hungary. *Acta Theriologica* **35**: 17-24.

KING, J.M. 1983. Abundance, biomass and diversity of benthic macroinvertebrates in a Western CAPE river, South Africa. *Transactions of the Royal Society of South Africa* **45**: 11-34.

KREBS, C.J. 1985. *Ecology: The experimental analysis of distribution and abundance.* Harper and Row, New York.

KREBS, J.R. & KACELNIK, A. 1991. Decision making. In: *Behavioural ecology an evolutionary approach*, (eds) J.R. Krebs, & N.B. Davies, Blackwell Scientific Publications, Oxford.

KRUUK, H. 1995. *Wild otters: Predation and populations.* Oxford University Press, Oxford.

KRUUK, H. & CONROY, J.W.H. 1991. Mortality of otters (*Lutra lutra*) in Shetland. *Journal of Applied Ecology* **28**: 83-94.

KRUUK, H. & GOUDSWAARD, P.C. 1990. Effects of changes in fish populations in Lake Victoria on the food of otters (*Lutra maculicollis* Schinz and *Aonyx capensis* Lichtenstein). *African Journal of Ecology* **28**: 322-329.

KRUUK, H. & MOORHOUSE, A. 1990. Seasonal and spatial differences in food selection by otters (*Lutra lutra*) in Shetland. *Journal of Zoology, London* **221**: 621-637.

KRUUK, H., CONROY, J.W.H. & MOORHOUSE, A. 1987. Seasonal reproduction, mortality and food of otters (*Lutra lutra* L.) in Shetland. *Symposia of the Zoological Society of London* No. 58: 263-278.

KRUUK, H., CONROY, J.W.H. & MOORHOUSE, A. 1991. Recruitment to a population of otters (*Lutra lutra*) in Shetland, in relation to fish abundance. *Journal of Applied Ecology* **28**: 95-101.

KRUUK, H., TAYLOR, P.T. & MOM, G.A.T. 1997. Body temperature and foraging behaviour of the Eurasian otter (*Lutra lutra*), in relation to water temperature. *Journal of Zoology, London* **241**: 689-697.

KRUUK, H., CARSS, D.N., CONROY, J.W.H. & DURBIN, L. 1993. Otter (*Lutra lutra* L.) numbers and fish productivity in rivers in north-east Scotland. *Symposia of the Zoological Society of London* No. 65: 171-191.

KRUUK, H., KANCHANASAKA, B., O'SULLIVAN, S. & WANGHONGSA, S. 1994. Niche separation in three sympatric otters *Lutra perspicillata, L. lutra* and *Aonyx cinerea* in Huai Kha Khaeng, Thailand. *Biological Conservation* **69**: 115-120.

LANSZKI, J. & KÖRMENDI, S. 1996. Otter diet in relation to fish availability in a fish pond in Hungary. *Acta Theriologica* **41**: 127-136.

LIGTHART, M.F., NEL, J.A.J. & AVENANT, N.L. 1994. Diet of Cape clawless otters in part of the Breede River system. *South African Journal of Wildlife Research* **24**: 38-39.

LOWRY, L.F. & PEARSE, J.S. 1974. Abalones and sea urchins in an area inhabited by sea otters. *Marine Biology* **23**: 312-319.

MACARTHUR, R.H. & PIANKA, E.R. 1966. On optimal use of a patchy environment. *American Naturalist* **100**: 603-609.

MACLEAN, G.L. 1985. *Roberts' birds of southern Africa*. John Voelcker Bird Book Fund, Cape Town.

MASON, C.F. & MACDONALD, S.M. 1986. *Otters: ecology and conservation*. Cambridge University Press, Cambridge.

MEDINA, G. 1998. Seasonal variations and changes in the diet of southern river otter in different freshwater habitats in Chile. *Acta Theriologica* **43**: 285-292.

MELQUIST, W.E. & HORNOCKER, M.G. 1983. Ecology of river otters in west central Idaho. *Wildlife Monographs* **83**: 1-60.

NAYERUL HAQUE, M.D. & VIJAYAN, V.S. 1995. Food habits of the smooth Indian otter (*Lutra perspicillata*) in Keoladeo National Park, Bharatpur, Rajasthan (India). *Mammalia* **59**: 345-348.

NEL, J.A.J. & SOMERS, M.J. In press. The status of otters in Africa: an assessment. *Habitat* **13**:

OSTFELD, R.S. 1982. Foraging strategies and prey switching in the California sea otter. *Oecologia* **53**: 170-178.

PERRIN, M.R. & CARUGATI, C. 2000. Food habits of coexisting Cape clawless otter and spotted-necked otter in the KwaZulu-Natal Drakensberg, South Africa. *South African Journal of Wildlife Research* **30**: 85-92.

PERRY, G. & PIANKA, E.R. 1997. Animal foraging: past, present and future. *Trends in Ecology and Evolution* **12**: 360-364.

POWER, M.E., TILMAN, D., ESTES, J.A., MENGE, B.A., BOND, W.J., MILLS, L.S., DAILY, G., CASTILLA, J.C., LUBCHENCO, J. & PAINE, R.T. 1996. Challenges in the quest for keystones. *BioScience* **46**: 609-620.

PULLIAM, H.R. 1989. Individual behavior and the procurement of essential resources. In: *Perspectives in ecological theory,* (eds) J. Roughgarden, R.M. May, & S.A. Levin, Princeton University Press, Princeton.

PURVES, M.G. & SACHSE, B. 1998. *The utilization of freshwater crabs by co-existing otter* (Aonyx capensis *Schinz) and water mongoose* (Atilax paludinosus *Cuvier) in the Drakensberg, South Africa.* Unpublished report, University of Stellenbosch, Stellenbosch.

PURVES, M.G., KRUUK, H. & NEL, J.A.J. 1994. Crabs *Potamonautes perlatus* in the diet of the otter *Aonyx capensis* and water mongoose *Atilax paludinosus* in a freshwater habitat in South Africa. *Zeitschrift für Säugetierkunde* **59**: 332-341.

RAÜBENHEIMER, C.D. 1986. Aspects of the biology of the freshwater crab, *Potamonautes sidneyi*, with particular reference to general seasonality and female aggression. M.Sc. thesis, University of Natal, Durban, South Africa.

ROWE-ROWE, D.T. 1975. Biology of Natal mustelids. M.Sc. thesis, University of Natal, Durban, South Africa.

ROWE-ROWE, D.T. 1977a. Food ecology of otters in Natal, South Africa. *Oikos* **28**: 210-219.

ROWE-ROWE, D.T. 1977b. Variation in the predatory behaviour of the clawless otter. *Lammergeyer* **23**: 22-27.

ROWE-ROWE, D.T. 1978. The small carnivores of Natal. *Lammergeyer* **25**: 1-48.

ROWE-ROWE, D.T. & SOMERS, M.J. 1998. Diet, foraging behaviour and coexistence of African otters and the water mongoose. *Symposia of the Zoological Society of London* No. 71: 215-227.

SCHOENER, T.W. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics* **2**: 369-404.

SKELTON, P.H. 1993. A *complete guide to the freshwater fishes of southern Africa*. Southern Book Publishers, Halfway House.

SOMERS, M.J. 1996. Cape clawless otters associated with the Riviersonderend and Breede Rivers. In: *The Riviersonderend: Situation assessment, with specific reference to the effects of Tweewaterskloof Dam on the riverine ecosystem*, (eds) Ractliffe, G., Snaddon, K. & Brown, C. Department of Water Affairs and Forestry, Cape Town.

SOMERS, M.J. 2000a. Foraging behaviour of Cape clawless otters (*Aonyx capensis*) in a marine habitat. *Journal of Zoology, London* **252**: 473-480.

SOMERS, M.J. 2000b. Seasonal variation in the diet of Cape clawless otters (*Aonyx capensis*) in a marine habitat. *African Zoology* **35**: 261-268.

SOMERS, M.J. & NEL, J.A.J. 1995. Otters as biological indicators of freshwater systems in South Africa: project description and some preliminary results. *Habitat* **11**: 18-21.

SOMERS, M.J. & NEL. J.A.J. 1998. Dominance and population structure of freshwater crabs (*Potamonautes perlatus* Milne Edwards). *South African Journal of zoology* **33**: 31-36.

SOMERS, M.J. & PURVES, M.G. 1996. Trophic overlap between three syntopic semi-aquatic carnivores: Cape clawless otter, spotted-necked otter, and water mongoose. *African Journal of Ecology* **34**: 158-166.

STEWART, B.A. 1997. Morphological and genetic differentiation between populations of river crabs (Decapoda: Potamonautidae) from the Western Cape, South Africa, with a taxonomic re-examination of *Gecarcinautes brincki*. *Zoological Journal of the Linnean Society* **119**: 1-21.

TUMLISON, R. & KARNES, M. 1987. Seasonal changes in food habits of river otters in southwestern Arkansas beaver swamps. *Mammalia* **51**: 225-231.

TURNBULL-KEMP, P.ST.J. 1960. Quantitative estimations of populations of river crab, *Potamon (Potamonautes) perlatus* (M. Edw.), in Rhodesian trout streams. *Nature, London* **185**: 481.

VAN DER ZEE, D. 1979. Food and status of the Cape clawless otter (*Aonyx capensis* Schinz 1821) in the Tsitsikama Coastal National Park. M.Sc. thesis, University of Pretoria, Pretoria, South Africa.

VAN DER ZEE, D. 1981. Prey of the Cape clawless otter (*Aonyx capensis*) in the Tsitsikama National Park, South Africa. *Journal of Zoology, London* **194**: 467-483.

VERWOERD, D.J. 1987. Observations on the food and status of the Cape clawless otter *Aonyx capensis* at Betty's Bay, South Africa. *South African Journal of Zoology* **22**: 33-39.

WEBB, J.B. 1975. Food of the otter (*Lutra lutra*) on the Somerset levels. *Journal of Zoology, London* **177**: 486-491.

WEBER, J.-M. 1990. Seasonal exploitation of amphibians by otters (*Lutra lutra*) in north-east Scotland. *Journal of Zoology, London* **220**: 641-651.

# CHAPTER 3

# VARIATIONS IN, AND FACTORS AFFECTING, HOME RANGE PARAMETERS OF INDIVIDUAL CAPE CLAWLESS OTTERS (*AONYX CAPENSIS*)

## INTRODUCTION

The concept of and methods for determining home range have been much debated (e.g. Burt 1943; Jewell 1966; Jennrich & Turner 1969; Brown & Orians 1970; Brown 1975; Anderson 1982; Boulanger & White 1990; Gautestad & Mysterud 1995; Seaman & Powell 1996; Bothma *et al.* 1997). Home range is defined as the area an animal uses in its normal activities of food gathering, mating and caring for young (Burt 1943). Most animals do not use their entire home range with equal intensity and tend to occupy certain areas with greater frequency than others (Dixon & Chapman 1980). This implies a core area of concentrated activity (Samuel *et al.* 1985) that is used more frequently, and with greater regularity, than other parts of the home range (Jewell 1966).

Single species studies on home ranges have found home ranges to vary owing to, amongst others, differences in habitats (Geffen *et al.* 1992; Somers *et al.* 1994), food availability (Melquist & Hornocker 1983; Mills 1990), interspecific relationships (Rasa 1983), intraspecific relationships (Rasa 1986), time in residence (Conner *et al.* 1999) sex of the animal (Green *et al.* 1984; Somers *et al.* 1994; Gehrt & Fritzell 1997; Conner *et al.* 1999), age of the animal (Ralls *et al.* 1995), anthropogenic influences (Weber & Dailly 1998) and vegetation cover (Gese *et al.* 1988; Bothma *et al.* 1997). Home ranges of animals may also shift with time (Doncaster & Macdonald 1991). Estimates of home range size and movement patterns of individual animals are useful in determining population density, habitat use, energy requirements, and social structure (Sanderson 1966) that in turn allow estimates of the carrying capacity of available habitat. As territoriality (the

action of defending an area) greatly affects the spatial organisation of animal populations (Lack 1954; Wynne-Edwards 1962) it is important to determine if this occurs in populations. Home range and territoriality data are needed to help determine the amount of suitable habitat required, and to realise a complete conservation management plan for a species.

If territorial, animals are expected to move over the minimum economically defendable area (Pyke et al. 1977; Maher & Lott 1995), which also satisfies their metabolic needs (McNab 1963, 1980; Nagy 1987). Home range size and territory size of animals generally increase with body size and metabolic requirements (McNab 1963; Clutton-Brock & Harvey 1977; Gittleman & Harvey 1992; Grant et al. 1992), but decrease with an increase in habitat productivity (Macdonald 1983). Broad diet has been recognised as the most important factor influencing home range size (Grant et al. 1992). For example, carnivores typically have larger home ranges than omnivores or herbivores of the same size (Grant et al. 1992). A possible reason for observed differences in home range size could be that species with undefended home ranges are usually larger than territories (Grant et al. 1992). An explanation for males having larger home ranges than females may be linked to males' ranging behaviour being primarily governed by access to potential mates (Emlen & Oring 1977; Wrangham 1980; Macdonald 1983; Davies & Lundberg 1984; Clutton-Brock 1989; Gehrt & Fritzell 1998).

The resource dispersion hypothesis (RDH) (Macdonald 1983; Carr & Macdonald 1986) tries to explain, within the limits of all constraints, interspecific and intraspecific variation in territories and group sizes in ecological terms. The RDH predicts that spatial organisation will be determined by dispersion of resources (particularly food) and that group size will be determined by the richness of these patches when animals occupy the smallest economically defendable area (Macdonald 1983; Kruuk & Macdonald 1985; Carr & Macdonald 1986). For Cape clawless otters *Aonyx capensis,* resource patches are assumed to be reed beds *Phragmites australis*. This assumption is made in light of

the results of chapters 2 & 4, which shows that *A. capensis* prefer these areas for foraging and that their preferred prey are more abundant here than in other habitat types sampled. Also most freshwater fish species use submerged macrophytes in which to breed and hide (Skelton 1993). I therefore predict a variation of spatial organisation of *A. capensis* owing to a variation in the distribution of reed beds.

*Aonyx capensis* are widely distributed in sub-Saharan Africa (Rowe-Rowe & Somers 1998; Nel & Somers in press) and occur mainly in freshwater habitats such as rivers, marshes, lakes and dams where they eat predominantly freshwater crabs (*Potamonautes* spp.). In South Africa, and elsewhere in Africa, however, these freshwater habitats are under serious and increasing threat (Davies & Day 1998).

Arden-Clarke (1983, 1986) provided home range data for seven male otters (radio-tracking data) and one female otter (using recovery of $^{65}$Zn-labelled spraints) in a marine habitat. No data are available on the home range size of *A. capensis* in freshwater habitats. The data of Arden-Clarke (1983, 1986) indicate that *A. capensis* do not conform to the standard mustelid spacing patterns, which is to have intrasexual territories where males are territorial against males, females against females (perhaps including most recent offspring), with extensive overlap between sexes and male territories being larger than those of females (Powell 1979). It appears that *A. capensis* mostly forage alone but occur in groups of up to five (Rowe-Rowe 1978; Arden Clarke 1983; Somers 2000b (Chapter 6)).

This study provides data, using radio telemetry, on movement parameters of individual *A. capensis* in two Western Cape Province rivers. The main objectives of this study were:

1. To determine, for the first time, home range sizes and movement parameters of *A. capensis* in freshwater habitats.
2. To determine spatial organisation, density and group sizes of *A. capensis* in freshwater habitats.
3. To test the hypothesis that *A. capensis* in freshwater habitats do not conform to the typical mustelid spacing

pattern (Powell 1979), and 4) To test predictions based on a hypothesis (RDH of Macdonald 1983) relating otter dispersion to the distribution of resources.

## MATERIALS & METHODS

Data were collected in the Eerste (near Stellenbosch (33° 56' S, 18° 52' E)) and Olifants (near Clanwilliam (32° 11' S, 18° 23' E)) rivers in the Western Cape Province, South Africa.

The Eerste River is a rocky, narrow river, which begins in pristine conditions in the Jonkershoek Mountains, but then flows through agricultural, industrial and urban areas. Most of the Eerste River has a stony bed, and consists of runs, riffles and occasional deep pools (Brown & Dallas 1995). The flow rate is variable depending on rainfall, which mostly occurs in winter. It reaches the sea about 40 km from its source. It is disturbed for *ca* 90% of its length by agriculture, industry and the urban environment. The main crops are vines, fruit, and vegetables, all of which are subject to heavy applications of fertilizers, herbicides and pesticides (Heinecken *et al.* 1983). Winery effluents are either irrigated onto pasturelands or sent to the Stellenbosch sewage works. Treated effluent from these works is discharged into a tributary (Veldwagters River) of the Eerste River (Heinecken *et al.* 1983). During heavy rainfall events overflow of the sewage works occurs and untreated sewage flows into the river below Stellenbosch (personal observations). The Eerste River and a number of its tributaries flow through the town of Stellenbosch, and these receive all the storm water run-off from the town. Pollution levels and eutrophication increases rapidly below Stellenbosch. The treated sewage from the towns of Macassar, Somerset West and Strand is also discharged into the estuary of the Eerste River (Heinecken *et al.* 1983). The riparian vegetation along the lower part of the river is mostly the invasive alien, *Acacia mearnsii*. For a detailed classification

and description of the Eerste River see Brown & Dallas (1995) and Eekhout *et al.* (1997).

The Olifants River is 285 km long and has a catchment area of 46 220 km². The part of the Olifants River used in this study is dominated by two impoundments: the Clanwilliam and Bulshoek Dams. There are holiday camps along the edge of both impoundments and recreational boating, swimming, and fishing takes place. The length of river between the two impoundments is 17.6 km and it is bordered by cattle and crops. There is, however, little disturbance along the water edge where mostly alien *Eucalyptus* trees grow. Just above Bulshoek Dam the river is slow flowing, has a sandy bank with reed beds, bulrushes *Typha capensis* and occasional sedges *Cyperus* spp along the edge. The river below Bulshoek Dam is slow flowing with marshlands, oxbows, large basins, large reed beds, bulrushes, and rocky pools of up to 6 m deep. Except for recreational activities on the dam (mostly during weekends and the summer holidays), there is minimal disturbance. The area down to *ca* 15 km below Bulshoek Dam is not intensively farmed, except for some cattle farming, again resulting in very little disturbance. For a detailed classification of the Olifants River see Harrison (1997) and Eekhout *et al.* (1997).

Seven otters (Table 3.1) were caught in standard carnivore traps (800 X 800 X 1400 mm) as described by van der Zee (1979, 1982) and Arden-Clarke (1983, 1986). The traps were baited with either fish and/or fresh spraints from another area. Fish bait used in the Eerste River was rainbow trout *Oncorhynchus mykiss,* and in the Olifants River shallow-water hake *Merluccius capensis*. The otters were anaesthetized with ketamine hydrochloride (Ketalar 50 mg/ml Parke Davis). Radio transmitters (IMP/300/L, implantable transmitter, 40g, 80 x 20 mm diameter cylinder (Telonics Inc., Arizona, USA)) were implanted by a veterinary surgeon into the otters following the same procedures as described by McKenzie *et al.* (1990). The transmitters were left free floating in the abdominal cavity. A Telonics TR-4 receiver and multidirectional whip antenna were used to find the general

locality of the otters. The TR-4 receiver and a RA - 2A antenna were then used to find their position. Otter M1 was found dead four months after the transmitter was implanted. There were skin punctures, which appeared to be a result of another animal. On post-mortem there appeared to be no physical abnormality associated with the transmitter.

Continuous radio-tracking (Harris *et al.* 1990), with fixes being taken at 10 min intervals, was carried out. This was done at times of usual otter activity and periodically on a 24 hour basis. Activity was detected as fluctuations in signal strength. Whenever possible, otters were visually observed using 10x42 binoculars. A total of 1579 h was spent radio-tracking between 1993 and 1995 of which 851 h were of active otters (Table 3.1). Observations and radio-tracking were conducted from a vehicle and on foot. The otters were located by triangulation (usually from the vehicle) or tracking (on foot) the path of increasing signal strength to within *ca* 20 m of the animal or closer.

The study areas were divided into numbered, 100 m stretches of river, and these drawn on 1 : 50 000 topographical maps and 1 : 10 000 orthophotographs of the study area. The position of the otters was continuously recorded on tape.

Four measures of home range were determined: the total length, core length, total area and core area of river used by each otter. Areas were measured by multiplying the mean width of the river by 100 m by the number of sections that the otter used. Mean width was determined from the mean of the two ends of the 100 m section. The amount of overlap in home range lengths was determined. Following Kruuk & Moorhouse (1991), core areas for the otters were taken as the shortest stretch where each otter spent more than 50% of its time.

Although it may not be logical to compare otters living along marine coasts with those in rivers (Kruuk 1995) it would be interesting to note any differences. The total home range lengths and areas found along the Tsitsikama coast (Arden-Clarke 1983, 1986) were therefore statistically compared with the results from the present study.

The amount and distribution of preferred *A. capensis* habitat (reed beds) (Chapter 4) were measured in the otters' home ranges. These and body size of the otters (Table 3.1) were correlated to the various measures of home range size.

The number of reed beds and the mean distance to the nearest reed bed (patch distribution) was measured using the 1: 10 000 orthophotographs. Only reed beds large enough to be seen on the orthophotographs were counted. These were assumed to be large enough to be a significant source of food to the otters and were consistent over years. Reed beds that stretched over more than one 100 m section were counted as the number of sections over which they stretched.

Following Durbin (1996a), for each tracking session the rate of range use = L/T, and revisit index = D/L were measured. D is the total distance travelled by the otter during the session (including revisited areas), T is the time it spent active during the session and L is the length of range that it used. These movement parameters were correlated to the various measures of home range size.

To determine density of the otters along the Olifants River the detection of isotopes in spraints (isotope-based Lincoln Index), as used for European otters *Lutra lutra* (Durbin 1993; Kruuk *et al.* 1993), was used. One otter (F2) was injected with $^{65}$Zn. Fifty five spraints were collected within the following two weeks and tested for radioactivity. Thereafter the laboratory, which did the tests for me, unfortunately closed.

## RESULTS

### Home ranges

Except for otter F1, the range expansion over time radio-tracked shows that longer study periods would have had minimal effect on measured home range length (Fig. 3.1 & 3.2).

**Table 3.1.** Radio-tracking of Cape clawless otters *Aonyx capensis* in the (a) Eerste and (b) Olifants Rivers, Western Cape Province, South Africa. M = male; F = female.

| Animal | Tracking dates (day/mon/yr) | Tracking period (h) | Otter activity (h) | Sessions tracked partial | complete | total |
|---|---|---|---|---|---|---|
| **(a)** | | | | | | |
| M1 (12.2 kg sub-adult) | 20/07/93 – 16/11/93 | 216 | 140 | 46 | 22 | 48 |
| F1 (10 kg adult) | 10/08/93 – 13/08/93 | 25 | 11 | 4 | 2 | 6 |
| M2 (18 kg adult) | 18/02/94 – 20/07/94 | 246 | 57 | 48 | 33 | 82 |
| **(b)** | | | | | | |
| M3 (14 kg adult) | 24/03/94 – 05/12/94 | 189 | 105 | 33 | 12 | 45 |
| M4 (14 kg adult) | 23/04/94 – 13/05/95 | 208 | 123 | 28 | 20 | 48 |
| F2 (11.5 kg adult) | 18/05/94 – 12/04/95 | 447 | 248 | 61 | 49 | 110 |
| F3 (10 kg adult) | 22/11/94 – 31/08/95 | 248 | 167 | 28 | 18 | 46 |
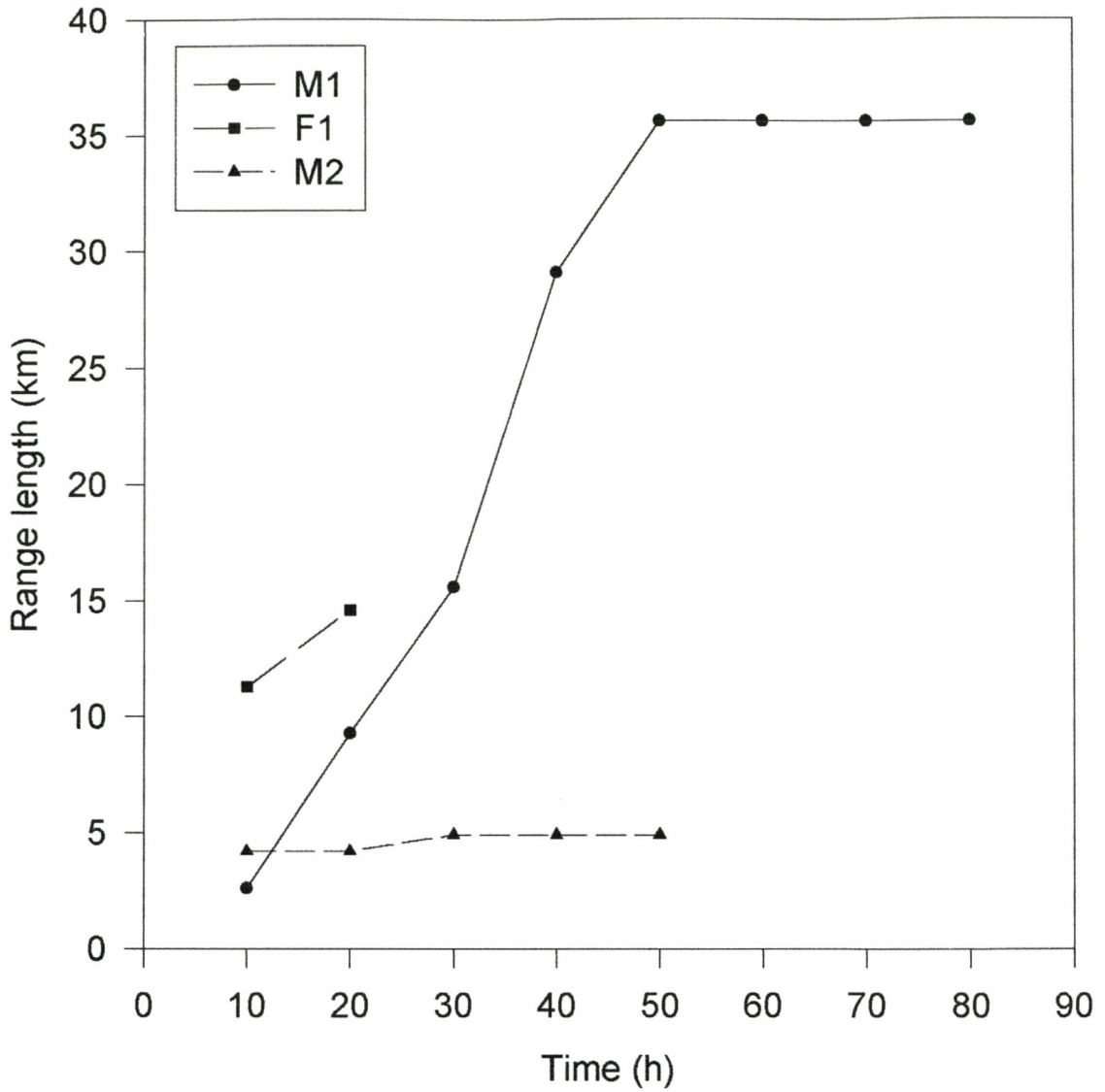
**Fig. 3.1.** Cumulative home range length against time radio-tracking active Cape clawless *Aonyx capensis* otters in the Eerste River.
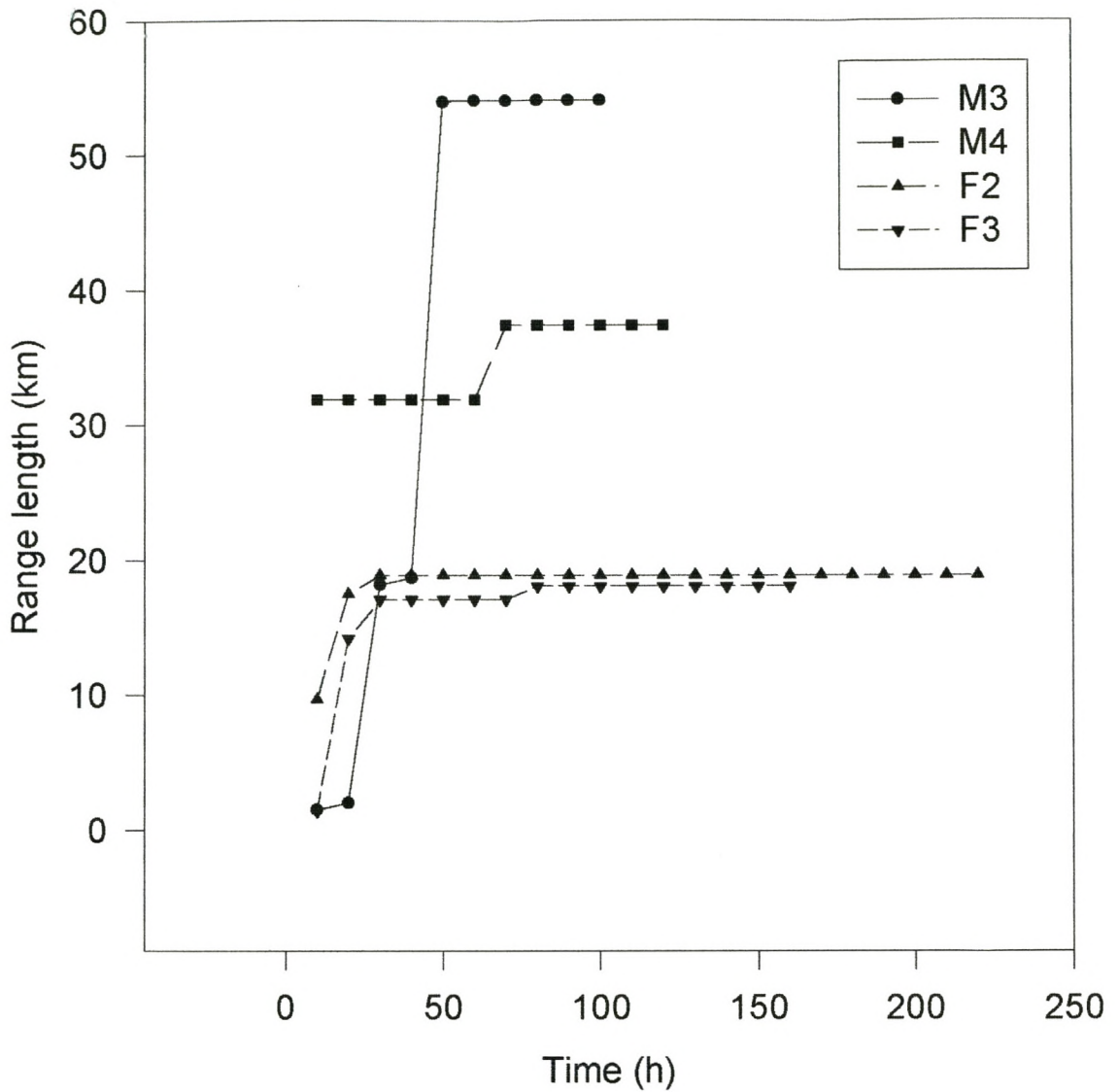
**Fig. 3.2.** Cumulative home range length against time radio-tracking active Cape clawless otters *Aonyx capensis* in the Olifants River.

The otters were never seen or radio-located more than *ca* 5 m away from water. Total home range length varied from 4.9 to 54.1 km, and core home range length varied from 0.2 to 9.8 km (Table 3.2; Fig. 3.1 & 3.2). Total home range area varied from 4.9 to 1062.5 ha, while core home range area varied from 1.1 to 138.9 ha. The total and core home ranges of otter M2 were short (4.9 & 0.2 km respectively) and small (4.9 & 1.1 ha respectively) mainly owing to his habit of leaving his resting place and moving *ca* 200 m to a floating rainbow trout tank from which he fed almost exclusively. Excluding otter M2 from the analyses below, the total home range length of males was significantly longer than that of females ($t$ = 4.17, d.f. = 4, $P$ = 0.014) (Table 3.2).

This was not the case with core home range length ($t$ = 2.04, d.f. = 4, $P$ = 0.11, power of test with alpha = 0.275) (As the power of this test was below the desired 0.8 the negative finding should be interpreted with caution. This applies to other tests where the power of the test is given and is below 0.8).

Males and females did not have significantly different sized total or core home range areas (total area: $t$ = 1.11, d.f. = 4, $P$ = 0.331, power of test = 0.07) (core area: $t$ = 1.30, d.f. = 4, $P$ = 0.265, power of test = 0.01) (Table 3.2). Combining sexes, total and core home range lengths were not significantly different between the Eerste and Olifants Rivers (total home range length: $t$ = -0.49, d.f. = 4, $P$ = 0.651, power of test with alpha = 0.05) (core home range length: $t$ = -1.69, d.f. = 4, $P$ = 0.166, power of test with alpha = 0.182) (Table 3.2). However, otters in the Olifants River using the Clanwilliam and Bulshoek dams as part of their home ranges occupied areas that were much larger (mean = 416.5, range = 119.8-1062.5 ha) than those in the Eerste River (mean = 16.9, range = 4.9-32.0 ha). Despite this, total and core home range areas were not significantly different between the Eerste and Olifants Rivers (total home range area: Mann-Whitney $U$ = 12, d.f. = 6, $P$ = 0.06) (core home range area: Mann-Whitney $U$ = 12, d.f. = 6, $P$ = 0.06) (Table 3.2). Total home ranges of the radio-tracked male otters in both rivers overlapped considerably.

**Table 3.2.** Various measures of home range size of Cape clawless otters *Aonyx capensis* in the (a) Eerste and (b) Olifants Rivers, Western Cape Province, South Africa.

| River<br>Animal | Total length<br>(km) | Core length<br>(km) | Total area<br>(ha) | Core area<br>(ha) |
|---|---|---|---|---|
| **(a)** | | | | |
| M1 | 35.6 | 3.7 | 32.0 | 3.9 |
| F1 | 14.6 | 1.0 | 13.8 | 1.3 |
| M2 | 4.9 | 0.2 | 4.9 | 1.1 |
| **(b)** | | | | |
| M3 | 54.1 | 9.8 | 1062.5 | 138.9 |
| F2 | 18.9 | 4.2 | 200.3 | 63.0 |
| M4 | 37.4 | 7.9 | 283.5 | 129.6 |
| F3 | 18.1 | 3.6 | 119.8 | 25.2 |
| Mean sizes: | 26.2 | 4.3 | 245.3 | 51.9 |

The males also overlapped the total home range lengths of the females. Core home range lengths of males overlapped with other males and females but the two female core home ranges in the Olifants River only overlapped with one 100 m section (Fig. 3.3 & 3.4; Table 3.3). Despite the spatial overlap (Table 3.3) between the total home ranges of otters F2 and F3, no temporal overlap occurred in the section common to both.

Otters F1 and M1 used the Eerste River in the urban environment of Stellenbosch town. All the otters used human disturbed parts of the Eerste and Olifants Rivers and Clanwilliam and Bulshoek dams, which were in their home ranges. As there was a significant difference in total home range lengths between males and females in the present study only males were compared with those of Arden-Clarke (1983, 1986). There was a significant difference between the total home range lengths of males between the two habitats (t = -2.66, d.f. = 8, $P$ = 0.03). As there was no significant difference between the total home range areas of males and females in the present study, these data were pooled and compared with those of Arden-Clarke (1983, 1986). There was no significant difference between total home range areas of the otters living in the marine environment of Tsitsikama and those in the present study area.

Members of both sexes foraged and rested independently of others. Only once did tracked otters spend time together. Otters F3 and M4 were together from 15:00 to 21:50 on 14 March 1995. They were resting together from at least 15:00 until 19:10 after which they were foraging together until 21:50. At 10:20 on 2 November 1994 otter M4 was seen swimming in one of the large deep pools below Bulshoek Dam. With him were five other otters. They did not appear to be foraging, but swimming and diving together. At 11:40 another two otters approached from upriver. The otters vocalised with whistles and squeaks while swimming rapidly around each other. They all moved off into a reed bed and were not seen again. At 12:20, two otters (presumably the two that had just arrived) swam out of the reeds and went off.
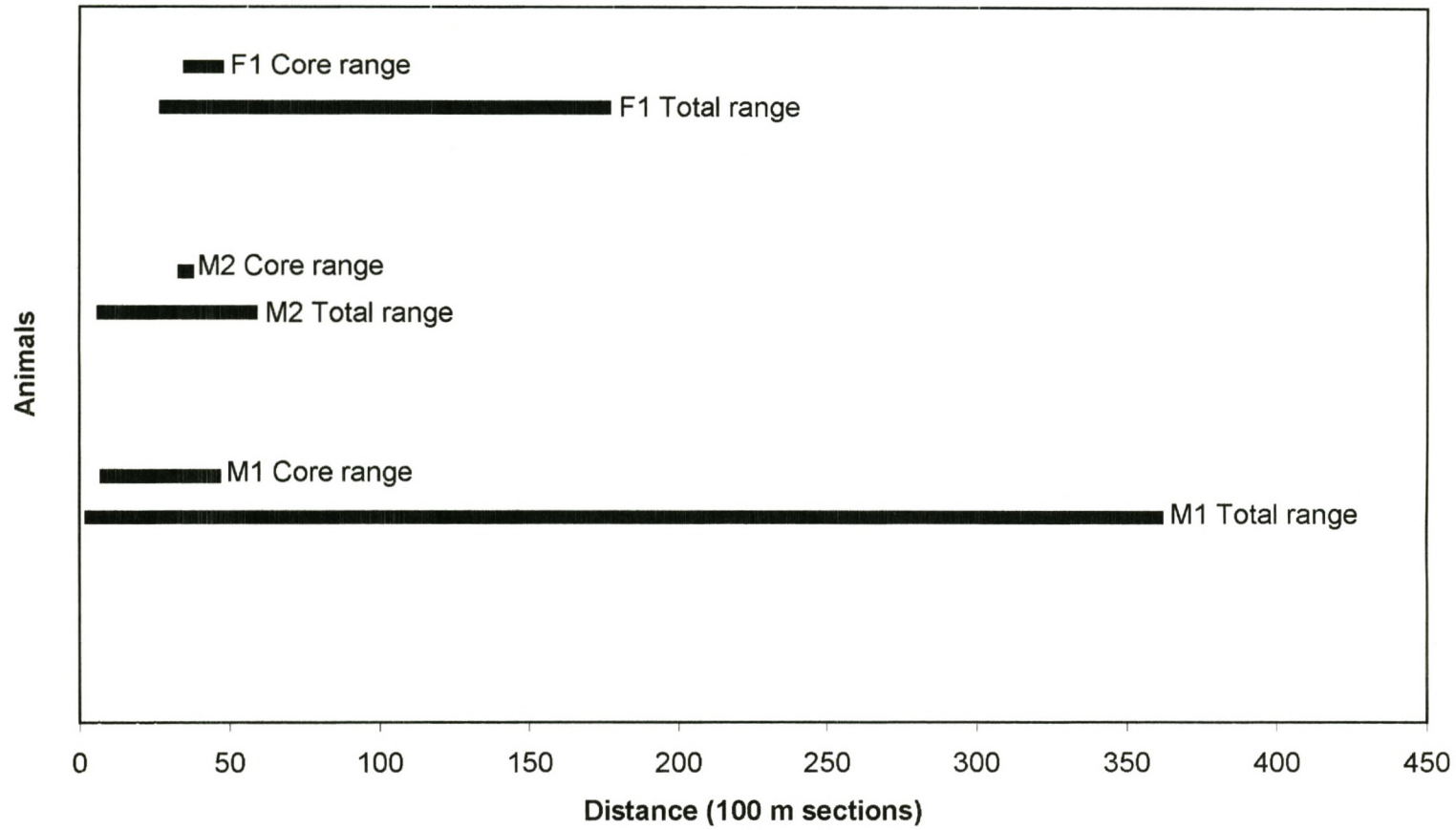
**Fig. 3.3.** Total home range, core ranges and home range overlap of three radio-tracked Cape clawless otters *Aonyx capensis* in the Eerste River, Western Cape Province, South Africa.
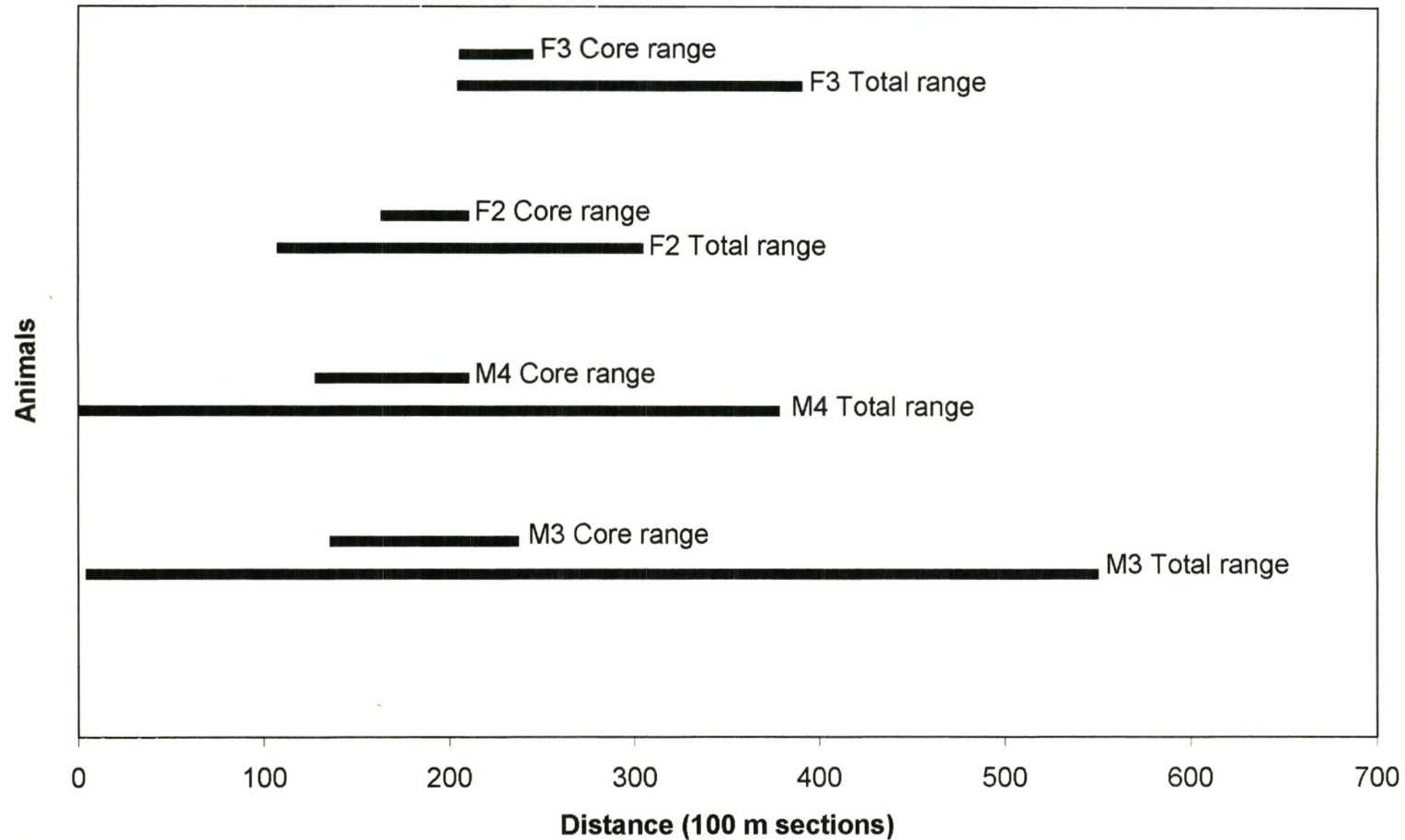
**Fig. 3.4.** Total home range, core ranges and home range overlap of four radio-tracked Cape clawless otters *Aonyx capensis* in the Olifants River, Western Cape Province, South Africa.

**Table 3.3.** The spatial overlap of linear home ranges (total and core) between individual Cape clawless otters *Aonyx capensis* in the (a) Eerste and (b) Olifants Rivers, Western Cape Province, South Africa.

| River Animals | Total home range length (km) | (%:%) | Core home range length (km) | (%:%) |
|---|---|---|---|---|
| **(a)** | | | | |
| M1:F1 | 14.6 | 41.0:100.0 | 0.9 | 24.3: 90.0 |
| M1:M2 | 4.9 | 13.8:100.0 | 0.2 | 5.4:100.0 |
| M2:F1 | 2.8 | 19.2: 57.1 | 0.0 | |
| **(b)** | | | | |
| M3:F2 | 18.9 | 34.9:100.0 | 4.2 | 42.9:100.0 |
| M3:F3 | 18.1 | 33.5:100.0 | 3.6 | 36.7:100.0 |
| M3:M4 | 37.0 | 68.4: 98.9 | 7.1 | 72.4: 89.9 |
| F2:F3 | 9.5 | 50.3: 52.5 | 0.1 | 2.4: 2.8 |
| M4:F2 | 18.9 | 100.0: 50.5 | 4.2 | 53.2:100.0 |
| M4:F3 | 16.9 | 54.8: 93.4 | 0.1 | 1.3: 2.8 |

From their size they appeared to be a female and a cub. The signal of otter M4 showed he was resting from 13:00. Otter M4 was not seen the next day but remained in the area. Excluding radio-tracked otters, single otters were seen more often than groups of otters (Fig. 3.5).

When observed, the otters appeared to use only the edges of the rivers and dams and short distances in from the edges in which to forage. They occasionally crossed to the opposite side, both in the rivers and dams. Radio-tracked otters were never observed foraging in tributaries of either river. Otter F2 (Olifants River) and M1 (Eerste River), however, had resting places short distances up tributaries.

Spraints were not found near these resting places but were found at the mouths of the tributaries. The otters in the Eerste River used a small tributary to access the trout dams in the trout farm, where they foraged.

As expected, there was significantly (Mann Whitney $U = 0$, d.f. = 13, $P < 0.001$) more reed beds in the total areas (mean = 76.1, S.E. = 25.33, range = 20-175), than in the core areas (mean = 7.43, S.E. = 1.57, range = 2-13) (Table 3.4). There was, however, no significant difference (Mann Whitney $U = 21$, d.f. = 13, $P = 0.71$) in the mean reed bed nearest neighbour either in the total ranges (mean = 276.0, S.E. = 70.9, range = 100-679 m), or in the core areas (mean = 287.6, S.E. = 100.86, range = 100-786 m) (Table 3.4).

There were no significant correlations between any of the measures of home range size and body weight (Table 3.5).

There was a highly significant correlation between the numbers of reed beds and total length and total area used (Table 3.5). The mean reed bed nearest neighbour was correlated to total home range length but none of the other measures of home range size (Table 3.5).
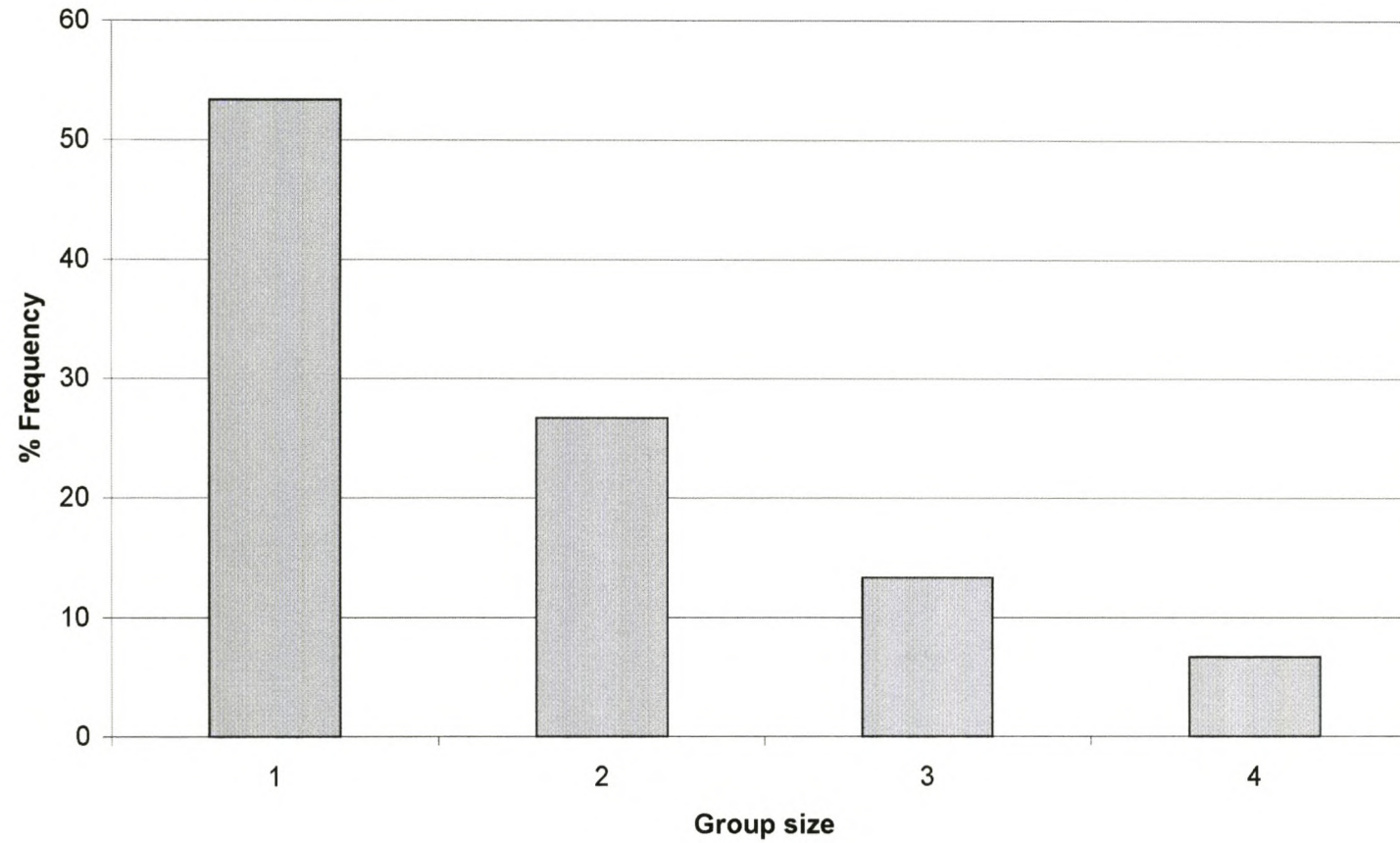
**Fig. 3.5.** The percentage frequency distribution of group size classes of Cape clawless otters *Aonyx capensis* seen in the Olifants ($n = 13$) and Eerste Rivers ($n = 2$), Western Cape Province, South Africa, between July 1993 and August 1995.

**Table 3.4.** The number of reed beds and mean reed bed nearest neighbour distance in the total and core home range areas of individual Cape clawless otters Aonyx *capensis* in the (a) Eerste River and (b) Olifants River, Western Cape Province, South Africa.

| Animal (home range type) | No reed beds | Mean (± S.E.) nearest neighbour distance (m) |
|---|---|---|
| (a) | | |
| M1 (Total) | 49 | 679.2 ± 300.9 |
| M1 (Core) | 13 | 100 ± 0.0 |
| F1 (Total) | 23 | 220.8 ± 120.8 |
| F1 (Core) | 10 | 100 ± 0.0 |
| M2 (Total) | 20 | 100 ± 0.0 |
| M2 (Core) | 2 | 100 |
| (b) | | |
| M3 (Total) | 175 | 278.9 ± 56.7 |
| M3 (Core) | 10 | 470.0 ± 144.6 |
| M4 (Total) | 169 | 168.0 ± 35.85 |
| M4 (Core) | 7 | 785.7 ± 430.1 |
| F2 (Total) | 61 | 262.5 ± 78.6 |
| F2 (Core) | 2 | 100 |
| F3 (Total) | 36 | 222.2 ± 73.2 |
| F3 (Core) | 8 | 357.1 ± 110.0 |

**Table 3.5.** Spearman rank correlations between various measures of home range size and body weight, preferred habitat (reed bed) patch number and dispersal (mean nearest neighbour distance between reed beds) for seven Cape clawless otters *Aonyx capensis*.

| Variable | Total length | | Core length | | Total area | | Core area | |
|---|---|---|---|---|---|---|---|---|
| | $r$ | $P$ | $r$ | $P$ | $r$ | $P$ | $r$ | $P$ |
| Body weight (kg) | 0.04 | 0.91 | 0.09 | 0.78 | 0.00 | 0.97 | 0.00 | 0.97 |
| No reed beds | 0.89 | <0.001 | 0.11 | 0.78 | 0.93 | <0.001 | 0.67 | 0.10 |
| Mean nearest neighbour | 0.79 | 0.03 | 0.49 | 0.22 | 0.50 | 0.22 | 0.59 | 0.12 |

Total home range length and core home range length were correlated ($r$ = 0.96, $n$ = 7, $P$ < 0.001). However, core length was correlated with number of reed beds in the total length ($r$ = 0.96, $n$ = 7, $P$ < 0.001) but not with number of reed beds in the core length (Table 3.5).

## Density

Of the 55 spraints collected and tested for the presence of $^{65}$Zn, three (5.45%) proved positive. These spraints were collected from 12 km of the Olifants River. With these few data the density of otters was estimated to be 1.53 otters per km.

## Movement parameters

The furthest an otter was recorded moving in one activity session was 10.5 km (otter M1). This was continuous movement by the otter from above Stellenbosch to below the town. The longest activity session lasted 11.7 h (otter F2). The otters were active from dawn for 2.6 (S.E. = 0.1) h and moved a mean of 0.9 (S.E. = 0.1) km during this period, i.e. a mean of 350 m/h. They were also active from sunset for a mean of 2.3 (S.E. = 0.1) h moving a mean of 1.3 (S.E. = 0.2) km, i.e. 565 m/h. There was no significant difference in the length of home range used between morning and evening activity bouts (Mann-Whitney $U$ = 2951, d.f. = 155, $P$ = 0.85). However, the otters were active significantly longer during the morning than during the evening sessions (Mann-Whitney $U$ = 4881, d.f. = 155, $P$ = 0.013). Distance travelled per session varied from a mean of 0.4 to 2.8 km between individuals (Table 3.6), and the mean activity periods from 1.6 to 3.1 h (Table 3.6).

Kruskal-Wallis One Way Analysis of Variance on Ranks showed a significant difference in time active among individual otters ($H$ = 36.84, d.f. = 6, $P$ < 0.001). An all pairwise multiple comparison (Dunn's method) isolated otter M2 as the individual to be less active than the other otters. Otter M2 was the otter that fished almost exclusively for trout (see above).

**Table 3.6.** Mean distances moved and activity periods of individual Cape clawless otters *Aonyx capensis* during complete tracking sessions in the (a) Eerste and (b) Olifants Rivers, Western Cape Province, South Africa. Means are given ± standard error. Ranges are given in parenthesis.

| River | | | Activity session | |
|---|---|---|---|---|
| Animal | | *n* | Distance (km) | Activity period (h) |
| (a) | | | | |
| | M1 | 22 | 1.5 ± 0.6 (0.1-10.5) | 2.6 ± 0.2 (0.7-3.8) |
| | F1 | 2 | 1.0 ± 0.1 (0.9-1.1) | 2.3 ± 1.2 (1.2-3.5) |
| | M2 | 33 | 0.4 ± 0.1 (0.1-1.6) | 1.6 ± 0.1 (1.0-3.0) |
| (b) | | | | |
| | M3 | 12 | 2.8 ± 0.8 (0.5-9.4) | 2.3 ± 0.2 (1.3-3.3) |
| | F2 | 49 | 1.2 ± 0.3 (0.1-6.0) | 2.7 ± 0.3 (0.3-11.7) |
| | M4 | 20 | 1.4 ± 0.3 (0.1-4.0) | 3.1 ± 0.2 (2.0-4.7) |
| | F3 | 18 | 0.6 ± 0.1 (0.1-1.6) | 2.2 ± 0.2 (0.8-3.3) |
| | All | 156 | 1.2 ± 0.1 | 2.4 ± 0.1 |

Excluding M2 there was no significant difference between individuals with regards time active ($H$ = 9.97, d.f. = 6, $P$ = 0.126).

Range use rate varied between 0.2 and 1.2 km/h between individuals (Table 3.7). There was a significant difference between range use rate among individuals ($H$ = 19.7, d.f. = 6, $P$ = 0.003). An all pairwise multiple comparison isolated otter M3 as the individual to differ from the others with regards range use rate.

Revisit index varied between 1.0 and 1.7 among individuals (Table 3.7). There was a significant difference in the revisit index among individual otters ($H$ = 44.2, d.f. = 6, $P$ < 0.001). An all pairwise multiple comparison isolated otter M2 as the individual to differ from the others with regards the revisit index.

Table 3.8 provides the Spearman correlations between the movement parameters and the various measures of home range size. There was a significant correlation between distance travelled and the total and core home range lengths. Total home range length was correlated to range use rate. The other correlations were not significant (Table 3.8).

## DISCUSSION

The most striking result found was the long total home ranges used by some of the males. Otter home ranges are, however, probably better expressed as area of water used (Kruuk & Moorhouse 1991; Kruuk 1995). Although it is convenient to measure otter home ranges in terms of length, comparisons with other areas should be made with caution (Kruuk & Moorhouse 1991). From the results and following discussion it is evident that the use of both home range length and home range area are appropriate in analysing home range of *A. capensis*.

**Table 3.7.** Movement parameters of individual Cape clawless otters *Aonyx capensis* otters in the (a) Eerste and (b) Olifants Rivers, Western Cape Province, South Africa. Means are given ± standard error. Ranges are given in parenthesis.

| Animal | n | Mean range use rate (km/h) | Revisit index km/km |
|--------|-----|----------------------------|---------------------|
| (a) | | | |
| M1 | 22 | 0.5 ± 0.2 (0.1-3.4) | 1.3 ± 0.2 (1.0-5.0) |
| F1 | 2 | 0.5 ± 0.2 (0.3-0.8) | 1.0 ± 0.0 (1.0-1.0) |
| M2 | 33 | 0.2 ± 0.0 (0.1-1.1) | 1.7 ± 0.1 (1.0-2.0) |
| (b) | | | |
| M3 | 12 | 1.2 ± 0.2 (0.3-2.8) | 1.2 ± 0.1 (1.0-1.5) |
| F2 | 49 | 0.4 ± 0.1 (0.0-1.8) | 1.2 ± 0.1 (0.1-2.2) |
| M4 | 20 | 0.5 ± 0.1 (0.0-1.7) | 1.0 ± 0.0 (1.0-1.1) |
| F3 | 18 | 0.3 ± 0.1 (0.0-0.8) | 1.2 ± 0.1 (1.0-2.0) |

**Table 3.8.** Spearman rank correlations between various measures of home range size and movement parameters of seven Cape clawless otters *Aonyx capensis*.

| Variable | Total length | | Core length | | Total area | | Core area | |
|---|---|---|---|---|---|---|---|---|
| | $R$ | $P$ | $r$ | $P$ | $R$ | $P$ | $r$ | $P$ |
| Time active | 0.63 | 0.09 | 0.67 | 0.07 | 0.56 | 0.15 | 0.56 | 0.15 |
| Distance travelled | 0.93 | <0.001 | 0.86 | 0.006 | 0.71 | 0.05 | 0.71 | 0.05 |
| Range use rate | 0.78 | 0.03 | 0.70 | 0.05 | 0.59 | 0.12 | 0.59 | 0.12 |
| Revisit index | -0.26 | 0.55 | -0.34 | 0.44 | -0.41 | 0.30 | -0.41 | 0.30 |

As in *L. lutra* (Kruuk 1995) and other species (references given in the introduction) spatial organisation of *A. capensis* is expected to be variable. Even within broadly similar habitats there is considerable intraspecific variation in carnivore home range sizes (Macdonald 1983). The large variation in area used in the two rivers may be a result of *A. capensis* not using large surface areas for foraging, but mostly the edges of dams and rivers. It is unclear why they did not use the central parts of the dams. It may simply be too deep for the otters, or there were fewer crabs further away from the edge (Chapter 2). Although crab density was higher in the Olifants River than in the Eerste River (Chapter 2) home ranges were smaller (although not significantly so) in the Eerste River. Increased prey would be expected to affect group size but not home range size (Macdonald 1983). I did not have enough sightings of otters in the Eerste River to statistically test if there were differences between group sizes in the two rivers. The prediction of the RDH that group size increases with increased richness of resources is supported by the data of Perrin *et al*. (2000). They found that in an area where food from the river was supplemented by dams artificially stocked with trout 70% of groups seen comprised 3 or more otters (*n* = 73), whereas at Stillerust (river, reed beds, oxbows) 77% comprised 2 Otters and 3 were seen on only two occasions (*n* = 31). The RDH also takes resource dispersion into account. From the RDH we would predict that home range size increases with increased dispersal of reed beds, which is what was found for total length of rivers used by the otters. The fact that the otters did not use most of the dam's surface may explain why the correlations for the other home range areas were not significant.

As in *L. lutra* in Scotland (Kruuk 1995; Durbin 1996a, 1996b) males of *A. capensis* used longer home ranges than females. Kruuk (1995) stated that as male *L. lutra* are 1.5X heavier than females this alone might explain the difference in home range sizes between the sexes (McNab 1963; Clutton-Brock & Harvey 1977; Grant *et al*. 1992). As intersexual differences in social behaviour and spacing behaviour are common in mammals (Wilson 1975; Crook *et*

*al.* 1976) they are not unexpected here. The reasons may vary but size of species, diet or dispersal of resources may all affect the various species. There was, however, no relationship between body size and home range size for the otters in the present study. Other explanations must therefore be explored. As both sexes of *A. capensis* appear to have similar diets I would not expect diet to affect intersexual home range size of *A. capensis*. The variation in intersexual home range size may be a result of undefended home ranges usually being larger than defended home ranges (Grant *et al.* 1992). Total home ranges of the radio-tracked otters in the two rivers overlapped considerably between and within sexes, which with the finding that home ranges of otters F2 and F3 were exclusive when they were radio-tracked concurrently and only shared one 100 m section of core length, is evidence that they have evolved a variation of the typical mustelid spacing pattern as described above (Powell 1979). The pattern of female home ranges is suggestive of territoriality. Although there was no evidence for the areas being defended, thus being territories as defended areas (Burt 1943), the areas were exclusive (Schoener 1968). Kruuk (1995) described turnaround points or boundaries for female spatial groups. Although this may be the case with *A. capensis*, I never saw another female in the core areas of otters F2 or F3. More direct radio-tracking data and direct observations would be needed to determine if the females were defending their home ranges. If, however, the females are territorial, as seems likely, and have defended home ranges, there would be a cost to defending a home range and the smaller the home range the smaller the cost. As other females would be excluded, there would be fewer competitors in the range. The home ranges could therefore be smaller than those of the males, who have to share with other males and females. Some evidence against this explanation, however, is that core lengths or areas were not significantly different between sexes, which are what females appear to be defending.

As members of both sexes of *A. capensis* tended to forage and rest independently of other adults, this study supports the notion that *A. capensis* are solitary. Most species of carnivores are, however, solitary, with single females defending territories against other females, and single males using larger areas, which overlap the ranges of several females but exclude other males (Kruuk & Macdonald 1985). In Somers (2000b) (Chapter 6), the largest foraging group observed consisted of three individuals, which is less than found by Arden-Clarke (1983) who recorded three groups of four and one group of five ($n = 67$). The results found here were more consistent with those found by Arden-Clarke (1983) than those found by Somers (2000b (Chapter 6)). These data suggest that *A. capensis* have similar group structures in the rivers and marine habitats so far investigated.

The fact that body size and home range size was not correlated and that males had larger home ranges than females, indicates that home ranges of males were larger than needed to meet energetic requirements, suggesting that distribution of females may be important in the spacing of the males. As female *A. capensis* appear to be spread out, males are expected not to compete and therefore not form male alliances as happens in some other carnivores (e.g. Cheetah (Caro 1994)). The males with overlapping home ranges may be co-operating in defending a home range with many females. Each male by himself may not be able to patrol the area and keep it scent-marked adequately. This would, however, only happen if there was no shortage of females. They may, however, not be co-operating but the costs to each of expelling the others may be too great (Macdonald & Carr 1989). This may select for the formation of male group home ranges. If this were the case we would expect group size to decrease in habitats with decreased prey richness.

*Lutra lutra* females and males overlap with no territories in either sex (Kruuk & Moorhouse 1991; Kruuk 1995). Female core areas were, however, like *A. capensis*, exclusive. However, in *L. lutra* there were exclusive group ranges. There has not been

enough female *A. capensis* radio-tracked to determine if this is also the case with this species.

The data of Arden-Clarke (1986) suggest the existence of a clan-type social organization. Kruuk (1978) described a clan as a group of animals (he uses badgers *Meles meles*) jointly inhabiting an area where females may use only part of that area. Data are at present too few to elucidate this. Broadly, the males may have empires and the females may have enclaves (Kruuk & Macdonald 1985).

The spatial organization I have described where males overlap males, possibly forming male group ranges, and males overlap many females, with the females being possibly territorial is common in mustelids (Powell 1979). This intraspecific variation in spatial patterns within my study animals, as well as those of Arden-Clarke (1996), is consistent with the general mammalian spatial patterns as described above.

Similar to this study, the size of badger territories is closely correlated with the distance between feeding patches (Kruuk & Parish 1982) (reed beds in the present case). The number of badgers per clan was correlated with the biomass of earthworms per territory and with the biomass of earthworms per field or patch (Kruuk & Parish 1982). I could not determine prey richness but would predict from the RDH that the number of males in a range would be less where prey richness is less.

Male North American river otters *Lutra canadensis* have been suggested to move in groups of males ('bachelor groups') or in home range groups (Melquist & Hornocker 1983; Larsen 1983 cited in Kruuk 1995). In the often-sympatric *L. maculicollis* there is intrasexual and intersexual overlap in home ranges (Perrin *et al.* 2000) but the existence of group home ranges is uncertain.

The largest male otter (M2) was expected to have the largest home range. His use of the abundant trout in the trout tank, however, enabled him to use only a small home range. This observed small home range of M2 therefore suggests that the benefits of an abundant food resource was possibly, at least during the time radio-tracked, more beneficial to it than

covering as large an area as possible to gain access to many females.

There appears to be some differences between the coastal living otters and those living in freshwater, at least in total home range lengths of males. Rowe-Rowe (1992) predicted that as coastal-living freshwater otters occur at higher densities in the marine environment (Estes 1989) the same would apply to *A. capensis* and they would have greater area requirements in a freshwater system. This appears not to be the case. The otters in fresh water had longer, but not larger home ranges. Arden-Clarke (1993) estimated that the otters he studied never foraged more than 100 m from the coast. Whether they use all 100 m equally, however, is unknown. The presence of the large Bulshoek and Clanwilliam Dams in the Olifants River almost certainly caused the home range areas in the present study to be inflated. The Tsitsikama marine reserve is probably more productive than the two rivers, which could explain the different home range lengths. Food patches may also be closer together in the marine environment, which could explain the smaller home ranges. The comparison between home range parameters of marine and freshwater environments therefore remains inconclusive.

Other otter species have varying home range sizes. In freshwater habitats in northeast Scotland the much smaller *L. lutra* have been found to have a mean home range length of 34.8 km for males (*n* = 6) and 20.0 km for females (*n* = 2, range = 18.2-84.4 km) (Durbin 1993, 1996a, 1996b; Kruuk 1995). Another study found them to range over distances of 39.1 km for a male and 18 km for females (*n* = 2) (Green *et al.* 1984). Core lengths of *L. lutra* vary from 5.4-38.0 km (Durbin 1993, 1996a). A young male and adult female were radio-tracked in Spain for 20.7 and 11.8 km respectively (Ruiz-Olmo *et al.* 1995). Home range areas range from 66.5-276.3 ha (Green *et al.* 1984) and 10.2-35.6 ha (Durbin 1996a). *Lutra canadensis* have total home range lengths from 10-81 km (mean = 39.8, S.E. = 4.0) (Melquist & Hornocker 1983). Spotted-Necked otters *Lutra maculicollis* which occur in South Africa, but not the Western Cape, and which are mostly

piscivorous (Rowe-Rowe & Somers 1998) have total home range lengths with a mean of 14.8 km (range = 6.9-23.2 km), home range areas of 114.0-1714.0 ha and core areas of 100.0-941.0 ha (Perrin *et al.* 2000). The home range areas were, however, 100% Minimum Convex Polygon measures. As this included more land than water it cannot be used for comparisons for the other measures of home range areas used here and in the other studies cited. Four radio-tracked smooth-coated otters *Lutra perspicillata* (weight = 7-11 kg; Harris 1968) have been found to use short (mean = 7.3, S.E. = 0.5, 5.5-11.3 km) and small (mean = 2.8, S.E. = 0.5, range = 2.1-4.4 ha) home ranges (Hussain & Choudhury 1995). These were, however, all juvenile or sub-adult animals. Other individuals, not radio-tracked, had estimated home ranges of 17.0 km and 6.6 ha (adult male) and 5.5 km and 2.1 ha (a mother and cub) respectively (Hussain & Choudhury 1995).

Although the use of different methods and large intraspecific variations in home range sizes from this study and the other species make predicting trends difficult, *A. capensis* do not appear to have larger home ranges than the other, smaller (Foster-Turley *et al.* 1990), freshwater species.

Other factors such as human disturbance may also play a significant role in determining home-range size (Ciucci *et al.* 1997), especially in shy species such as otters. The home ranges of the otters studied here included areas of high human impact (town, camping sites and dams). They have, therefore, adapted, although to an unknown extent, to an altered environment. These results show the Lutrinae to be adaptable with regards to some aspects of spatial use.

Other authors (Van der Zee 1979, 1982; Arden-Clarke 1983, 1986; Verwoerd 1987) have estimated one otter for every two km of marine coast. Estimates for freshwater habitats are one otter per 1.25-2.5 km (Carugati 1995), one otter per 3-4 km (Rowe-Rowe 1992) and one otter per 8-10 km of river (Butler & du Toit 1994). Butler & du Toit (1994) predicted that the low density in Zimbabwe was a result of the poor productivity of freshwater crabs. The estimated density of one otter per 0.65 km found in

the present study was higher than these other studies. This may be real or a result of the high crab densities in the Olifants River, or the estimate may not be accurate. With only one otter marked and only 55 spraints sampled this result should be taken as incomplete.

Total home range length was correlated to range use rate, suggesting the otters with larger home ranges were attempting to cover their home range as quickly as those with smaller home ranges. Excluding otter M2, males, besides having larger home range sizes, had larger range sizes per activity bout, perhaps because they were searching for females. Otter M3, besides having the longest recorded distance moved, also had the highest range use rate further suggesting he was looking for mates or male intruders rather than just searching for good foraging sites. Otter M2 had the highest revisit index owing to his habit of feeding at the same place (trout tank) during most activity sessions.

An underlying assumption of most radio-tracking studies is that the instrumented animals are moving through the environment, responding to stimuli, and behaving in a similar way to non-instrumented animals (White & Garrott 1990). As there was no evidence that the otters in the present study were affected by the implants I confidently accepted this assumption. The main shortcoming of the data was the small sample size of seven otters. This either prevented statistical analysis or reduced the power of some of the tests, which caused some results to be inconclusive and difficult to interpret. To measure the availability of resources, such as prey, is also notoriously difficult (Macdonald 1983) and this study was no exception. The large home ranges and deep waters made it impossible to measure absolute prey densities. The distribution of food was therefore measured indirectly by counting the number of reed beds and their mean nearest neighbour distance.

As the otters certainly foraged in other areas of the rivers and dams besides the reed beds, this analysis is imperfect. Also, even where different habitat types have different prey

availability, such as in this study (Chapter 2), spatial and temporal variation in aggregation within habitats would have important implications for home range configuration (Johnson *et al.* 2001). The RDH is also based on the assumption that the populations in question are limited by food, or other resource availability (Kruuk & Macdonald 1985). One of the assumptions leading to the RDH predictions tested here is that the number of patches (reed beds) correlates with home range size. This is expected since larger home ranges are more likely to incorporate more patches. It was, however, specifically tested since it is an assumption crucial to deriving the above predictions (Johnson *et al.* 2001). This assumption is supported with highly significant results in this study, but only for total length and total area used by the otters. This, like so many other studies (see Johnson *et al.* 2001 for refs), however, remains an imperfect test of the RDH. Although more data are needed to use the RDH to predict and explain the group structure of *A. capensis,* we can make some preliminary predictions on the data we have.

The large home ranges found show that large stretches of rivers would need to be protected to effectively conserve otters. The use of the entire Eerste River by otter M1 shows that this may even include whole rivers and not just large stretches. This is important when planning an effective conservation management plan for the species. In South Africa, and elsewhere in Africa, freshwater habitats are under serious and increasing threat (Davies & Day 1998). In South Africa, e.g., at best, with the slowest estimated population growth and the smallest demand for water, fresh water supplies will no longer be able to meet demand some time between 2020 (use of all surface water) and 2040 (use of surface and ground water). At worst, with the highest population growth and water demand, supplies will be fully committed some time between 2003 and 2015 (Davies & Day 1998). As almost all of the water used in South Africa comes from rivers (Davies & Day 1998) the potential impact on *A. capensis* habitat is of immediate and great concern. Elsewhere in Africa and the world, rapidly expanding human populations and accelerated water

extraction for industry and agriculture, yields an equally dismal scenario (see Tilman *et al*. 2001).

Otters often cause damage to trout farms and domestic fowl and are therefore caught and either relocated or killed. The present results show that there will probably be other otters in the area and the problem will not be solved by killing or translocations. The results suggest that areas with widely dispersed reed beds will have otters ranging over greater distances. Longer stretches of river would need to be conserved if otters were taken into consideration for conservation.

If, as it seems, females have exclusive home ranges, they are probably density dependent. Habitat loss will directly affect total population size and productivity. The increased silting up of South African rivers is also of concern. This causes loss of reed beds and may cause otters to range over larger areas to fulfil their requirements.

## REFERENCES

ANDERSON, D.J. 1982. The home range: A new nonparametric estimation technique. *Ecology* **63**: 103-112.

ARDEN-CLARKE, C.H.G. 1983. Population density and social organisation of the Cape clawless otter, *Aonyx capensis* Schinz, in the Tsitsikama Coastal National Park. M.Sc. thesis, University of Pretoria, Pretoria, South Africa.

ARDEN-CLARKE, C.H.G. 1986. Population density, home range size and spatial organization of the Cape clawless otter, *Aonyx capensis*, in a marine habitat. *Journal of Zoology, London* **209**: 201-211.

BOTHMA J. DU P., KNIGHT M.H., LE RICHE, E.A.N. & VAN HENSBERGEN H.J. 1997. Range size of southern Kalahari leopards. *South African Journal Of Wildlife Research* **27**: 94-99.

BOULANGER, J.G. & WHITE, G.C. 1990. A comparison of home-range estimators using Monte Carlo simulation. *Journal of Wildlife Management* **54**: 310-315.

BROWN, C.A. & DALLAS, H.F. 1995. *Eerste River, Western Cape: situation assessment of the riverine ecosystem.* CSIR, Stellenbosch.

BROWN, J.L. 1975. *The evolution of behavior.* W.W. Norton & Company, New York.

BROWN, J.L. & ORIANS, G.H. 1970. Spacing patterns in mobile animals. *Annual Review of Ecological Systems* **1**: 239-262.

BURT, W.H. 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* **24**: 346-352.

BUTLER, J.R.A. & DU TOIT, J.T. 1994. Diet and conservation of Cape clawless otters in eastern Zimbabwe. *South African Journal of Wildlife Research* **24**: 41-47.

CARO, T.M. 1994. *Cheetahs of the Serengeti Plains*, University of Chicago Press, Chicago.

CARR, R.J. & MACDONALD, D.W. 1986. The sociality of solitary foragers: a model based on resource dispersion. *Animal Behaviour* **34**: 1540-1549.

CARUGATI, C. 1995. Habitat, prey, and area requirements of otters (*Aonyx capensis* and *Lutra maculicollis*) in the Natal Drakensberg. M.Sc. thesis, University of Natal, Pietermaritzburg, South Africa.

CIUCCI, P., BOITANI, L., FRANCISCI, F. & ANDREOLI, G. 1997. Home range, activity and movements of a wolf pack in central Italy. *Journal of Zoology, London* **243**: 803-812.

CLUTTON-BROCK, T.H. 1989. Mammalian mating systems. *Proceedings of the Royal Society of London* B **236**: 339-372.

CLUTTON-BROCK, T.H. & HARVEY, P.H. 1977. Primate ecology and social organisation. *Journal of Zoology, London* **183**: 1-39.

CONNER, M.M., PLOWMAN, B.P., LEOPOLD, B.D. & LOVELL, C. 1999. Influence of time-in-residence on home range and habitat use of bobcats. *Journal of Wildlife Management* **63**: 261-269.

CROOK, J.H., ELLIS, J.E. & GOSS-CUSTARD, J.D. 1976. Mammalian social systems: structure and function. *Animal Behaviour* **24**: 261-274.

DAVIES, B.R. & DAY, J.A. 1998. *Vanishing waters*. University of Cape Town Press, Cape Town.

DAVIES, N.B. & LUNDBERG, A. 1984. Food distribution and a variable mating system in the Dunnock *Prunella modularis*. *Journal of Animal Ecology* **53**: 895-912.

DIXON, K.R. & CHAPMAN, J.A. 1980. Harmonic mean measure of animal activity areas. *Ecology* **61**: 1040-1044.

DONCASTER, C.P. & MACDONALD, D.W. 1991. Drifting territoriality in the red fox *Vulpes vulpes*. *Journal of Animal Ecology* **60**: 423-439.

DURBIN, L.S. 1993. Food and habitat utilization of otters (*Lutra lutra* L.) in a riparian habitat. D.Phil thesis, University of Aberdeen, Aberdeen, Scotland.

DURBIN, L.S. 1996a. Individual differences in spatial utilization of a river-system by otters *Lutra lutra*. *Acta Theriologica* **41**: 137-147.

DURBIN, L.S. 1996b. Some changes in the habitat use of free-ranging female otter *Lutra lutra* during breeding. *Journal of Zoology, London* **240**: 761-764.

EEKHOUT, S., KING, J.M. & WACKERNAGEL, A. 1997. *Classification of South African river, volume 1.,* Department of Environment Affairs and Tourism, Pretoria.

EMLEN, S.T. & ORING, L.W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* **197**: 215-223.

ESTES, J.A. 1989. Adaptations for aquatic living by carnivores. In: *Carnivore behavior, ecology and evolution,* (ed) J.L. Gittleman, Chapman and Hall, London.

FOSTER-TURLEY, P., MACDONALD, S. & MASON, C. 1990. *Otters: an action plan for their conservation*. IUCN/SSC Otter Specialist Group, Gland.

GAUTESTAD, A.O. & MYSTERUD, I. 1995. The home range ghost. *Oikos* **74**: 195-204.

GEFFEN, E., HEFNER, R., MACDONALD, D.W. & UCKO, M. 1992. Habitat selection and home range in the Blanford's fox *Vulpes cana:* compatibility with the resource dispersion hypothesis. *Oecologia* **91**: 75-81.

GEHRT, S.D. & FRITZELL, E.K. 1997. Sexual differences in home ranges of raccoons. *Journal of Mammalogy* **78**: 921-931.

GEHRT, S.D. & FRITZELL, E.K. 1998. Resource distribution, female home range dispersion and male spatial interactions: group structure in a solitary carnivore. *Animal Behaviour* **55**: 1211-1227.

GESE, E.M., RONGSTAD, O.J. & MYTTON, W.R. 1988. Home range and habitat use of coyotes in southeastern Colorado. *Journal of Wildlife Management* **52**: 640-646.

GITTLEMAN, J.L. & HARVEY P.H. 1992. Carnivore home-range size, metabolic needs and ecology. *Behavioural Ecology and Sociobiology* **10**: 57-83.

GRANT, J.W.A., CHAPMAN, C.A. & RICHARDSON, K.S. 1992. Defended versus undefended home range size of carnivores, ungulates and primates. *Behavioral Ecology and Sociobiology* **31**: 149-161.

GREEN, J., GREEN, R. & JEFFERIES, D.J. 1984. A radio-tracking survey of otters *Lutra lutra* on a Perthshire river system. *Lutra* **27**: 85-145.

HARRIS, C.J. 1968. *Otters: A study of the recent Lutrinae.* Weidenfeld and Nicolson, London.

HARRIS, S., CRESSWELL, W.J., FORDE, P.G., TREWHELLA, W.J., WOOLLARD, T. & WRAY, S. 1990. Home-range analysis using radio-tracking data - a review of problems and techniques particularly as applied to the study of mammals. *Mammal Review* **20**: 97-123.

HARRISON, T.D. 1997. A preliminary survey of coastal river systems on the South African west coast, Orange River - Groot Berg, with particular reference to the fish fauna. *Transactions of the Royal Society of South Africa* **52**: 277-321.

HEINECKEN, T.J.E., BICKERTON, I.B. & HEYDORN, A.E.F. 1983. *A Summary of Studies of the Pollution Input by Rivers and Estuaries Entering False Bay.* CSIR, Stellenbosch.

HUSSAIN, S.A. & CHOUDHURY, B.C. 1995. Seasonal movement, home range, and habitat use in smooth coated otters in National Chambal Sanctuary, India. *Habitat* **11**: 45-55.

JENNRICH, R.I. & TURNER, F.B. 1969. Measurement of non-circular

home range. *Journal of Theoretical Biology* **22**: 227-237.

JEWELL, P.A. 1966. The concept of home range in mammals. *Symposia of the Zoological Society of London* No. 18: 85-109.

JOHNSON, D.D.P., BAKER, S., MORECROFT, M.D. & MACDONALD, D.W. 2001. Long-term resource variation and group size: A large-sample field test of the Resource Dispersion Hypothesis. *BMC Ecology* **1**: 2.

KRUUK, H. 1978. Spatial organization and territorial behaviour of the European badger *Meles meles*. *Journal of Zoology, London* **184**: 1-19.

KRUUK, H. 1995. *Wild otters: Predation and populations*. Oxford University Press, Oxford.

KRUUK, H. & MACDONALD, D.W. 1985. Group territories of carnivores: empires and enclaves. In: *Behavioural ecology: ecological consequences of adaptive behaviour*, (eds) R.M. Sibly & R.H. Smith, Blackwell Scientific Publications, Oxford.

KRUUK, H. & MOORHOUSE, A. 1991. The spatial organization of otters *(Lutra lutra)* in Shetland. *Journal of Zoology, London* **224**: 41-57.

KRUUK, H. & Parish, T. 1982. Factors affecting population density, group size and territory of the European badger, *Meles meles*. *Journal of Zoology, London* **196**: 31-39.

KRUUK, H., CARSS, D.N., CONROY, J.W.H. & DURBIN, L.S. 1993. Otter *(Lutra lutra* L.) numbers and fish productivity in rivers in north-east Scotland. *Symposia of the Zoological Society of London* No. 65: 171-191.

LACK, D. 1954. *The natural regulation of animal numbers*. Oxford University Press, Oxford.

MACDONALD, D.W. 1983. The ecology of carnivore social behaviour. *Nature, London* **301**: 379-384.

MACDONALD, D.W. & CARR, G.M. 1989. Food security and the rewards of tolerance. In: *Comparative socioecology: The behavioural ecology of humans and animals*, (eds) V. Standen & R.A. Foley, Blackwell Scientific, Oxford.

MAHER, C.R. & LOTT, D.F. 1995. Definitions of territoriality used in the study of variation in vertebrate spacing systems. *Animal Behaviour* **49**: 1581-1597.

MCKENZIE, A.A., MELTZER, D.G.A., LE ROUX, P.G. & GOSS, R.A. 1990. Use of implantable radio transmitters in large African carnivores. *South African Journal of Wildlife Research* **20**: 33-35.

MCNAB, B.E. 1963. Bioenergetics and the determination of home range size. *American Naturalist* **97**: 133-140.

MCNAB, B.E. 1980. Food habits, energetics, and the population biology of mammals. *American Naturalist* **116**: 106-124.

MELQUIST, W.E. & HORNOCKER, M.G. 1983. Ecology of river otters in west central Idaho. *Wildlife Monographs* **83**: 1-60.

MILLS, M.G.L. 1990. *Kalahari hyaenas: The comparative behavioural ecology of two species*. Unwin Hyman, London.

NAGY, K.A. 1987. Field metabolic rates and food requirements scaling in mammals and birds. *Ecological Monographs* **57**: 111-128.

PERRIN, M.R., D'INZILLO CARRANZA, I. & LINN, I.J. 2000. Use of space by the spotted-necked otter in the Natal Drakensberg, South Africa. *South African Journal of Wildlife Research* **30**: 15-21.

POWELL, R.A. 1979. Mustelid spacing patterns: variations on a theme by *Mustela*. *Zeitschrift für Tierpsychologie* **50**: 153-163.

PYKE, G.H., PULLIAM, H.R. & CHARNOV, E.L. 1977. Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology* **52**: 137-254.

RALLS, K., HATFIELD, B.B. & SINIFF, D.B. 1995. Foraging patterns of California sea otters as indicated by telemetry. *Canadian Journal of Zoology* **73**: 523-531.

RASA, O.A.E. 1983. Dwarf mongoose and hornbill mutualism in the Taru Desert, Kenya. *Behavioral Ecology and Sociobiology* **12**: 181-190.

RASA, O.A.E. 1986. Ecological factors and their relationships to group size, mortality and behaviour in the dwarf mongoose *Helogale undulata* (Peters, 1852). *Cimbebasia* **8**: 15-21.

ROWE-ROWE, D.T. 1978. The small carnivores of Natal. *Lammergeyer* **25**: 1-48.

ROWE-ROWE, D.T. 1992. Survey of South African otters in freshwater habitat, using sign. *South African Journal of Wildlife Research* **22**: 49-55

ROWE-ROWE, D.T. & SOMERS, M.J. 1998. Diet, foraging behaviour and coexistence of African otters and the water mongoose. *Symposia of the Zoological Society of London* No. 71: 215-227.

RUIZ-OLMO, J., JIMENEZ, J. & LOPEZ-MARTIN, J.M. 1995. Radio-tracking of otters *Lutra lutra* in North-eastern Spain. *Lutra* **38**: 11-21.

SAMUEL, M.D., PIERCE, D.J. & GARTON, E.O. 1985. Identifying areas of concentrated use within the home range. *Journal of Animal Ecology* **54**: 711-719.

SANDERSON, G.C. 1966. The study of mammal movements - a review. *Journal of Wildlife Management* **30**: 215-235.

SCHOENER, T.W. 1968. Sizes of feeding territories among birds. *Ecology* **49**: 123-141.

SEAMAN, D.E. & POWELL, R.A. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* **77**: 2075-2085.

SKELTON, P.H. 1993. *A complete guide to the freshwater fishes of southern Africa*. Southern Book Publishers, Halfway House.

SOMERS, M.J. 2000a. Seasonal variation in the diet of Cape clawless otters (*Aonyx capensis*) in a marine habitat. *African Zoology* **35**: 261-268.

SOMERS, M.J. 2000b. Foraging behaviour of Cape clawless otters (*Aonyx capensis*) in a marine habitat. *Journal of Zoology, London* **252**: 473-480.

SOMERS, M.J., PENZHORN, B.L. & RASA, O.A.E. 1994. Home range size, range use and dispersal of warthogs in the eastern Cape, South Africa. *Journal of African Zoology* **108**: 361-373.

TILMAN, D., FARGIONE, J., WOLFF, B., D'ANTONIO, C., DOBSON, A., HOWARTH, R., SCHINDLER, D., SCHLESINGER, W.H., SIMBERLOFF, D. & SWACKHAMER, D. 2001. Forecasting agriculturally driven global environmental change. *Science* **292**: 281-284.

VAN DER ZEE, D. 1979. Food and status of the Cape clawless otter (*Aonyx capensis* Schinz 1821) in the Tsitsikama Coastal National Park. M.Sc. thesis, University of Pretoria, Pretoria, South Africa.

VAN DER ZEE, D. 1982. Density of Cape clawless otters *Aonyx capensis* (Schinz, 1821) in the Tsitsikama Coastal National Park. *South African Journal of Wildlife Research* **12**: 8-13.

VERWOERD, D.J. 1987. Observations on the food and status of the Cape clawless otter *Aonyx capensis* at Betty's Bay, South Africa. *South African Journal of Zoology* **22**: 33-39.

WEBER, J.-M. & DAILLY, L. 1998. Food habits and ranging behaviour of a group of farm cats (*Felis catus*) in a Swiss mountainous area. *Journal of Zoology, London* **245**: 234-237.

WHITE, G.C. & GARROTT, R.A. 1990. *Analysis of wildlife radio-tracking data*. Academic Press, San Diego.

WILSON, E.O. 1975. *Sociobiology The new synthesis*. Belknap Press of Harvard University Press, Cambridge.

WRANGHAM, R. 1980. An ecological model of female-bonded primate groups. *Behaviour* **75**: 262-300.

WYNNE-EDWARDS, V.C. 1962. *Animal dispersion in relation to social behaviour*. Oliver & Boyd, Edinburgh.

# CHAPTER 4

# HABITAT SELECTION BY CAPE CLAWLESS OTTERS (*AONYX CAPENSIS*) IN RIVERS

## INTRODUCTION

As habitat selection by animals provides a theoretical basis for habitat management decisions (Kopp *et al.* 1998) it is a common and important aspect of wildlife science (Alldredge & Ratti 1986). Habitat selection is determined by identifying the disproportionate use of habitats (Johnson 1980). Common aims of habitat use studies are to determine whether a species uses habitats available at random, to rank habitats in order of relative use, to compare use by different groups of animals, to relate use to variables such as food abundance, or to examine the effects of habitat on movement and home range size (Aebischer *et al.* 1993). Animal movements and habitat use are related to both the acquisition of primary resources (e.g. food, shelter, mate, and host) and the avoidance of sources of stress (e.g. predators, thermal extremes, dehydration) (Barbaresi *et al.* 1997). Differences in habitat use by carnivores can vary owing to, amongst others, differences in geographic locality (Crooks & Van Vuren 1995), geomorphology (shelter) (Waller & Mace 1997), food availability (Melquist & Hornocker 1983; Mills 1990), interspecific relationships (Rasa 1983), intraspecific relationships (Rasa 1986), time in residence (Conner *et al.* 1999), sex of the animal (Green *et al.* 1984; Conner *et al.* 1999), age of the animal (Ralls *et al.* 1995); anthropogenic influences (Weber & Dailly 1998) and vegetation cover (Gese *et al.* 1988).

Knowledge of a species' use of habitat can be helpful to conservation efforts. Ralls (1997) gives the sea otter *Enhydra lutris* as an example of this, showing that they selected areas much further offshore and in deeper water than had previously

been thought. These new habitat selection data, from radiotelemetry (Ralls *et al.* 1995), facilitated legislation prohibiting set-net fishing in the otters' hunting areas, so as to prevent them from drowning in the nets (Ralls 1997).

Radiotelemetry, as used in the present study, is one of the most powerful tools available to wildlife biologists (Aebischer *et al.* 1993) particularly to get insight into the ecology of elusive species such as otters. In environments intensively used by humans, thorough and reliable data on space and habitat selection by otters can be obtained only by radiotelemetry, and this information is critical not only to understanding the ecology of these species, but also to planning effectively for their conservation.

Our understanding of otter habitat selection comes mainly from studies on the distribution and abundance of otter spraints and resting places (reviewed by Mason & Macdonald 1986). However, Green *et al.* (1984); Kruuk *et al.* (1986) and Conroy & French (1987) show that for European otters *Lutra lutra* the position of spraints is an unreliable indication of where otters spend their time. They are, however, an indication of how the otters use land, which is important for semi-aquatic otters. Data from radiotelemetry would therefore compliment these data, giving a better understanding of how the otters use their habitat.

There have been numerous radiotelemetry habitat selection studies done on otters such as *L. lutra* (e.g. Green *et al.* 1984; Durbin 1993, 1996a, 1996b, 1998; Kruuk 1995), North American river otters *Lutra canadensis* (Melquist & Hornocker 1983), spotted-necked otters *Lutra maculicollis* (Perrin & D'Inzillo Carranza 2000; Perrin *et al.* 2000), *E. lutris* (Ralls *et al.* 1995) and smooth coated otters *Lutra perspicillata* (Hussain & Choudhury 1995). Only Arden-Clarke (1986) and Somers (Chapter 3) provide data on Cape clawless otters *Aonyx capensis* using radiotelemetry. Although he did not look at habitat variables, Arden-Clarke (1986) did show differential use of the home range of *A. capensis* along the Tsitsikama coast. Somers (Chapter 3), in the present

study area, showed that *A. capensis* could range over distances as long as 54.1 km.

*Aonyx capensis* are semi-aquatic predators, which occur over most of sub-Saharan Africa (Rowe-Rowe & Somers 1998; Nel & Somers in press). In most areas crustaceans are the most important prey type, but fish, frogs, insects, birds, reptiles, molluscs, dung (ungulate) and mammals are also eaten (Rowe-Rowe & Somers 1998; Perrin & Carugati 2000a; Somers 2000a, 2000b; (Chapters 5 & 6)). This is in contrast to most otters, which are mainly piscivorous (Estes 1989).

Perrin & Carugati (2000b) analysed habitat selection by *A. capensis* by comparing sites of otter activity on land with environmental variables. They found that the otters select, for time spent on land, undisturbed areas with rock cover and natural dense vegetation. Rowe-Rowe (1992) and Butler & du Toit (1994) give densities of spraints and resting places but do not relate these to habitat variables. Van der Zee (1981); Arden-Clarke (1986) and Verwoerd (1987) also give densities and distribution of sign of *A. capensis* along the coast but again do not quantitatively relate these to habitat characteristics. Along the coast there is evidence that *A. capensis* select places of activity on land to be near thick vegetation, an abundant food resource and fresh water (van der Zee 1982; Arden-Clarke 1986; van Niekerk *et al.* 1998). Just as *L. lutra* use spraints as scent marks (Kruuk 1992) so may *A. capensis*. This implies that the analysis of habitat selection from sprainting sites may indicate only areas that the otters select as scent marking stations and not general habitat selection.

Although Kruuk *et al.* (1998) point out that limiting factors should be of primary concern for conservation of otters, it is not known what limits *A. capensis* numbers. However, Kruuk *et al.* (1998) also point out that it is important to identify habitat preferences and to establish what kind of role the particular factors are likely to play, either as habitat requirements or as mere preferences. This is because if the main limiting factor (e.g. food) is abundant and therefore not limiting numbers the

population will increase until another factor becomes limiting (Kruuk *et al.* 1993).

Owing to loss of energy while in the water (Kruuk *et al.* 1997) it would be expected that otters would always maximise the net rate of energy gain. Optimal foraging theory states that foraging strategies may involve behaviours that maximise the net rate of food intake, or of some other measure of foraging efficiency (Emlen 1966; MacArthur & Pianka 1966; Krebs & Kacelnik 1991). An otter should therefore use its habitat to the optimum and select those parts that allow it to best maximise its inclusive fitness. It is therefore predicted that otters select some habitat types over others.

In this chapter I report on the habitat selection by seven *A. capensis*, as determined by radio-tracking in the Olifants and Eerste Rivers, Western Cape Province, South Africa. The hypothesis being tested is that active otters do not select for any particular habitat.

## MATERIALS & METHODS

Data were collected in the Eerste (near Stellenbosch (33° 56' S, 18° 52' E)) and Olifants (near Clanwilliam (32° 11' S, 18° 23' E)) rivers in the Western Cape Province, South Africa.

The Eerste River is a rocky, narrow river, which rises in pristine conditions in the Jonkershoek Mountains, but then flows through agricultural, industrial and urban areas. The flow rate is variable depending on rainfall, which is mostly in winter. It reaches the sea about 40 km from its source. It is disturbed for *ca* 90% of its length by agriculture, industry and the urban environment. The main crops are vines, fruit, and vegetables, all of which are subject to heavy applications of fertilizers, herbicides and pesticides (Heinecken *et al.* 1983). Winery effluents are either irrigated onto pasturelands or accepted into the Stellenbosch sewage works. Treated effluent from these works is discharged into a tributary of the Eerste River (Heinecken *et al.* 1983). During heavy rainfall events, overflow of the sewage

works occurs and untreated sewage flows into the river below Stellenbosch (personal observations). The Eerste River and a number of its tributaries flow through the town of Stellenbosch, and these receive all the storm water run-off from the town. Pollution levels and eutrophication increases rapidly below Stellenbosch. The treated sewage from the towns of Macassar, Somerset West and Strand is also discharged into the estuary of the Eerste River (Heinecken *et al.* 1983). For a detailed classification of the Eerste River see Eekhout *et al.* (1997).

The Olifants River is 285 km long and has a catchment area of 46 220 km$^2$. The part of the Olifants River used in this study is dominated by two impoundments: the Clanwilliam and Bulshoek Dams. There are holiday camps along the edge of the two impoundments and recreational boating, swimming and fishing takes place. The length of river between the two dams is 17.6 km and bordered by cattle and crops. There is, however, little disturbance along the water edge where mostly exotic *Eucalyptus* trees grow. Just above Bulshoek Dam the river is slow flowing, has a sandy bank with reed beds *Phragmites australis*, bulrushes *Typha capensis* and occasional sedges *Cyperus* spp along the edge. The river below Bulshoek Dam is slow flowing with marshlands, oxbows, large basins, large reed beds and rocky pools of up to 6 m deep. Except for recreational activities on the dam (mostly during weekends and the summer holidays) there is not much disturbance. The area down to *ca* 15 km below Bulshoek Dam is not intensively farmed, except for some cattle farming, resulting in very little disturbance. Further down (out of the present study area) the river has extensive agriculture in the form of vines, fruit and vegetables along the edge. For a detailed classification of the Olifants River see Harrison (1997) and Eekhout *et al.* (1997).

Seven otters (Table 4.1) were caught in standard carnivore traps (800 X 800 X 1400 mm) as described by van der Zee (1982) and Arden-Clarke (1986). The traps were baited with either fish and/or fresh spraints from another area. Fish bait used in the Eerste River was rainbow trout *Oncorhynchus mykiss,* and in the Olifants River shallow-water hake *Merluccius capensis*. The otters

were anaesthetized with ketamine hydrochloride (Ketalar 50 mg/ml Parke Davis). Radio transmitters (IMP/300/L, implantable transmitter, 40g, 80 x 20 mm diameter cylinder (Telonics Inc., Arizona, USA)) were implanted by a veterinary surgeon into the otters following the same procedures as described by McKenzie *et al.* (1990). The transmitters were left free floating in the abdominal cavity. A Telonics TR-4 receiver and multidirectional whip antenna were used to find the general locality of the otters. The TR-4 receiver and a RA - 2A antenna were then used to find their position.

Otter M1 was found dead four months after the transmitter was implanted. There were skin punctures, which appeared to be a result of another animal. On post-mortem there appeared to be no physical abnormality associated with the transmitter.

Continuous radio-tracking (Harris *at al.* 1990) with fixes being taken at 10 min intervals was carried out. This was done at times of usual otter activity and periodically on a 24-hour basis. Most radio-tracking habitat use studies combine both active and non-active data, which underestimates foraging habitat, with potentially important management and/or ecological consequences (Palomares & Delibes 1992). This study avoided this problem by only using data from active otters. Activity was detected as fluctuations in signal strength. Whenever possible otters were visually observed using 10 x 42 binoculars. A short un-quantified description of their foraging is provided. A total of 1579 h was spent radio-tracking between 1993 and 1995 of which 851 h were of active otters (Table 4.1).

Observations and radio-tracking were conducted from a vehicle and on foot. The otters were located by triangulation (usually from the vehicle) or tracking (on foot) the path of increasing signal strength.

**Table 4.1.** Radio-tracking effort on Cape clawless otters *Aonyx capensis* in (a) the Eerste and (b) Olifants Rivers, Western Cape Province, South Africa. M = male; F = female.

| Animal | Tracking dates (day/mon/yr) | Tracking period (h) | Otter activity (h) | Sessions tracked | | |
|---|---|---|---|---|---|---|
| | | | | partial | complete | total |
| (a) | | | | | | |
| M1 (sub-adult) | 20/07/93 – 16/11/93 | 216 | 140 | 46 | 22 | 48 |
| F1 (adult) | 10/08/93 – 13/08/93 | 25 | 11 | 4 | 2 | 6 |
| M2 (adult) | 18/02/94 – 20/07/94 | 246 | 57 | 48 | 33 | 82 |
| (b) | | | | | | |
| M3 (adult) | 24/03/94 – 05/12/94 | 189 | 105 | 33 | 12 | 45 |
| M4 (adult) | 23/04/94 – 13/05/95 | 208 | 123 | 28 | 20 | 48 |
| F2 (adult) | 18/05/94 – 12/04/95 | 447 | 248 | 61 | 49 | 110 |
| F3 (adult) | 22/11/94 – 31/08/95 | 248 | 167 | 28 | 18 | 46 |

The study areas were divided into numbered, 100 m stretches of river, and these drawn on 1: 50 000 topographical maps and 1 : 10 000 orthophotographs. The position of the otters when active was continuously recorded on tape. Following Durbin (1993), two 100 m sections were combined and these 200 m sections were used for the present analyses.

The surveys were done during 1995 and 1996. This was during summer when the rivers were not in flood. To prevent Type II statistical errors the numbers of habitat variables were limited (Alldredge & Ratti 1986). This restricts the number of usable variables and makes deciding which ones to use critical. The variables decided on were those thought to be of importance to the otters. The importance was subjectively decided by reference to the literature and to direct observations of the otters (personal observations).

For each 200 m section, the areas or lengths of the various variables (Table 4.2) were estimated by eye, and following Durbin (1993) assigned to the following percentage classes using the midpoint scores: 3 = 0-5%; 13 = 6-25%; 35 = 26-50%; 73 = 51-95%; 98 = 96-100%. Within 100 m of the bank, surrounding land uses were quantified by estimating the length of bank adjacent to particular habitat types (Table 4.2). Variables such as channel width and bank vegetation change temporarily during the rainy season. Water levels would, however, usually return to normal within a few days of rainfall events.

Following Durbin (1993) and Kruuk et al. (1993) the mean width of each section was calculated from two measurements at the upstream and downstream boundaries. This was done by direct measurement (narrow sections) or from the 1 : 10 000 orthophotographs (wide sections). An estimate was made of the number of trees (>2.0 m high) overhanging the water. The minimum distance of each section from roads and buildings were measured using the 1: 10 000 orthophotographs. The length of canalised bank was measured from the 1 : 10 000 orthophotographs.

**Table 4.2.** The habitat variables used for analysis of habitat selection by Cape clawless otters *Aonyx capensis*.

| Variable | Code | Description | Measurement | Log-conversion |
|---|---|---|---|---|
| **Substrate** | | | | |
| soil | SOIL | < 20 mm maximum diameter | %A | $\ln(x/(100-x))$ |
| gravel | GRAV | 20-60 mm | %A | $\ln(x/(100-x))$ |
| stones | STON | 60-200 mm | %A | $\ln(x/(100-x))$ |
| boulders | BOUL | > 200 mm | %A | $\ln(x/(100-x))$ |
| | | | | |
| **Bank vegetation** | | | | |
| over-hanging | OVER | No. trees >2.0 m | | |
| over-hanging | Count | | | $\ln(x+1(\text{mean}+1)$ |
| emergent | EMER | length of bank | %L | $\ln(x/(100-x))$ |
| reeds | REED | m$^2$ | %A | $\ln(x/(100-x))$ |
| | | | | |
| **Surrounding area** | | | | |
| arable | ARAB | length of bank | %L | $\ln(x/(100-x))$ |
| fynbos | FYNB | length of bank | %L | $\ln(x/(100-x))$ |

**Table 4.2** Continued:

| Variable | Code | Description | Measurement | Log-conversion |
|----------|------|-------------|-------------|----------------|
| **Channel width** | WIDT | mean width | In m | $\ln(x/\text{mean})$ |
| **Canalisation** | CANA | length of bank | %L | $\ln(x/(100-x))$ |
| **Roads** | ROAD | minimum distance from road | In m | $\ln(x/\text{mean})$ |
| **Buildings** | BUIL | minimum distance from building | In m | $\ln(x/\text{mean})$ |

%A = percentage area class; %L = per cent length class; x = habitat variable score

Although there are various methods for analysing habitat use data from radio-tracking (see Alldredge & Ratti 1986, 1992 for comparisons) there are shortcomings affecting the validity of their analysis (see Aebischer *et al.* 1993). In order to minimise problems with analysis, analysis of data closely followed that used by Durbin (1998) for *L. lutra*. Minor differences between this study and that of Durbin (1998) in methods and the reasons for them are outlined below. As the exact habitat type (e.g. reed bed) that the otters were foraging in could seldom be determined the method used here provides the most powerful analysis possible.

The total amount of active time *(T)* spent in each section was calculated. These patterns of utilization were compared with models based on the uniform use of habitat length $(T^l)$ and area $(T^a)$. As Durbin (1998) points out, both these models may be appropriate, as the riverine habitat is clearly linear but varies in width. This is especially true with the data collected in the Olifants River, where the two dams were included in the study area (Durbin personal communication). The predicted values for each section were calculated in a Microsoft Excel spreadsheet as follows:

$$T^l = T^t(S^l/R^l),$$

$$T^a = T^t(S^a/R^a),$$

where $T^t$ = total amount of active time that the otter was tracked, $S^l$ = length of the section (200 m), $R^l$ = total length of otter's range, $S^a$ = area of the section (200 m X width), and $R^a$ = area of the otter's range. Two preference indices were then calculated for each section using natural log ratios of the observed to predicted values:

*PL* (deviation from uniform use of length) = $\ln(T/T^l)$, and

*PA* (deviation from uniform use of area) = $\ln(T/T^a)$.

Sections with indices greater than zero were interpreted as being used more than expected, and those with values less than zero were used less than expected. Sections with indices of zero were used as predicted. As with Durbin (1998), associations between habitat variable scores and levels of preference had dependence problems because some habitat variables were inter-correlated (Table 4.3). All the variables were still used as they were considered to be of possible relevance to the otter's use of habitat.

To be compatible with the preference indices the habitat variable scores were log converted (see Table 4.2). Regressions between the preference indices with habitat variables were done for each otter. Significant regressions were taken to indicate that the habitat variable concerned, or some correlated variable, was affecting the otter's use of its range (Durbin 1998).

Although the number of radiolocations per animal determines the accuracy with which its habitat use is estimated, it is the number of animals tracked that determines the sample size upon which to test the hypothesis that the otters were selecting for various habitat types (Aebischer *et al.* 1993; Durbin 1998). Habitat preference was inferred on the basis of consistency between the samples of otters. For this analysis the Mann-Whitney U test was used to test the hypothesis that the median coefficient for a particular habitat variable was zero across the sample of seven otters. A significant result indicated a general pattern for the seven otters, and the sign of the mean coefficient defined the relationship between observed vs expected (i.e. as a preference or avoidance) (Durbin 1998).

## RESULTS

The mean width of the part of the Eerste River used by the radio-tracked otters was 8.9 m (S.E. = 1.3, range = 2-110, $n$ = 178) and of the Olifants River (including dams) was 182.8 m (S.E. = 12.07, range = 10-1250, $n$ = 270).

**Table 4.3.** Correlation matrix of habitat variables from two Western Cape Rivers.

| | GRAV | STON | BOUL | OVER | EMER | REED | ARAB | FYNB | WIDT | CANA | ROAD | BUIL |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SOIL | -0.25 | -0.38 | -0.26 | 0.14 | 0.18 | 0.45 | 0.48 | 0.05 | 0.05 | -0.10 | -0.04 | 0.02 |
| GRAV | | -0.18 | -0.16 | 0.03 | 0.08 | -0.03 | 0.20 | 0.16 | 0.01 | -0.12 | -0.08 | 0.06 |
| STON | | | -0.23 | 0.15 | 0.06 | -0.09 | 0.05 | 0.06 | -0.14 | 0.16 | -0.14 | 0.08 |
| BOUL | | | | 0.11 | 0.10 | -0.13 | -0.20 | 0.13 | 0.78 | -0.19 | -0.09 | 0.16 |
| OVER | | | | | 0.07 | 0.37 | -0.11 | 0.11 | -0.37 | 0.55 | -0.04 | -0.07 |
| EMER | | | | | | 0.19 | -0.01 | -0.01 | 0.25 | -0.87 | -0.02 | -0.18 |
| REED | | | | | | | 0.28 | 0.03 | 0.02 | -1.00 | -0.01 | 0.22 |
| ARAB | | | | | | | | 0.56 | 0.07 | -1.00 | 0.07 | 0.23 |
| FYNB | | | | | | | | | 0.15 | -0.40 | -0.05 | 0.54 |
| WIDT | | | | | | | | | | -0.95 | -0.01 | -0.08 |
| CANA | | | | | | | | | | | 0.93 | 0.95 |
| ROAD | | | | | | | | | | | | 0.76 |

Excluding Bulshoek and Clanwilliam dams, the mean width of the Olifants River used by the radio-tracked otters was 50.1 m (S.E. = 2.01, range = 10-145, $n$ = 161).

Observations showed that, as in the marine habitat (Somers 2000a) (Chapter 6), two modes of hunting or foraging could be recognised. In the first, the otters, selecting open water within $ca$ 8 m of the shore, would dive and surface with or without prey. The second type of hunting involved the otters moving into shallow water ($ca$ 0.2 m deep), and walking along the substrate feeling for prey with their feet, disturbing possible prey items, which were then caught with the forefeet. They occasionally submerged their heads, presumably looking for food. For a more detailed description see Somers (2000b) (Chapter 6).

In the rivers, the second type of hunting in shallow water seemed more common than that of hunting in open water. The otters often "swam fished" along the shore, while occasionally coming closer to the shore and foraging in the reeds, stones, boulders or emergent vegetation. They would occasionally cross to the opposite bank, usually without diving. The otters did not appear to forage in tributaries, but F2 and M1 had resting places short distances up tributaries (Chapter 3).

Among the regressions using the index PL (related to the amount of time spent active per unit length of river) the variables that showed consistent relationships with all seven otters were, boulders (mean coefficient = 0.37, S.E. = 0.1, range = 0.07-0.75; Mann-Whitney $U$ = 0, d.f. = 13, $P$ < 0.001) and reeds (mean coefficient = 0.37, S.E. = 0.07, range = 0.08-0.66; Mann-Whitney $U$ = 0, d.f. = 13, $P$ < 0.001) (Table 4.4). The three otters in the Eerste River showed a preference for areas with overhanging vegetation, which was not the case for all the otters in the Olifants River (Table 4.4). Except for otter M2 and F2 the otters did not select for wide areas.

**Table 4.4.** Regression statistics for relationships between preference indices (a) PL, (b) PA, and habitat scores. Significant coefficients are indicated in bold.

| Animal | Habitat variables | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | SOIL | GRAV | STON | BOUL | OVER | EMER | REED | ARAB | FYNB | WIDT | CANA | ROAD | BUIL |
| **(a)** | | | | | | | | | | | | | |
| **M1** | | | | | | | | | | | | | |
| $r^2$ | **0.10** | **0.10** | **0.05** | **0.33** | **0.19** | **0.35** | 0.02 | 0.00 | 0.04 | 0.06 | **0.37** | 0.01 | **0.05** |
| b | **0.16** | **0.12** | **0.21** | **0.68** | **0.38** | **0.29** | 0.08 | −0.00 | 0.09 | −0.05 | **−0.76** | 0.09 | **−0.31** |
| **F1** | | | | | | | | | | | | | |
| $r^2$ | **0.05** | 0.03 | 0.02 | **0.25** | **0.09** | 0.00 | **0.11** | **0.08** | 0.00 | 0.00 | **0.26** | **0.18** | **0.10** |
| b | **−0.19** | −0.05 | 0.08 | **0.75** | **0.23** | 0.01 | **0.18** | **−0.15** | −0.01 | 0.02 | **−0.46** | **−0.29** | **−0.17** |
| **M2** | | | | | | | | | | | | | |
| $r^2$ | 0.03 | 0.06 | 0.00 | **0.10** | **0.03** | 0.00 | **0.20** | **0.11** | 0.00 | **0.04** | 0.00 | **0.13** | 0.00 |
| b | 0.09 | 0.12 | 0.03 | **0.29** | **0.14** | −0.05 | **0.37** | **−0.34** | 0.03 | **0.16** | 0.00 | **0.22** | 0.00 |
| **M3** | | | | | | | | | | | | | |
| $r^2$ | 0.06 | **0.09** | 0.00 | 0.06 | 0.00 | 0.01 | **0.28** | 0.00 | 0.00 | **0.08** | 0.00 | 0.00 | 0.00 |
| b | −0.10 | **−0.21** | −0.02 | 0.07 | −0.04 | 0.12 | **0.54** | −0.00 | −0.01 | **−0.21** | 0.00 | −0.08 | 0.09 |
| **M4** | | | | | | | | | | | | | |
| $r^2$ | **0.03** | 0.02 | **0.05** | **0.11** | **0.08** | 0.00 | **0.28** | 0.00 | 0.07 | 0.00 | 0.00 | 0.03 | 0.00 |
| b | **0.16** | −0.16 | **−0.14** | **0.25** | **0.14** | −0.01 | **0.38** | 0.02 | −0.11 | −0.02 | 0.00 | −0.08 | 0.02 |
| **F2** | | | | | | | | | | | | | |
| $r^2$ | 0.04 | **0.06** | **0.15** | 0.02 | 0.03 | 0.01 | **0.25** | 0.00 | 0.00 | **0.14** | 0.00 | **0.04** | **0.01** |
| b | 0.10 | **0.16** | **0.46** | 0.15 | −0.08 | 0.08 | **0.38** | 0.00 | −0.05 | **0.45** | 0.00 | **−0.14** | **−0.23** |
| **F3** | | | | | | | | | | | | | |
| $r^2$ | **0.05** | **0.06** | 0.00 | **0.11** | 0.00 | −0.02 | **0.31** | **0.08** | **0.07** | **0.05** | 0.00 | 0.00 | **0.02** |
| b | **0.12** | **0.17** | 0.00 | **0.38** | −0.05 | 0.14 | **0.66** | **−0.17** | **−0.13** | **−0.15** | 0.00 | −0.06 | **0.12** |

Table 4.4 continued

| Animal | Habitat variables | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | SOIL | GRAV | STON | BOUL | OVER | EMER | REED | ARAB | FYNB | WIDT | CANA | ROAD | BUIL |
| (b) | | | | | | | | | | | | | |
| **M1** | | | | | | | | | | | | | |
| $r^2$ | **0.01** | 0.14 | **0.07** | **0.13** | **0.11** | **0.35** | **0.03** | 0.00 | 0.01 | 0.03 | **0.17** | 0.01 | **0.03** |
| b | **0.06** | 0.17 | **0.12** | **0.57** | **0.22** | **0.15** | **0.14** | −0.00 | 0.04 | −0.04 | **−0.56** | 0.04 | **−0.06** |
| **F1** | | | | | | | | | | | | | |
| $r^2$ | 0.00 | 0.00 | **0.01** | **0.14** | **0.21** | 0.00 | **0.06** | **0.09** | 0.01 | 0.00 | **0.16** | **0.17** | **0.11** |
| b | −0.03 | 0.02 | **0.05** | **0.44** | **0.35** | 0.01 | **0.15** | **−0.25** | −0.04 | −0.03 | **−0.39** | **−0.32** | **−0.19** |
| **M2** | | | | | | | | | | | | | |
| $r^2$ | 0.04 | 0.03 | 0.00 | **0.10** | 0.02 | 0.01 | **0.17** | 0.11 | 0.00 | **0.15** | 0.00 | **0.02** | 0.00 |
| b | 0.09 | 0.12 | 0.03 | **0.39** | **0.18** | −0.07 | **0.44** | −0.24 | −0.03 | **0.27** | 0.00 | **0.10** | 0.00 |
| **M3** | | | | | | | | | | | | | |
| $r^2$ | 0.04 | 0.05 | 0.01 | **0.06** | **0.21** | 0.01 | **0.15** | 0.00 | **0.20** | **0.06** | 0.00 | 0.00 | 0.00 |
| b | 0.10 | −0.15 | −0.07 | **0.21** | **0.33** | −0.15 | **0.38** | 0.00 | **−0.06** | **−0.14** | 0.00 | −0.08 | 0.07 |
| **M4** | | | | | | | | | | | | | |
| $r^2$ | **0.03** | 0.01 | 0.03 | **0.08** | 0.04 | 0.03 | **0.29** | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.00 |
| b | **0.12** | −0.10 | 0.10 | **0.15** | **0.19** | **0.12** | **0.48** | −0.09 | −0.02 | −0.07 | 0.00 | −0.03 | −0.05 |
| **F2** | | | | | | | | | | | | | |
| $r^2$ | **0.09** | 0.02 | 0.00 | 0.12 | 0.06 | **0.11** | **0.39** | 0.00 | 0.00 | **0.10** | 0.00 | 0.01 | **0.01** |
| b | **0.19** | 0.05 | −0.02 | 0.08 | 0.07 | **0.23** | **0.56** | 0.00 | −0.01 | **0.35** | 0.00 | −0.04 | **−0.23** |
| **F3** | | | | | | | | | | | | | |
| $r^2$ | **0.01** | 0.03 | 0.00 | 0.01 | 0.05 | **0.01** | **0.31** | 0.04 | **0.05** | 0.03 | 0.00 | **0.02** | 0.01 |
| b | **0.32** | 0.27 | −0.00 | 0.03 | 0.11 | **0.08** | **0.76** | 0.07 | **−0.13** | 0.18 | 0.00 | **0.08** | −0.10 |

When controlling for area using the index PA (related to the amount of time spent active per unit area of river) the variables that showed consistent relationships with all seven otters were boulders (mean coefficient = 0.27, S.E. = 0.8, range = 0.03-0.0.57; Mann-Whitney $U$ = 0, d.f. = 13, $P$ < 0.001), reeds (mean coefficient = 0.42, S.E. = 0.08, range = 0.14-0.76; Mann-Whitney $U$ = 0, d.f. = 13, $P$ < 0.001) and overhanging vegetation (mean coefficient = 0.21, S.E. = 0.04, range = 0.07-0.35; Mann-Whitney $U$ = 0, d.f. = 13, $P$ < 0.001). The four otters in the Olifants River showed a preference for areas with soil. Although the pattern did not extend to the otters of the Eerste River the relationship across all the otters was significant (mean coefficient = 0.12, S.E. = 0.04, range = -0.03-0.32; Mann-Whitney $U$ = 7, d.f. = 13, $P$ = 0.03). Otters M2, F2 and F3 selected for wide areas.

## DISCUSSION

Both indexes show that the seven otters selected habitats with reeds and boulders. Personal observations confirmed this, as the otters would forage in and around individual patches of reeds – sometimes for hours.

*Aonyx capensis* occur over most of sub-Saharan Africa (Rowe-Rowe & Somers 1998; Nel & Somers in press) using diverse habitats, from the mangrove forests of KwaZulu-Natal Province (personal observation) to the desert conditions of the upper Doring River and Fish River in southern Namibia (Nel unpublished data). It appears that only where there is no fresh water, do they not occur. They have been found in towns (e.g. Stellenbosch) and cities (e.g. Port Elizabeth, Cape Town) (personal observations). They occur in rivers with high pollution and eutrophication levels (Heath & Claassen 1999; Nel & Somers unpublished data). No data are, however, available on their relative densities in these areas and the present data are the first on their habitat selection.

Irrespective of the width of the rivers or dams, there was a general trend for the otters to spend a greater proportion of their time in areas with reed beds and boulders. When controlling for area the otters also selected areas with overhanging vegetation. Except for otter M2 and F2 the otters did not select for wide areas. Otters M2 and F2 extensively used Kleinplaas and Bulshoek dams respectively while foraging (Chapter 3). When controlling for area, otter F3 also selected for width. This otter extensively used the upper part of Bulshoek dam. The reason the otters avoided canals may be that crab density is much reduced in canals (Mayfield 1993). As refuge size and availability are important in determining population structure of many aquatic organisms (Beck 1995 and references therein), size distribution of the crab population may be determined by the availability of refuges created by the number and size of substrate particles. This has been supported by Somers & Nel (1998) who showed that where there are fewer, larger substrate particles, there are fewer but larger crabs. This indicates that substrate size may be of critical importance to otters. As crab size increases the amount of vegetable material in their diet increases (Raübenheimer 1986; Hill & O'Keeffe 1992). The reed beds may therefore be a source of refugia for the crabs and a source of food for the larger crabs. The otters therefore appear to be selecting habitats with high prey density. There are also more crabs in reed beds than in open, sandy or rocky areas (Chapter 2). The importance of the conservation of crab habitat for the conservation of *A. capensis* is therefore critical. These results also emphasise the need for further work on the ecology of African freshwater crabs, of which little is known.

In environments with low human populations, habitat use by otters may reflect the search for prey only. In the conditions studied here the selection of reed beds and overhanging vegetation may be a means of increasing safety from humans, while living in close proximity to them.

This study offers an opportunity to compare the results with those where habitat selection was implied from the distribution

and density of otters sign (e.g. Carugati 1995; Perrin & Carugati 2000b). The methods used by Carugati (1995) and Perrin and Carugati (2000b) are quicker, less expensive and less invasive to the otters and would therefore be preferred, if proved reliable estimates of habitat use by *A. capensis*. Perrin & Carugati (2000b) found the otters select, for time spent on land, undisturbed areas with rock cover and natural dense vegetation. This is similar to the results of the present radio-tracking study. A notable exception is that the otters did not seem to avoid disturbed areas as reported by Perrin & Carugati (2000b). The reason for this may be that although otters forage near anthropogenic disturbances they do not use these areas for sprainting or resting (i.e. landing). Another explanation may be that the otters in the present study areas are more habituated to anthropogenic influences because there is more disturbance than in the study area of Perrin & Carugati (2000b). Further supporting the present findings is the evidence that along the marine coasts *A. capensis* select places of activity on land to be near thick vegetation, abundant food resource and fresh water (van der Zee 1982; Arden-Clarke 1986; van Niekerk *et al.* 1998).

Durbin (1998) shows a trend towards narrow areas with trees being selected. In the terrestrial habitat of freshwater areas *L. lutra* show preference for islands and for reed beds, but they rest or sleep almost anywhere with a cover of vegetation or rocks. While foraging, they prefer narrow parts of rivers that are shallow, with a high fish biomass, or marshy areas with amphibians (Kruuk *et al.* 1998).

As with Durbin (1998), the results are based on consistent patterns between a few individuals (seven in the present study), resulting in the conclusions being conservative. This means that habitat selection at the population level might be missed. These two studies, however, were done in two rivers with habitats which differ, which somewhat obviates this limitation. The present results may, however, only be applicable to rivers in the Western Cape Province. As 200-m sections were used, some detailed patterns of small-scale habitat use will have been lost.

Consistent relationships, however, indicate a behavioural response and may be of conservation significance (Durbin 1998). The importance of scale in habitat use studies has been stressed by many (e.g. Morris 1987; Orians & Wittenberger 1991). Studies done at several scales improve the resolution of factors that determine ecological patterns and their interrelationships among scales (Wiens 1989). Data on otter densities in different river systems, which are presently lacking, are needed to determine large-sale habitat selection. Owing to the difficulty of observing the otters in freshwater systems it would also be extremely difficult to measure small-scale habitat selection. Some attempt at detailed habitat use in the marine environment has been made (Somers 2000a, 2000b (Chapters 5 & 6)). In these studies, however, the otters were not radio-tracked and habitat use could only be determined in a limited area and in one habitat type. There was differential use of depths by the otters and the otters selected specific depths in which to forage (Somers 2000b (Chapter 6)). The present data, although only on one scale, are useful in determining which habitat types are preferred. From these data, predictions as to how other systems would be used by *A. capensis,* can be made. The data also provide direction for future research.

Although the use of the models based on the amount of time spent per unit length and space may seem appropriate for otters (Durbin 1998), *A. capensis* seldom forage more than *ca* 8 m from the shore (personal observations). The use of the area index may therefore be inappropriate for the wide Olifants River where most of the water surface area is not used by the otters (see also Chapter 3).

Although South Africa has international legal obligations through the "Convention on Biological Diversity" treaty to protect its biological diversity, its rivers are in a state of critical conservation status (Davies & Day 1998). With the ever-decreasing quality of freshwater systems in South Africa and elsewhere in Africa (Davies & Day 1998), increasing water use by invading alien plants (Le Maitre *et al.* 2000) and impending

climate change (Schmandt 1992), the fate of many aquatic species is unclear. Most of Southern Africa is expected to become considerably more arid (Schmandt 1992), probably affecting most taxa. The affects on aquatic organisms are likely to be severe as river systems change or dry up totally.

Scientists are being asked what these affects are going to be and what can be done to avoid or minimize them. For many aquatic species there are very few data on how they use their habitats. These data are needed to predict the affects of future changes. For example the present results suggest that submerged macrophytes are important habitat types for otters. With increasing silting up of rivers (Davies & Day 1998) these habitat types are at risk through increased flooding (Colloty *et al.* 2000).

The results show, that the otters radio-tracked did not use the entire home range uniformly and their presence was most frequent in areas with reeds and boulders: The hypothesis can therefore be rejected.

## REFERENCES

AEBISCHER, N.J., ROBERTSON, P.A. & KENWARD, R.E. 1993. Composition analysis of habitat use from animal radio-tracking data. *Ecology* **74**: 1313-1325.

ALLDREDGE, J.R. & RATTI, J.T. 1986. Comparison of some statistical techniques for analysis of resource selection. *Journal of Wildlife Management* **50**: 157-165.

ALLDREDGE, J.R. & RATTI, J.T. 1992. Further comparison of some statistical techniques for analysis of resource selection. *Journal of Wildlife Management* **56**: 1-9.

ARDEN-CLARKE, C.H.G. 1986. Population density, home range size and spatial organization of the Cape clawless otter, *Aonyx capensis*, in a marine habitat. *Journal of Zoology, London* **209**: 201-211.

117

BARBARESI, S., GHERARDI, F. & VANNINI, M. 1997. Movement patterns of river crabs (Decapoda, Potamoidea) in the field: predictable and unpredictable components. *Journal of Zoology, London* **242**: 247-259.

BECK, M.W. 1995. Size-specific shelter limitation in stone crabs: a test of the demographic bottleneck hypothesis. *Ecology* **776**: 968-980.

BUTLER, J.R.A. & DU TOIT, J.T. 1994. Diet and conservation of Cape clawless otters in eastern Zimbabwe. *South African Journal of Wildlife Research* **24**: 41-47.

CARUGATI, C. 1995. Habitat, prey, and area requirements of otters (*Aonyx capensis* and *Lutra maculicollis*) in the Natal Drakensberg. M.Sc. thesis, University of Natal, Pietermaritzburg, South Africa

COLLOTY, B.M., ADAMS, J.B. & BATE, G.C. 2000. The use of a botanical importance rating to assess changes in the flora of the Swartkops Estuary over time. *Water SA* **26**: 171-180.

CONNER, M.M., PLOWMAN, B.P., LEOPOLD, B.D. & LOVELL, C. 1999. Influence of time-in-residence on home range and habitat use of bobcats. *Journal of Wildlife Management* **63**: 261-269.

CONROY, J.W.H. & FRENCH, D.D. 1987. The use of spraints to monitor populations of otters (*Lutra lutra* L.). *Symposia of the Zoological Society of London* No. 58: 247-262.

CROOKS, K.R. & VAN VUREN, D. 1995. Resource utilization by two insular endemic mammalian carnivores, the island fox and spotted skunk. *Oecologia* **104**: 301-307.

DAVIES, B.R. & DAY, J.A. 1998. *Vanishing waters*. University of Cape Town Press, Cape Town.

DURBIN, L.S. 1993. Food and Habitat Utilization of Otters (*Lutra Lutra L.)* in a Riparian Habitat. D. Phil. thesis, University of Aberdeen, Aberdeen, Scotland.

DURBIN, L.S. 1996a. Some changes in the habitat use of free-ranging female otter *Lutra lutra* during breeding. *Journal of Zoology, London* **240**: 761-764.

DURBIN, L.S. 1996b. Individual differences in spatial utilization of a river-system by otters *Lutra lutra*. *Acta Theriologica*

**41:** 137-147.

DURBIN, L.S. 1998. Habitat selection by five otters *Lutra lutra* in rivers of northern Scotland. *Journal of Zoology, London* **245:** 85-92.

EEKHOUT, S., KING, J.M. & WACKERNAGEL, A. 1997. *Classification of South African river, volume 1.* Department of Environment Affairs and Tourism, Pretoria.

EMLEN, J.M. 1966. The role of time and energy in food preference. *American Naturalist* **100:** 611-617.

ESTES, J.A. 1989. Adaptations for aquatic living by carnivores. In: *Carnivore behavior, ecology and evolution,* (ed) J.L. Gittleman, Chapman and Hall, London.

GESE, E.M., RONGSTAD, O.J. & MYTTON, W.R. 1988. Home range and habitat use of coyotes in southeastern Colorado. *Journal of Wildlife Management* **52:** 640-646.

GREEN, J., GREEN, R. & JEFFERIES, D.J. 1984. A radio-tracking survey of otters *Lutra lutra* on a Perthshire river system. *Lutra* **27:** 85-145.

HARRIS, S., CRESSWELL, W.J., FORDE, P.G., TREWHELLA, W.J., WOOLLARD, T. & WRAY, S. 1990. Home-range analysis using radio-tracking data - a review of problems and techniques particularly as applied to the study of mammals. *Mammal Review* **20:** 97-123.

HARRISON, T.D. 1997. A preliminary survey of coastal river systems on the South African west coast, Orange River - Groot Berg, with particular reference to the fish fauna. *Transactions of the Royal Society of South Africa* **52:** 277-321.

HEATH, R.G.M. & CLAASSEN, M. 1999. *An overview of the pesticide and metal levels present in populations of the larger indigenous fish species of selected South African rivers.* WRC Report No. 428/1/99, Water Research Commission, Pretoria.

HEINECKEN, T.J.E., BICKERTON, I.B. & HEYDORN, A.E.F. 1983. A *summary of studies of the pollution input by rivers and estuaries entering False Bay.* Council for Scientific and Industrial Research, Stellenbosch.

HILL, M.P. & O'KEEFFE, J.H. 1992. Some aspects of the ecology of the freshwater crab (*Potamonautes perlatus* Milne Edwards) in the upper reaches of the Buffalo River, eastern Cape Province, South Africa. *South African Journal of Aquatic Sciences* **18**: 42-50.

HUSSAIN, S.A. & CHOUDHURY, B.C. 1995. Seasonal movement, home range, and habitat use by smooth coated otters in National Chambal Sanctuary, India. *Habitat* **11**: 45-55

KOPP, S.D., GUTHERY, F.S., FORRESTER, N.D. & COLE, L.C. 1998. Habitat selection modeling for northern bobwhites on subtropical rangeland. *Journal of Wildlife Management* **62**: 884-895.

KREBS, J.R. & KACELNIK, A. 1991. Decision making. In: *Behavioural ecology an evolutionary approach*, (eds) J.R. Krebs, & N.B. Davies, 3rd edn, Blackwell Scientific Publications, Oxford.

KRUUK, H. 1992. Scent marking by otters (*Lutra lutra*): signaling the use of resources. *Behavioral Ecology* **3**: 133-140.

KRUUK, H. 1995. *Wild otters: Predation and populations*. Oxford University Press, Oxford.

KRUUK, H., CARSS, D.N., CONROY, J.W.H. & DURBIN, L.S. 1993. Otter (*Lutra lutra* L.) numbers and fish productivity in rivers in north-east Scotland. *Symposia of the Zoological Society of London* No. 65: 171-191.

KRUUK, H., TAYLOR, P.T. & MOM, G.A.T. 1997. Body temperature and foraging behaviour of the Eurasian otter (*Lutra lutra*), in relation to water temperature. *Journal of Zoology, London* **241**: 689-697.

KRUUK, H., CARSS, D.N., CONROY, J.W.H. & GAYWOOD, M.J. 1998. Habitat use and conservation of otters (*Lutra lutra*) in Britain: a review. *Symposia of the Zoological Society of London* No. 71: 119-133.

KRUUK, H., CONROY, J.W.H., GLIMMERVEEN, U. & OUWERKERK, E.J. 1986. The use spraints to survey populations of otter *Lutra lutra*. *Biological Conservation* **35**: 187-194.

JOHNSON, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* **61**: 65-71.

LE MAITRE, D.C., VERSFELD, D.B. & CHAPMAN, R.A. 2000. The impact of invading alien plants on surface water resources in South Africa: A preliminary assessment. *Water SA* **26**: 397-408.

MACARTHUR, R.H. & PIANKA, E.R. 1966. On optimal use of a patchy environment. *American Naturalist* **100**: 603-609.

MASON, C.F. & MACDONALD, S.M. 1986. *Otters: ecology and conservation.* Cambridge University Press, Cambridge.

MAYFIELD, S. 1993. Aspects of the distribution, population structure and feeding biology of the freshwater crab *Potamonautes perlatus* (Milne Edwards) (Decapoda: Potamonidae) in the Liesbeek River, western Cape, South Africa. B.Sc. (Hons) thesis, University of Cape Town, Cape Town, South Africa.

MCKENZIE, A.A., MELTZER, D.G.A., LE ROUX, P.G. & GOSS, R.A. 1990. Use of implantable radio transmitters in large African carnivores. *South African Journal of Wildlife Research* **20**: 33-35.

MELQUIST, W.E. & HORNOCKER, M.G. 1983. Ecology of river otters in west central Idaho. *Wildlife Monographs* **83**: 1-60.

MILLS, M.G.L. 1990. *Kalahari hyaenas: The comparative behavioural ecology of two species.* Unwin Hyman, London.

MORRIS, D.W. 1987. Ecological scale and habitat use. *Ecology* **68**: 362-369.

NEL, J.A.J. & SOMERS, M.J. In press. The status of otters in Africa: an assessment. *Habitat* No. 13:

ORIANS, G.H. & WITTINGER, J.F. 1991. Spatial and temporal scales in habitat selection. *American Naturalist* **137(supplement):** 29-49.

PALOMARES, F. & DELIBES, M. 1992. Data analysis design and potential bias in radio-tracking studies of animal habitat use. *Acta Oecologica* **13**: 221-226.

PERRIN, M.R. & CARUGATI, C. 2000a. Food habits of coexisting Cape clawless otter and spotted-necked otter in the KwaZulu-Natal

Drakensberg, South Africa. *South African Journal of Wildlife Research* **30**: 85-92.

PERRIN, M.R. & CARUGATI, C. 2000b. Habitat use by the Cape clawless otter and the spotted-necked otter in the KwaZulu-Natal Drakensberg, South Africa. *South African Journal of Wildlife Research* **30**: 103-113.

PERRIN, M.R. & D'INZILLO CARRANZA, I. 2000. Habitat use by spotted-necked otters in the KwaZulu-Natal Drakensberg, South Africa. *South African Journal of Wildlife Research* **30**: 8-14.

PERRIN, M.R., D'INZILLO CARRANZA, I. & Linn, I.J. 2000. Use of space by the spotted-necked otter in the Natal Drakensberg, South Africa. *South African Journal of Wildlife Research* **30**: 15-21.

RALLS, K. 1997. On becoming a conservation biologist: autobiography and advice. In: *Behavioral approaches to conservation in the wild,* (eds) J.R. Clemmons & R. Buchholz, Cambridge University Press, Cambridge.

RALLS, K., HATFIELD, B.B. & SINIFF, D.B. 1995. Foraging patterns of California sea otters as indicated by telemetry. *Canadian Journal of Zoology* **73**: 523-531.

RASA, O.A.E. 1983. Dwarf mongoose and hornbill mutualism in the Taru Desert, Kenya. *Behavioral Ecology and Sociobiology* **12**: 181-190.

RASA, O.A.E. 1986. Ecological factors and their relationships to group size, mortality and behaviour in the dwarf mongoose *Helogale undulata* (Peters, 1852). *Cimbebasia* **8**: 15-21.

RAÜBENHEIMER, C.D. 1986. Aspects of the biology of the freshwater crab, *Potamonautes sidneyi*, with particular reference to general seasonality and female aggression. M.Sc. thesis, University of Natal, Durban, South Africa.

ROWE-ROWE, D.T. 1992. Survey of South African otters in freshwater habitat, using sign. *South African Journal of Wildlife Research* **22**: 49-55.

ROWE-ROWE, D.T. & SOMERS, M.J. 1998. Diet, foraging behaviour and coexistence of African otters and the water mongoose. *Symposia of the Zoological Society of London* No. 71: 215-227.

SCHMANDT, J. 1992. *The regions and global warming impacts and response strategies*. Oxford University Press, New York.

SIEGEL, S. 1956. *Nonparametric statistics for the behavioral sciences*. McGraw-Hill Book Company, New York.

SOMERS, M.J. 2000a. Seasonal variation in the diet of Cape clawless otters (*Aonyx capensis*) in a marine habitat. *African Zoology* **35**: 261-268.

SOMERS, M.J. 2000b. Foraging behaviour of Cape clawless otters (*Aonyx capensis*) in a marine habitat. *Journal of Zoology, London* **252**: 473-480.

VAN DER ZEE, D. 1981. Prey of the Cape clawless otter (*Aonyx capensis*) in the Tsitsikama National Park, South Africa. *Journal of Zoology, London* **194**: 467-483.

VAN DER ZEE, D. 1982. Density of Cape clawless otters *Aonyx capensis* (Schinz, 1821) in the Tsitsikama Coastal National Park. *South African Journal of Wildlife Research* **12**: 8-12.

VAN NIEKERK, C.H., SOMERS, M.J. & NEL, J.A.J. 1998. Freshwater availability and distribution of Cape clawless otter spraints and resting places along the south-west coast of South Africa. *South African Journal of Wildlife Research* **28**: 68-72.

VERWOERD, D.J. 1987. Observations on the food and status of the Cape clawless otter *Aonyx capensis* at Betty's Bay, South Africa. *South African Journal of Zoology* **22**: 33-39.

WALLER, J.S. & MACE, R.D. 1997. Grizzly bear habitat selection in the swan mountains, Montana. *Journal of Wildlife Management* **61**: 1032-1039.

WEBER, J.-M. & DAILLY, L. 1998. Food habits and ranging behaviour of a group of farm cats (*Felis catus*) in a Swiss mountainous area. *Journal of Zoology, London* **245**: 234-237.

WIENS, J.A. 1989. Spatial scaling in ecology. *Functional Ecology* **3**: 385-397.

# CHAPTER 5[*]

# SEASONAL VARIATION IN THE DIET OF CAPE CLAWLESS OTTERS (*AONYX CAPENSIS*) IN A MARINE HABITAT

## INTRODUCTION

Optimal foraging theory (MacArthur & Pianka 1966; Stephens & Krebs 1986) predicts that when food is scarce, individuals cannot be as particular about what they eat as when food is abundant. As a result, diets are predicted to be broader during 'lean seasons' than during 'rich seasons'. This is probably optimal foraging theory's most robust theorem to date (Perry & Pianka 1997). The diets of animals are therefore expected to change with the seasons, being more diverse in winter than in summer. In certain circumstances this may, however, be reversed with the leaner period being summer. For piscivorous predators the leaner period may also be related to the ability of the predator to catch prey, rather than prey abundance. Colder water enables fish to be caught more easily as they are more lethargic (Rowe-Rowe 1977a). In cold water, piscivorous predators could therefore afford to be more selective than in warmer water where the prey can move faster. In False Bay, Western Cape Province, South Africa, sea temperature in winter is significantly colder than in other seasons, but neither the total number nor the overall densities of fish fluctuate seasonally (Clark *et al.* 1996). This locality therefore affords an opportunity to test the hypothesis that diversity (i.e. the number of prey species, their relative

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contribution, and size distribution) in the diet of piscivorous predators is influenced by their ability to catch prey, rather than just prey abundance. One such predator feeding on fish and crustaceans in the surf zone in False Bay is the Cape clawless otter *Aonyx capensis* (Schinz, 1821).

*Aonyx capensis* weigh between 10 and 18 kg, males being larger than females. They use freshwater habitats extensively (see Rowe-Rowe & Somers 1998 for a review) but also use marine habitats for food such as Cape rock crab *Plagusia chabrus*, shore crab *Cyclograpsus punctatus*, Cape rock lobster *Jasus lalandii*, octopus *Octopus granulatus,* and various species of fish (Van der Zee 1981; Arden-Clarke 1983; Verwoerd 1987). Of these studies only Van der Zee (1981) provides seasonal data on four prey species and their relation to availability. As has been shown for European otters *Lutra lutra* (Kruuk 1995), *A. capensis* also appear to only use marine habitats in the presence of fresh water (van Niekerk *et al.* 1998). In the marine habitat of Tsitsikama National Park, Eastern Cape Province, South Africa, they are mainly nocturnal (Arden-Clarke 1983). Crustaceans have been shown in most studies to be the most common prey of *A. capensis* in freshwater ecosystems, supplemented with lesser amounts of frogs, fish, and aquatic insects (Rowe-Rowe & Somers 1998 and references therein). Birds, reptiles, molluscs, dung (ungulate) and mammals are all minor items, seldom eaten. In freshwater habitats *A. capensis* are active mainly during late afternoon, early evening, and early morning (Rowe-Rowe 1977a, 1978; Chapter 3).

This study quantifies sizes of marine crustaceans eaten by *A. capensis*, using length of eyestalks found in spraints (Purves *et al.* 1994). The sizes of the fish eaten are also determined, using the diameter of otoliths (Smale *et al.* 1995) in the spraints. Otoliths have long been recognised as a tool for determining the diet of piscivorous predators (Fitch & Brownell 1968; Ross 1984), but have not previously been used for otters. The energetics of prey capture, however, fall outside the scope of this chapter; no data are available on energetic requirements of *A. capensis*, or the energetic content of different prey species.

In this chapter I present data on the seasonal diet of *A. capensis* in a marine habitat as determined by spraint analysis.

As little is known about use of marine environments by *A. capensis* (Estes 1994) this chapter also aims to contribute to the knowledge on which future conservation management plans for the species could be based.

## MATERIALS & METHODS

Spraints were collected, and visual observations made, on *A. capensis* foraging and feeding, from 7 September 1995 to 10 October 1996, along a 2-km stretch of the southwestern corner of False Bay, just South West of Rooi-Els (33° 19' S, 26° 05' E), Western Cape Province, South Africa.

The coast here is highly exposed, with broad (up to 40 m) surf zones. Four small, perennial, freshwater streams (*ca* 0.5-2 m wide and *ca* 50-500 mm deep, depending on season) enter the sea within this 2 km stretch. A road parallel to the coast and 3-5 m above and 15-20 m away from the high water mark, facilitates access.

The mean sea temperature varies with season: summer, 21.5°C; spring, 18.2°C; autumn, 17.1°C; and winter, 13.2°C. Winter sea temperature is significantly lower than that of the other seasons (Clark *et al.* 1996). The climate type is Mediterranean with cold, wet winters and hot, dry summers (Schulze 1965). The mean tidal range in False Bay is 1.48 m (Spargo 1991) and mean salinities range from *ca* 35.0-35.3‰ (Atkins 1970).

Identification of *A. capensis* spraints in the field was based on their characteristic odour, diameter and appearance (Rowe-Rowe 1992). Two hundred and four spraints were collected during the study. Spraints were air-dried, teased apart and prey remains identified using a stereomicroscope (X 10-100 magnification). Prey items were sorted into the following categories: *P. chabrus*, *C. punctatus*, freshwater crab *Potamonautes perlatus*, *J. lalandii*, *O. granulatus*, fish, frog, mammal, and unidentified items. The

presence of mammals was based on hair, crabs from carapaces, fish from bones, scales and otoliths, and frogs from bones. Otoliths were removed and identified to species level (Smale *et al.* 1995). Misidentification may occur when using otoliths to identify fish but this was circumvented (Smale *et al.* 1995) by identifying those fishes that occur in the area (Smith & Heemstra 1986; Clark *et al.* 1996). Two hundred and six otoliths were found in 103 spraints. Of these, 16 were complete yet unidentifiable, 45 were broken but identifiable, 109 were undamaged, measurable and identifiable and 36 broken and unidentifiable.

The presence of each prey category in each spraint was scored, and the percentage occurrence of each prey category calculated. Scores for each category were also added and expressed as a percentage of the total number of scores of all categories, yielding relative percentage occurrence. This method has been shown to closely approximate the proportions of different items actually consumed by *L. lutra* (Erlinge 1968) and *A. capensis* (Rowe-Rowe 1977b). Carss & Parkinson (1996), however, showed that for *L. lutra* it should only be used to rank importance of prey in the diet.

For comparisons with direct observations (Somers 2000 (Chapter 6)) and other studies, the rank order of all fish species, all crab species, *J. lalandii* and *O. granulatus* in the diet was determined using relative percentage occurrence data.

For each spraint the dominant prey type was also determined by volumetric analysis of remains of prey items. For this analysis, in a spraint consisting mainly of crab remains, crab would be the dominant prey type and the other prey items ignored. The different dominant prey items were then added and expressed as a percentage of the total number of spraints (Kruuk *et al.* 1994; Purves *et al.* 1994; Somers 2000 (Chapter 6)).

The diet was determined for the four seasons: winter (June-August); spring (September-November); summer (December-February) and autumn (March-May).

Following Arden-Clarke (1983), gastropods, isopods, amphipods, insects and unidentified crustacean larvae were

excluded from these analyses. These were all minor items in the spraints and were probably not food, but had entered the spraints after defaecation, or were attached to prey. They were, however, combined as an "other" category.

Prey diversity was, based on an analysis of 21, 58, 83 and 42 spraints respectively, compared between seasons using the Shannon-Wiener index (Krebs 1985).

$$H = -\sum_{i=1}^{S} (p_i)(\log_2 p_i)$$

Where,

$H$ = index of species diversity,

$S$ = number of species

and $p_i$ = proportion of total sample belonging to the $i$th species.

Diversity was also calculated using Simpson's diversity index

$$D = 1 - \sum_{i=1}^{s} (Pi)^2$$

where $D$ = Simpson's index of diversity and $p_i$ = proportion of individual of species $i$ in the community (Krebs 1985).

Equitability or evenness of representation E (range 0-1) of each species was calculated as

$$E = H/H_{max}$$

where $H_{max}$ is $\log_2 S$ and $H$ = observed diversity (Krebs 1985).

*Jasus lalandii* ($n$ = 12, mean carapace length = 79.1 mm, S.E. = 5.0 mm, range = 70.2-89.9 mm), *P. chabrus* ($n$ = 10, mean carapace length = 32.7 mm, S.E. = 2.6 mm, range 20.0-45.0 mm) and *C. punctatus* ($n$ = 7, mean carapace length = 39.0 mm, S.E. = 5.0 mm, range = 22.8-60.1 mm) were collected from shallow areas or found dead on the beach. *Jasus lalandii* and crabs were air-dried. The maximum carapace length of the *J. lalandii* and maximum carapace widths of the crab species were measured with callipers

and eyestalk lengths were measured with an ocular ruler in a stereo microscope. Regressions were calculated for carapace size and eyestalk lengths (Purves *et al.* 1994).

For *J. lalandii* there was a significant linear relationship ($r^2 = 0.84$, $n = 12$, S.E. = 2.10%, $P < 0.001$) for which C = 49.25+(15.81*E), where C = carapace length (mm) and E = eye stalk length (mm). For *C. punctatus* there was a significant linear relationship ($r^2 = 0.96$, $n = 7$, S.E. = 2.95%, $P < 0.001$) for which C = -10.65+(6.8*E). For *P. chabrus* there was a significant linear relationship ($r^2 = 0.95$, $n = 10$, S.E. = 2.0%, $P < 0.001$) for which C = -7.2 (7.11*E). For *P. perlatus* the regression, determined for crabs in the Olifants River, Western Cape Province, (Purves *et al.* 1994) was used: C = -11.48+(8.33*E). This correlation was also significant ($r^2 = 0.99$, $n = 66$, $P < 0.001$).

Lengths of eyestalks of all four crustacean species found in the spraints, were measured. The equations were then used to determine size of crabs and *J. lalandii* eaten by the otters. The sizes of the fishes were also determined, from published regressions using otolith diameter (Smale *et al.* 1995).

The amount of fish in the diet was compared with their availability during the different seasons, as determined by Clark *et al.* (1996).

Statistical tests used are mentioned at appropriate points in the text, the level of significance being *p* = 0.05. Statistical tests were done using the computer programme SigmaStat for Windows 95 version 2.0, Jandel Corporation©.

## RESULTS

Nearly all prey of *A. capensis* in False Bay were benthic marine species (Tables 5.1–5.4). Using the relative per cent occurrence data to rank the various prey the most common prey species of *A. capensis* was *P. chabrus* during all seasons, followed by *J. lalandii*.

**Table 5.1.** Prey items recorded in 21 Cape clawless otter *Aonyx capensis* spraints collected from False Bay during winter (June, July and August 1996), as percentage occurrence, relative frequency occurrence, and percentage of spraints dominated by a prey.

| Prey | Observed | % Occur. | Rel. freq. Occur. | % Dominance |
|---|---|---|---|---|
| **Crustacean** | 16 | 76.2 | 44.4 | 55.0 |
| *Plagusia chabrus** | (11) | (52.4) | (30.6) | (40.0) |
| *Potamonautes perlatus** | (1) | (4.8) | (2.8) | (5.0) |
| *Jasus lalandii** | (4) | (19.0) | (11.1) | (15.0) |
| **Fish** | 19 | 90.5 | 52.8 | 40.0 |
| *Clinus superciliosus** | (4) | (19.0) | (11.1) | |
| *Coryphaena hippurus* | (1) | (4.8) | (2.8) | |
| *Sarpa salpa* | (2) | (9.5) | (5.6) | |
| Unidentified | (6) | (28.6) | (16.7) | |
| **Mammal** | 1 | 4.8 | 2.8 | |
| **Other** (non food) | 9 | | | |

*Benthic species

**Table 5.2.** Prey items recorded in 58 Cape clawless otter *Aonyx capensis* spraints collected from False Bay during spring (September, October and November 1996), as percentage occurrence, relative per cent occurrence, and percentage of spraints dominated by a prey.

| Prey | Observed | % Occur. | Rel. freq. Occur. | % Dominance |
|---|---|---|---|---|
| **Crustacean** | 52 | 89.6 | 52.5 | 63.8 |
| *Plagusia chabrus** | (30) | (51.7) | (30.3) | (43.1) |
| *Cyclograpsus punctatus** | (2) | (3.4) | (2.0) | (1.7) |
| *Potamonautes perlatus** | (1) | (1.7) | (1.0) | |
| *Jasus lalandii** | (19) | (32.8) | (19.2) | (19.0) |
| **Fish** | 45 | 77.6 | 45.5 | 36.2 |
| *Cheilodactylus fasciatus** | (4) | (6.9) | (4.0) | |
| *Chirodactylus brachydatylus** | (1) | (1.7) | (1.0) | |
| *Chorisochismus dentex** | (2) | (3.5) | (2.1) | |
| *Clinus superciliosus** | (7) | (12.1) | (7.1) | |
| *Galeichthys feliceps** | (1) | (1.7) | (1.0) | |
| *Gonorynchus gonorynchus** | (1) | (1.7) | (1.0) | |
| *Halidesmus scapularis** | (1) | (1.7) | (1.0) | |
| *Heteromycteris capensis** | (1) | (1.7) | (1.0) | |
| *Pomatomus saltatrix* | (1) | (1.7) | (1.0) | |
| *Serranus cabrilla* | (1) | (1.7) | (1.0) | |
| Unidentified | (12) | (20.7) | (12.1) | |
| **Frog** | 1 | 1.7 | 1.0 | |
| **Mammal** | 1 | 1.7 | 1.0 | |
| **Other** (non food) | 28 | | | |

*Benthic species

**Table 5.3.** Prey items recorded in 83 Cape clawless otter *Aonyx capensis* spraints collected from False Bay during summer (December 1995, January and February 1996), as percentage occurrence, per cent frequency occurrence, and percentage of spraints dominated by a prey.

| Prey | Observed | % Occur. | Rel. freq. Occur. | % Dominance |
|---|---|---|---|---|
| **Crustacean** | 70 | 84.3 | 49.0 | 56.6 |
| *Plagusia chabrus*\* | (44) | (53.0) | (30.8) | (37.3) |
| *Cyclograpsus punctatus*\* | (1) | (1.2) | (0.7) | |
| *Potamonautes perlatus*\* | (5) | (6.0) | (3.5) | (3.6) |
| *Jasus lalandii*\* | (20) | (24.0) | (13.9) | (15.7) |
| **Mollusc** | | | | |
| *Octopus granulatus*\* | 7 | 8.4 | 4.9 | |
| **Fish** | 66 | 79.5 | 46.2 | 43.4 |
| *Cheilodactylus fasciatus*\* | (14) | (16.9) | (26.92) | |
| *Chorisochismus dentex*\* | (2) | (2.4) | (3.85) | |
| *Clinus supercilious*\* | (7) | (8.4) | (13.46) | |
| *Galeichthys feliceps*\* | (4) | (4.8) | (7.69) | |
| *Gilchristella aestuaria* | (1) | (1.2) | (1.92) | |
| *Halidesmus scapularis*\* | (1) | (1.2) | (1.92) | |
| *Heteromycteris capensis*\* | (1) | (1.2) | (1.92) | |
| *Pomatomus saltatrix* | (3) | (3.6) | (5.77) | |
| *Rhabdosargus holubi* | (1) | (1.2) | (1.92) | |
| *Sarpa salpa* | (2) | (2.4) | (3.85) | |
| *Serranus cabrilla* | (1) | (1.2) | (1.92) | |
| *Solea bleekeri*\* | (1) | (1.2) | (1.92) | |
| Unidentified | (16) | (19.3) | (26.92) | |
| **Other** (non food) | 52 | | | |

\*Bottom-dweller

**Table 5.4.** Prey items recorded in 42 Cape clawless otter *Aonyx capensis* spraints collected from False Bay during autumn (March, April and May 1996), as percentage occurrence, per cent frequency occurrence, and percentage of spraints dominated by a prey.

| Prey | Observed | % Occur. | Rel. freq. Occur. | % Dominance |
|---|---|---|---|---|
| **Crustacean** | 23 | 54.8 | 32.8 | 31.0 |
| *Plagusia chabrus** | 11 | (26.2) | (15.7) | (19.0) |
| *Potamonautes perlatus** | 2 | (4.8) | (2.9) | (4.8) |
| *Jasus lalandii** | 10 | (23.8) | (14.3) | (7.1) |
| **Mollusc** | | | | |
| *Octopus granulatus** | 9 | 21.4 | 12.8 | |
| **Fish** | 38 | 90.5 | 54.3 | 69.0 |
| *Atherina breviceps* | (1) | (2.4) | (1.4) | |
| *Cheilodactylus fasciatus** | (8) | (19.1) | (11.4) | |
| *Chorisochismus dentex** | (5) | (11.9) | (7.1) | |
| *Clinus superciliosus** | (7) | (16.7) | (10.0) | |
| *Diplodus sargus capensis* | (1) | (2.4) | (1.4) | |
| *Heteromycteris capensis** | (1) | (2.4) | (1.4) | |
| *Pomatomus saltatrix* | (3) | (7.1) | (4.3) | |
| *Sarpa salpa* | (1) | (2.4) | (1.4) | |
| *Umbrina canariensis* | (1) | (2.4) | (1.4) | |
| Unidentified | (14) | (33.3) | (20.0) | |
| **Other** (non food) | 29 | | | |

*Benthic species

In winter the fish *Clinus superciliosus* was of equal importance. Other prey included the crustaceans *C. punctatus*, and *P. perlatus*, the mollusc *O. granulatus*, and an additional 17 fish species, frogs and mammals (Tables 5.1-5.4). Using rank and percentage dominance, fish was the most important prey category in winter and autumn while crustacean was the most important in spring and summer (Tables 5.1-5.4). When separating *J. lalandii* from the crab species, the ranking of the three most important prey categories was (1) fish (2) crabs (3) *J. lalandii* for all seasons (Table 5.5).

Only for *Cheilodactylus fasciatus* and *C. superciliosus* were sample sizes large enough for seasonal comparison. For these two fish species Kruskal-Wallis one way analysis of variance on ranks indicated that there were no significant differences in the size of fish represented in the spraints in different seasons ($H = 0.68$, d.f. $= 2$, $P = 0.712$; $H = 0.59$, d.f. $= 3$, $P = 0.900$) respectively. There was also no significant difference in the sizes of all fish species combined ($H = 7.65$, d.f. $= 3$, $P = 0.054$) during the different seasons.

However, when comparing only summer and winter fish, there was a significant difference between the sizes of fish found in the spraints (Mann-Whitney $U = 285$, d.f. $= 48$, $P = 0.007$, two-tailed test). In addition, *A. capensis* also ate the widest size range of fish (Table 5.7), and preyed on the largest number of species (Tables 5.1-5.4), in summer.

Seasonal sample sizes of the two crustaceans (*P. chabrus* and *P. perlatus*) were large enough to allow statistical comparison. There were significant differences in size of *Plagusia chabrus* ($H = 12.43$, d.f $= 3$, $P = 0.006$) and *P. perlatus* ($H = 8.96$, d.f. $= 3$, $P = 0.03$) during the various seasons, with the largest *P. chabrus* being eaten in spring and the largest *P. perlatus* being eaten in winter.

**Table 5.5.** Relative percentage occurrence data and rank (in parenthesis) of most important prey categories of Cape clawless otters *Aonyx capensis* for this study and various other localities.

| Sampled area | crab species | *Jasus lalandii* | fish species | *Octopus granulatus* |
|---|---|---|---|---|
| False Bay (Winter) | 33 (2) | 11 (3) | 53 (1) | 0 (4) |
| False Bay (Spring) | 32 (2) | 19 (3) | 46 (1) | 0 (4) |
| False Bay (Summer) | 35 (2) | 14 (3) | 46 (1) | 5 (4) |
| False Bay (Autumn) | 19 (2) | 3 (4) | 54 (1) | 13 (3) |
| Tsitsikama[1] | 38 (2) | 1 (4) | 52 (1) | 7 (3) |
| Tsitsikama[2] | 63 (1) | 0 (4) | 33 (2) | 4 (3) |
| Betty's Bay[3] | 31 (2) | 18 (3) | 36 (1) | 11 (4) |

[1] van der Zee (1981), [2] Arden-Clarke (1983), [3] Verwoerd (1987).

**Table 5.6.** Sizes of crustaceans and fish found in spraints of Cape clawless otters *Aonyx capensis* in False Bay during the various seasons. Measurements (mm) are given ± SE with sample size in parenthesis. For fish total lengths are given. For crabs and *Jasus lalandii* maximum carapace widths and lengths, respectively, are given.

|  | Winter | Spring | Summer | Autumn |
|---|---|---|---|---|
| **Crustaceans:** | | | | |
| *Plagusia chabrus* | 21.1±4.9 (4) | 31.3±1.8 (7) | 29.4±1.5 (12) | 22.8±1.6 (14) |
| *Cyclograpsus punctatus* | - | 17.9±3.8 (2) | - | - |
| *Potamonautes perlatus* | 39.33 (1) | 27.7±7.1 (3) | 26.5±2.75 (8) | 37.0±1.43 (5) |
| *Jasus lalandii* | 96.68 (1) | 142.5 (1) | 80.9 (1) | - |
| **Fish:** | | | | |
| *Atherina breviceps* | - | - | - | 51.8(1) |
| *Cheilodactylus fasciatus* | - | 115.3±25.4(3) | 127.2±11.0(13) | 124.2±5.4 (9) |
| *Chirodactylus brachydatylus* | - | 252.0 (1) | - | - |
| *Chorisochismus dentex* | - | 53.2±16.2(2) | 43.9±25.5 (2) | 39.0±5.2 (5) |
| *Clinus superciliosus* | 75.8±12.5 (4) | 79.6±7.7(15) | 94.0±17.4 (9) | 92.1±16.9 (9) |
| *Coryphaena hippurus* | - | - | - | - |
| *Diplodus sargus capensis* | - | - | - | 43.8±6.3 (2) |
| *Galeichthys feliceps* | - | 709.1 (1) | 181.9±48.0 (9) | - |

**Table 5.6. Continued:**

| | Winter | | Spring | | Summer | | Autumn | |
|---|---|---|---|---|---|---|---|---|
| **Fish Continued:** | | | | | | | | |
| *Gilchristella aestuaria* | - | | - | | - | | - | |
| *Gonorynchus gonorynchus* | - | | 40.3 | (1) | - | | - | |
| *Halidesmus scapularis* | - | | 124.6 | (1) | 183.8 | (1) | - | |
| *Heteromycteris capensis* | - | | - | | - | | - | |
| *Pomatomus saltatrix* | - | | - | | 127.5±48.7 | (2) | 98.2±1.0 | (2) |
| *Rhabdosargus holubi* | - | | - | | 305.1 | (1) | - | |
| *Sarpa salpa* | 64.2±2.4 | (5) | - | | 62.6±2.3 | (2) | 38.3 | (1) |
| *Serranus cabrilla* | - | | - | | 2.6 | (1) | - | |
| *Solea bleekeri* | - | | - | | - | | - | |
| *Umbrina canariensis* | - | | - | | - | | - | |
| All species of fish: | 69.3±5.7 | (9) | 115.5±27.6 | (24) | 127.7±14.2 | (40) | 86.8±8.3 | (29) |

**Table 5.7.** The size distribution of fish eaten by Cape clawless otters *Aonyx capensis* in False Bay, Western Cape Province, South Africa. The figures represent the number of fish in each size category.

| Size of fish (TL mm) | Winter (*n* = 9) | Spring (*n* = 24) | Summer (*n* = 40) | Autumn (*n* = 30) |
|---|---|---|---|---|
| 0-9 | | | | |
| 10-19 | | | 2 | |
| 20-29 | | 1 | | 3 |
| 30-39 | | 3 | 2 | 4 |
| 40-49 | | 1 | | 2 |
| 50-59 | 3 | 1 | 1 | 4 |
| 60-69 | 4 | 2 | 3 | |
| 70-79 | | 3 | 1 | |
| 80-89 | | 4 | 4 | 2 |
| 90-49 | 2 | 2 | 9 | 2 |
| 100-54 | | | 1 | 3 |
| 110-59 | | 3 | 4 | 3 |
| 120-65 | | 2 | | 1 |
| 130-70 | | | 1 | 3 |
| 140-149 | | | 1 | 2 |
| 150-159 | | | 1 | |
| 160-169 | | 1 | 2 | |
| 170-179 | | | | |
| 180-189 | | | 1 | 1 |
| 190-199 | | | 3 | |
| 200-209 | | | | |
| 210-219 | | | | |
| 220-229 | | | 1 | |
| 230-239 | | | | |
| 240-249 | | | | |
| 250-259 | | 1 | | |
| 260-269 | | | | |
| 270-279 | | | | |
| 280-289 | | | | |
| 290-299 | | | | |
| 300-310 | | | 1 | |
| > 310 | | | 2 | |

Although the data are not suitable for statistical comparison, the comparison of the percentages of species caught (Clark *et al.* 1996) with those found in the spraints show a clear selection for certain species of fishes such as *C. superciliosus, C. fasciatus* and *Sarpa salpa* (Table 5.8). The abundant *Atherina breviceps* (Clark *et al.* 1996, Table 5.8) was not eaten except in autumn.

Diversity of prey (Tables 5.1-5.4), as measured by the Shannon-Wiener and Simpson's indices, was lowest in winter increasing through the seasons (Table 5.9). Equitability was higher in winter and autumn than in spring and summer (Table 5.9). None of the measures of diversity used increased significantly with seasonal increases in temperature (Table 5.9).

## DISCUSSION

The present data, although collected over a short period from a small sample of spraints do indicate which species were eaten, and some seasonal differences in diet. However, spraint analysis does not reveal the importance of various prey with regard to biomass or energy consumed.

Diet analysis using frequency of occurrence data in *L. lutra* has come under severe criticism, with Carss & Parkinson (1996) showing that these data should only be used to rank the importance of various prey categories rather than as an indication of relevant quantities in the diet. The frequency of occurrence data from the present study show the same rank of importance of the three most important prey categories as does (Somers 2000 (Chapter 6)) (1) fish (2) crabs (3) *J. lalandii.* Somers (2000; Chapter 6) used direct observations of *A. capensis* and found unidentified fish (50.0%); unidentified crabs (27.8%); *J. lalandii* (11.1%) and abalone *Haliotis midae* (5.6%) to be eaten by otters. As only the soft part of *H. midae* are eaten (Somers, pers. obs.), no remains of them would be have been found in spraints in the present study.

**Table 5.8.** The observed versus the expected percentage of individual species of fish found in the spraints of Cape clawless otters *Aonyx capensis* in False Bay, Western Cape Province, South Africa.

| Fish species | Winter O | Winter E | Spring O | Spring E | Summer O | Summer E | Autumn O | Autumn E |
|---|---|---|---|---|---|---|---|---|
| *Atherina breviceps* | 0.00 | 27.00 | 0.00 | 62.66 | 0.00 | 61.99 | 2.22 | 54.21 |
| *Cheilodactylus fasciatus* | 0.00 | 0.00 | 15.79 | 0.00 | 33.33 | 0.00 | 42.22 | 0.00 |
| *Chirodactylus brachydatylus* | 0.00 | 0.00 | 2.63 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Chorisochismus dentex* | 0.00 | 0.00 | 5.26 | 0.00 | 3.51 | 0.00 | 11.11 | 0.00 |
| *Clinus superciliosus* | 53.85 | 0.16 | 47.37 | 0.11 | 22.81 | 0.03 | 24.44 | 0.24 |
| *Coryphaena hippurus* | 7.69 | 0.00 | 0.00 | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Diplodus sargus capensis* | 0.00 | 0.23 | 0.00 | 0.02 | 0.00 | 0.05 | 24.44 | 0.02 |
| *Galeichthys feliceps* | 0.00 | 0.00 | 2.63 | 0.00 | 17.54 | 0.00 | 0.00 | 0.00 |
| *Gilchristella aestuaria* | 0.00 | 2.55 | 0.00 | 0.04 | 1.75 | 0.50 | 0.00 | 0.05 |
| *Gonorynchus gonorynchus* | 0.00 | 0.00 | 2.63 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Halidesmus scapularis* | 0.00 | 0.00 | 2.63 | 0.00 | 1.75 | 0.00 | 0.00 | 0.00 |
| *Heteromycteris capensis* | 0.00 | 0.09 | 2.63 | 0.10 | 1.75 | 0.22 | 2.22 | 0.05 |
| *Pomatomus saltatrix* | 0.00 | 0.20 | 15.79 | 0.41 | 8.77 | 0.11 | 8.89 | 0.12 |
| *Rhabdosargus holubi* | 0.00 | 0.01 | 0.00 | 0.01 | 1.75 | 0.00 | 0.00 | 0.03 |
| *Sarpa salpa* | 38.46 | 0.00 | 0.00 | 0.72 | 3.51 | 1.79 | 2.22 | 0.34 |
| *Serranus cabrilla* | 0.00 | 0.00 | 2.63 | 0.00 | 1.75 | 0.00 | 0.00 | 0.00 |
| *Solea bleekeri* | 0.00 | 0.01 | 0.00 | 0.00 | 1.75 | 0.00 | 0.00 | 0.22 |
| *Umbrina canariensis* | 0.00 | 0.29 | 0.00 | 0.02 | 0.00 | 0.03 | 2.22 | 0.05 |

* Percentage of catch as determined from Clark *et al.* (1996)

**Table 5.9.** Seasonal diversity of prey species recorded in Cape clawless otter *Aonyx capensis* spraints collected from False Bay, Western Cape Province, South Africa.

| Community parameter | Winter | Spring | Summer | Autumn | Simple linear regression of variables vs water temperature |
|---|---|---|---|---|---|
| Total number of species | 6 | 16 | 17 | 13 | $r^2 = 0.89$, $P = 0.055$[*] |
| Diversity (H) | 2.00 | 2.70 | 2.95 | 3.20 | $r^2 = 0.52$, $P = 0.282$[*] |
| Equitability (E) | 0.78 | 0.68 | 0.72 | 0.87 | $r^2 = 0.17$, $P = 0.592$[*] |
| Dominance (D) | 0.71 | 0.77 | 0.80 | 0.89 | $r^2 = 0.18$, $P = 0.571$[*] |

[*]As the powers of these tests are below 0.800 the findings should be interpreted with caution.

This supports previous findings (Erlinge 1968; Rowe-Rowe 1977b) that percentage occurrence is a reliable estimate of the diet, but as shown here only when per cent of prey categories caught is concerned. The results show that a combination of direct observation and spraint analysis will give a more complete description of diet. For example, in the present study prey such as abalone were not found in the spraints but observations indicated that they were eaten (Somers 2000 (Chapter 6)). On the other hand, crab and fish species data were not available from direct observations (Somers 2000 (Chapter 6)), but are from the spraint analysis.

The finding of a general seasonal shift in diets from crustaceans being more important than fish in summer and spring suggests a shift in diet as the water gets warmer. This supports the hypothesis that the otters are able to catch fish more easily during colder times.

Other studies (Table 5.5) on the diet of *A. capensis* in marine habitats yielded varying results. In Tsitsikama van der Zee (1981), who sampled all seasons, found fish to be the most important but later Arden-Clarke (1983), who sampled only autumn, found crabs to be the most important prey type. The reasons for this difference between these two studies in the same locality are unknown. Verwoerd (1987) found a similar rank in the importance of prey to that in the present study and Somers (2000; Chapter 6).

*Aonyx capensis* ate a wide size range of crustaceans, including specimens much larger than they eat in freshwater habitats (e.g. mean carapace width = 23.5 mm, range 3.1-65.5 mm) (Somers & Purves 1996 (Chapter 7)). This applies to fish as well with *A. capensis*, in fresh water, eating *Tilapia sparrmanii* with a mean fork length of only 20.5 mm (range 12.8-30.5) (Somers & Purves 1996 (Chapter 7)). Similarly, Rowe-Rowe (1997b) found that mainly small fish were eaten. This disparity in prey size could be related to differences in feeding behaviour of the otters, or to availability of the prey. However, the diet of otters does not

always reflect prey availability, but may be influenced by feeding preferences (van der Zee 1981; Kruuk & Moorhouse 1990).

The results from the analysis of spraints should be interpreted with caution and only measures of relative importance or rank (Carss & Parkinson 1996) used.

The comparison of what was eaten by *A. capensis* with what was available in the sea must also be made with care. Clark *et al.* (1996) sampled 1-40 m out from the beach, which includes most of where the otters were seen foraging (Somers 2000 (Chapter 6)), but prey species that occur close to shore and in rock pools may have been undercounted. For example, *S. salpa* was eaten by the otters during winter but was not caught by Clark *et al.* (1996) during this season. This species is common in the rock pools in False Bay (Bennett & Griffiths 1984). *Clinus superciliosus* is the most common species of fish caught during the winter when fish are more easily caught, and appears to be a favourite of *A. capensis* in False Bay. *Clinus superciliosus* is abundant (1.34 m$^{-2}$, 15.44 g m$^{-2}$) in rock pools in False Bay (Bennett & Griffiths 1984) but not throughout the intertidal zone (Clark *et al.* 1996). This suggests that the otters are feeding extensively in the shallow rock pools, though Somers (2000; Chapter 6) found otters foraging in False Bay mostly at depths deeper (1.5-2.5 m) than the rock pools (< 1.5 m) which *C. superciliosus* inhabit (Bennett & Griffiths 1984). The disparity of these results and those of Somers (2000; Chapter 6) remains unclear. Van der Zee (1981) also found *Clinus* species, including *C. superciliosus,* to be important in the diet of *A. capensis* in a marine habitat.

The results show that *A. capensis* seem to select benthic fish species such as *C. superciliosus* and *C. fasciatus.* Another benthic species, *Galeichthys feliceps,* represented in spraints mostly in summer, was larger than the more commonly eaten species and could therefore be as important in the diet of *A. capensis* during summer as *C. superciliosus* and *C. fasciatus.* Analysis by weight of prey caught was, however, not possible in the present study. Otter preferences could be related to the low escape ability of prey. Erlinge (1968) also concluded that *L. lutra*

catch fish in inverse proportion to their ability to escape. There are few easily caught benthic freshwater fish species in southern Africa (Skelton 1993) which may be the reason fish remain low in importance in the diet of *A. capensis* in freshwater habitats. In addition, *A. capensis* could also eat more *P. perlatus* in freshwater habitats because they are abundant (Somers & Nel 1998) and more easily caught than fish (Rowe-Rowe 1977a).

The relationship between the otters and their prey is complex. Local differences such as the water depth, substratum type, availability of alternative prey, floods or tides, or the density of the predators, probably all interact to determine which section of fish and crustacean populations are available to *A. capensis* in specific areas and seasons. These aspects need to be further studied.

*Aonyx capensis* are generally regarded as crab specialists in freshwater habitats (Rowe-Rowe 1977b), having broadened bunodont molars for crushing the exoskeletons of invertebrate prey. Their manual dexterity further enables them to feel for and capture prey under stones and in crevices (Rowe-Rowe 1977c), possibly facilitating capture of all sizes of crabs, and probably bottom-dwelling fishes as well (see Tables 5.1-5.4). The results presented here suggest little dietary change (e.g. more *J. lalandii* in the southwestern Cape) along the south and southwestern coast of South Africa. *Aonyx capensis*, by foraging in both marine and freshwater habitats, demonstrate that they can successfully exploit different types of aquatic environments and are capable of exploiting different kinds of prey in each. This is emphasised by the finding here, and in Tsitsikama (van der Zee 1981), of both freshwater and marine species of prey in the spraints. Because of this ability otters are regarded as opportunist predators, and therefore can exploit a wide variety of habitats. They, however, do exhibit a degree of specialisation, being primarily adapted to feed on crustaceans, but are able to make use of other suitable prey, such as slow-moving fishes.

The results presented here show the importance of crustaceans in the diets of these carnivores, emphasising, for the conservation management of otters, the need for more information about factors limiting prey populations, especially the commercially exploited (Branch & Branch 1981) and ecologically important (van Zyl *et al.* 1998 and references therein) *J. lalandii*. The role of otters in this system is at present unknown and deserves further study. None of the three main fishes consumed are used commercially (Smith & Heemstra 1986).

It is not possible, with the data available, to assess the impact of otters on prey populations in the marine environment. Detailed data of the prey populations need to be gathered. These are, however, difficult to collect in the rough surf zones of False Bay and other areas of southern Africa's coast.

## REFERENCES

ARDEN-CLARKE, C.H.G. 1983. Population density and social organisation of the Cape clawless otter, *Aonyx capensis* Schinz, in the Tsitsikama Coastal National Park. M.Sc. thesis, University of Pretoria, Pretoria, South Africa.

ATKINS, G.R. 1970. Thermal structure and salinity of False Bay. *Transactions of the Royal Society of South Africa* **34**: 11-128.

BENNETT, B.A. & GRIFFITHS, C.L. 1984. Factors affecting the distribution, abundance and diversity of rock-pool fishes on the Cape Peninsula, South Africa. *South African Journal of Zoology* **19**: 97-104.

BRANCH, G. & BRANCH, M. 1981. *The living shores of southern Africa*. C. Struik, Cape Town.

CARSS, D.N. & PARKINSON, S.G. 1996. Errors associated with otter *Lutra lutra* faecal analysis. I. Assessing general diet from spraints. *Journal of Zoology, London* **238**: 301-317.

CLARK, B.M., BENNETT, B.A. & LAMBERTH, S.J. 1996. Temporal variations in surf zone fish assemblages from False Bay, South Africa. *Marine Ecology Progress Series* **131**: 35-47.

ERLINGE, S. 1968. Food studies on captive otters *Lutra lutra* L.. *Oikos* **19**: 259-270.

ESTES, J.A. 1994. Conservation of marine otters. *Aquatic Mammals* **20**: 125-128.

FIELD, J.G., GRIFFITHS, C.L., GRIFFITHS, R.J., JARMAN, N., ZOUTENDYK, P., VELIMIROV, B. & BOWES, A. 1980. Variation in structure and biomass of kelp communities along the south-west Cape coast. *Transactions of the Royal Society of South Africa* **44**: 145-203.

FITCH, J.E. & BROWNELL, R.L. 1968. Fish otoliths in cetacean stomachs and their importance in interpreting feeding habits. *Journal of the Fisheries Research Board of Canada* **25**: 2561-2574.

KREBS, C.J. 1985. *Ecology: The experimental analysis of distribution and abundance*. Harper and Row, New York.

KRUUK, H. 1995. *Wild otters: predation and populations*. Oxford University Press, Oxford.

KRUUK, H. & MOORHOUSE, A. 1990. Seasonal and spatial differences in food selection by otters (*Lutra lutra*) in Shetland. *Journal of Zoology, London* **221**: 621-637.

KRUUK, H., KANCHANASAKA, B., O'SULLIVAN, S. & WANGHONGSA, S. 1994. Niche separation in three sympatric otters *Lutra perspicillata, L. lutra* and *Aonyx cinerea* in Huai Kha Khaeng, Thailand. *Biological Conservation* **69**: 115-120.

MACARTHUR, R.H. & PIANKA, E.R. 1966. On optimal use of a patchy environment. *American Naturalist* **100**: 603-609.

PERRY, G. & PIANKA, E.R. 1997. Animal foraging: past, present and future. *Trends in Ecology and Evolution* **12**: 360-364.

PURVES, M.G., KRUUK, H. & NEL, J.A.J. 1994. Crabs *Potamonautes perlatus* in the diet of the otter *Aonyx capensis* and water mongoose *Atilax paludinosus* in a freshwater habitat in South Africa. *Zeitschrift für Säugetierkunde* **59**: 332-341.

ROSS, G.J.B. 1984. The smaller cetaceans of the south east coast of southern Africa. *Annals of the Cape Province Museum* (Natural History) **15**: 173-410.

ROWE-ROWE, D.T. 1977a. Variation in the predatory behaviour of

the clawless otter. *Lammergeyer* **23**: 22-27.

ROWE-ROWE, D.T. 1977b. Food ecology of otters in Natal, South Africa. *Oikos* **28**: 210-219.

ROWE-ROWE, D.T. 1977c. Prey capture and feeding behaviour of South African otters. *Lammergeyer* **23**: 13-21.

ROWE-ROWE, D.T. 1978. The small carnivores of Natal. *Lammergeyer* **25**: 1-48.

ROWE-ROWE, D.T. 1992. Survey of South African otters in freshwater habitat, using sign. *South African Journal of Wildlife Research* **22**: 49-55.

ROWE-ROWE, D.T. & SOMERS, M.J. 1998. Diet, foraging behaviour and coexistence of African otters and the water mongoose. *Symposia of the Zoological Society of London* No. 71: 215-227.

SCHULZE, B.R. 1965. *Climate of South Africa, Part 8, General Survey*. Weather Bureau, Pretoria.

SKELTON, P.H. 1993. *The complete guide to the freshwater fishes of Southern Africa*. Southern Book Publishers, Halfway House.

SMALE, M.J., WATSON, G. & HECHT, T. 1995. *Otolith atlas of southern African marine fishes*. Ichthyological Monographs of the J.L.B. Smith Institute of Ichthyology, No. 1: 253 pp.

SMITH, M.M. & HEEMSTRA, P.C. 1986. *Smiths' sea fishes*. Macmillan, Johannesburg.

SOMERS, M.J. 2000. Foraging behaviour of Cape clawless otters (*Aonyx capensis*) in a marine habitat. *Journal of Zoology, London* **252**: 473-480.

SOMERS, M.J. & PURVES, M.G. 1996. Trophic overlap between three syntopic semi-aquatic carnivores: Cape clawless otter, spotted-necked otter, and water mongoose. *African Journal of Ecology* **34**: 158-166.

SOMERS, M.J. & NEL. J.A.J. 1998. Dominance and population structure of freshwater crabs (*Potamonautes perlatus* Milne Edwards). *South African Journal of Zoology* **33**: 31-36.

SPARGO, P.E. 1991. False Bay, South Africa - an historic and scientific overview. *Transactions of the Royal Society of South Africa* **47**: 363-375.

STEPHENS, D.W. & KREBS, J.R. 1986. *Foraging Theory*. Princeton

University Press, Princeton.

VAN DER ZEE, D. 1981. Prey of the Cape clawless otter (*Aonyx capensis*) in the Tsitsikama National Park, South Africa. *Journal of Zoology, London* **194**: 467-483.

VAN NIEKERK, C.H., SOMERS, M.J. & NEL, J.A.J. 1998. Freshwater availability and distribution of Cape clawless otter spraints and resting places along the south-west coast of South Africa. *South African Journal of Wildlife Research* **28**: 68-72.

VAN ZYL, R.F., MAYFIELD, S., PULFRISH, A. & GRIFFITHS, C.L. 1998. Predation by West coast rock lobster (*Jasus lalandii*) on two species of winkle (*Oxystele sinensis* and *Turbo cidaris*). *South African Journal of Zoology* **33**: 203-209.

VERWOERD, D.J. 1987. Observations on the food and status of the Cape clawless otter *Aonyx capensis* at Betty's Bay, South Africa. *South African Journal of Zoology* **22**: 33-39.

## CHAPTER 6[*]

# FORAGING BEHAVIOUR OF CAPE CLAWLESS OTTERS (*AONYX CAPENSIS*) IN A MARINE HABITAT

## INTRODUCTION

Differences in diving behaviour of aquatic mammals can vary owing to differences in prey type (Rowe-Rowe 1977a; Kvitek *et al.* 1993), prey availability (Kvitek *et al.* 1993), diving depth (Kvitek *et al. 1993*; Nolet *et al.* 1993), hunting tactics, locality (Ostfeld 1991), water turbidity (Rowe-Rowe 1977a) and age of the predator (Watt 1993).

Our understanding of otter diving behaviour comes mainly from studies on Eurasian otters *Lutra lutra* (e.g. Kruuk *et al.* 1990; Nolet *et al.* 1993; Watt 1993), and sea otters *Enhydra lutris* (e.g. Kvitek & Oliver 1988; Kvitek *et al.* 1993; Ralls *et al.* 1995). Partly because of the difficulties in watching otters, both at sea and in freshwater systems, most research on Cape clawless otters *Aonyx capensis* has been centred on feeding behaviour (reviewed in Rowe-Rowe & Somers 1998) and large scale movements (Arden-Clarke 1983, 1986). Although Rowe-Rowe (1977a) gave 16 dive times of *A. capensis* in freshwater, and Arden-Clarke (1983) and Verwoerd (1987) gave 26 and 12 dive times respectively of *A. capensis* in the sea, little is known of diving behaviour of this species.

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Observations on foraging and habitat use by *A. capensis* may be useful first for conservation management, to determine how the species copes with the decrease in the quality of aquatic ecosystems in South Africa (see Branch & Branch 1981; Davies & Day 1998). Second it would be interesting to compare their behaviour with those of other species of marine diving mammals. Furthermore, observations on diving behaviour have been shown to be useful in the assessment of efficiency of exploitation of food resources in different environments for *L. lutra* (Kruuk *et al.* 1990; Kruuk & Moorhouse 1990; Watt 1993) and platypus *Ornithorhynchus anatinus* (Kruuk 1993).

Optimality models have three main components: the currency, the constraints, and the decision variable (Krebs & Kacelnik 1991). In the case of diving organisms, the currencies could include maximising the rate of energy intake, maximising the rate of oxygen intake, minimising the risk of predation, or a combination of these. Constraints and variables could be: travel time (duration of time taken to get to the bottom), bottom or search time (duration of time searching on the bottom), unsuccessful dive time (travel and bottom time of an unsuccessful dive), successful dive time (travel and bottom time of a successful dive), recovery time (duration of time after surfacing from an unsuccessful dive to the start of the next dive), processing time (duration of time after surfacing from an successful dive to the start of the next dive), hunting success (HS: % of dives yielding prey), % time at surface, time preceding each catch, success or failure (capturing or not capturing prey) and whether to eat or reject a small prey.

Owing to loss of energy in the water (Kruuk *et al.* 1997) it would be expected that otters would always maximise the net rate of energy gain. Optimal foraging theory states that foraging strategies may involve decisions that maximise the net rate of food intake or of some other measure of foraging efficiency (Emlen 1966; MacArthur & Pianka 1966; Krebs & Kacelnik 1991). An extension is the marginal value theorem (Charnov 1976), which (briefly) states that an animal foraging for food in patches

spends much of its time travelling between patches, or searching for and handling food within patches. As a forager depletes the available food within a patch over time, the benefit of staying in the patch decreases. In order to forage optimally in a particular patch, the animal should therefore leave the patch when the expected net gain from staying drops to that expected from travelling to and searching in a new patch.

The optimal breathing hypothesis (Kramer 1988), which originates from the marginal value theorem, suggests that oxygen stores are replenished according to a curve of diminishing returns. The hypothesis predicts that both surface and dive time will increase with dives of greater depths, as will the percentage time spent at the surface. Optimal breathing strategies (Kramer 1988) are affected by such factors as body size, physiological abilities, feeding requirements, and whether a species is a single-prey or multi-prey loader (Kruuk 1993). As otters hunt for prey under water but feed on the surface, they are central place foragers as well as single prey loaders (Houston & McNamara 1985). Otters do not return to a fixed central place, for example a den, but do need to return to the surface.

*Aonyx capensis* weigh between 10 and 18 kg, with a mean of *ca* 13.0 kg and males being larger then females (Skinner & Smithers 1990). *Aonyx capensis* relies on sight for locating prey but also feels for prey that is hidden from view (Rowe-Rowe 1977b). *Aonyx capensis* dives directly to the bottom (Rowe-Rowe 1977b) where it captures prey with its dextrous forefeet (Rowe-Rowe 1977b; Van der Zee 1979 1981; Verwoerd 1987). In captivity, factors such as water temperature, depth, substratum, turbidity, and darkness do not greatly affect the ability of *A. capensis* to catch crabs and frogs in freshwater, but do for fish (Rowe-Rowe 1977c).

*Aonyx capensis* uses freshwater habitats extensively (Rowe-Rowe & Somers 1998) but also uses marine habitats for food (Van der Zee 1981; Arden-Clarke 1983; Verwoerd 1987). However, they appear to use marine habitats only in the presence of freshwater (van Niekerk *et al.* 1998). Crustaceans, including shore crabs

*Cyclograpsus punctatus*, Cape rock crabs *Plagusia chabrus* and Cape rock lobsters *Jasus lalandii*, are their main prey, in decreasing order of importance, in marine habitats along the southern and southeastern coasts of South Africa. These are supplemented with octopus (*Octopus granulatus*) and fishes (Van der Zee 1981; Arden-Clarke 1983; Verwoerd 1987). Freshwater crabs *Potamonautes* spp are their most common prey in freshwater ecosystems, with lesser amounts of frogs, fishes, aquatic insects, birds, reptiles, molluscs, dung (ungulate) and mammals being taken (Rowe-Rowe & Somers 1998).

This chapter provides the first detailed quantitative data on foraging by free swimming *A. capensis* in a marine habitat. It also aims to contribute information on which a future conservation management plan for the species could be based. Perry & Pianka (1997) suggested that optimal foraging studies would contribute most by (1) providing a prediction of optimum possible performance, and (2) an indication of potential avenues for further research. This chapter, therefore, (1) describes quantitative and qualitative aspects of foraging behaviour of *A. capensis* in a marine ecosystem; (2) determines if depth has an effect on diving behaviour and diet; (3) tests the optimal breathing hypothesis (Kramer 1988); and (4) compares diving behaviour of *A. capensis* with that of *L. lutra* in marine habitats. I hypothesised that *A. capensis* maximise their diving success rate and that they dive at depths where they get most prey for least effort. I predicted that due to differences in diet, there would be differences between *A. capensis* and *L. lutra* with regard to diving behaviour.

## MATERIALS & METHODS

Data were collected from 26 April 1994 to 2 October 1996, along a 2 km stretch of the south-west corner of False Bay, just South east of Rooi-Els (33° 19' S, 26° 05' E), Western Cape Province, South Africa.

The coast here is highly exposed, with broad surf zones. There are four small, perennial, freshwater streams (*ca* 0.5-2 m wide and *ca* 50-500 mm deep, depending on season) entering the sea within this 2 km stretch. The substrate in the area from which data were collected consisted of boulders. A road, which runs parallel to the coast, at 3-5 m above and 15-20 m away from the high water mark, facilitates observations. The area was chosen because the otters, when hunting in the sea, are easily watched without disturbance.

The mean sea temperature varies with season: summer, 21.5°C; spring, 18.2°C; autumn, 17.1°C; and winter, 13.2°C. Winter sea temperature is significantly lower than that of the other seasons (Clark, Bennett, & Lamberth 1996). The climate type is Mediterranean with cold, wet winters and hot, dry summers (Schulze 1965). The mean tidal range in False Bay is 1.48 m (Spargo 1991) and mean salinities range from *ca* 35.0-35.3‰ (Atkins 1970).

Observations using 10X40 binoculars were conducted on foot, during the day at low tide. As the age of individual *L. lutra* affects diving behaviour (Watt 1993), diving data from only adult *A. capensis* were used to avoid a possible similar situation with *A. capensis* affecting results. As it was usually impossible to identify individuals, repeated sightings of individual otters may have been included. Although the number of individuals observed could not be determined there appeared to be a high turnover of individuals over the 29 months study period. The longest one recognisable individual was observed in the area was three months. As distinguishing between individuals which are hunting together proved to be very difficult, and as they may be co-operating under water (Arden-Clarke 1983), only data from solitary otters were used to compare diving parameters at different depths. Group sizes were recorded for all sightings. I located otters by walking transects along the 2 km shoreline in both directions (i.e. 4 km) (*n* = 106), and scanning the sea and shore for otters. Focal otters were followed for as long as possible.

The success or failure of dives was recorded. Duration of dives, recovery times and processing times were measured by stopwatch from tape recordings. Diving depths were allocated to the following depth categories: 0.0-0.5, 0.5-1.5, 1.5-2.5 and 2.5-3.5 m. This was possible after diving in the area and measuring the depth at 5 m intervals perpendicular to the shore. Depths were also estimated during calm spring tides. A map was produced showing approximate depths of the area for later estimation. It was, however, normally possible to estimate depth without the map. The area covered by particular depth categories was determined from the map. The percentage of dives at a given depth was correlated with the available area of that depth category (within 40 m of the shore).

The per cent time at the surface and time foraging before each catch were calculated at various depths. A hunt was regarded as the interval that elapsed between the time an otter was first seen foraging to when it was last seen foraging. The beginning and end of hunts were not always seen. When possible, the behaviour of otters was also recorded when they exited the sea.

Prey items that the otters were seen to catch were identified to the lowest taxonomic category possible. Occasionally, prey could not be identified while being handled and eaten. Prey length was estimated relative to otter head width (*ca* 150 mm for adults). Small prey were regarded as those < 50 mm, medium 50-100 mm and large > 100 mm (after Kvitek *et al*. 1993 for *E. lutris*). Quantitative data were collected from diving otters only. Occasionally, when the otters were foraging while walking in shallow water, they were difficult to observe without disturbing.

Qualitative data of foraging behaviour were recorded, and presented in a descriptive form.

Statistical tests used are mentioned at appropriate points in the text, the level of significance being $P = 0.05$. Statistical tests were done by hand using Siegel (1956), or by computer using the programme SigmaStat for Windows 95 version 2.0, Jandel Corporation©.

## RESULTS

Two forms of hunting or foraging mode were recognised. In the first, the otters would dive and surface with or without prey. Diving from the surface, or looping, is done by dorsal bending of the body, lifting the back and tail out of the water. Just after leaving the surface, there was paddling followed by dorsoventral flexion of the body and tail. Dives occurred either at the place the otter surfaced, or after the otter swam on the surface for a few metres. The most common foraging pattern appeared to be 'swim-fishing' (Kruuk 1995) which is when the otters swim on the surface, then dive and emerge some distance ahead, still travelling in the same direction. Swimming on the surface was either by paddling or by lateral undulations of the body and tail. The details of how the limbs were used could not be clearly determined. After unsuccessful dives otters would sometimes 'porpoise' in and out of the water. Occasionally they would simply submerge their heads and loop underwater. They occasionally dived vertically down, but usually at a slight angle, estimated to be *ca* 60°.

The second type of hunting involved the otters moving into shallow water (*ca* 0.2 m deep), and walking along the substrate feeling for prey with their feet, disturbing possible prey items, which were then caught with the forefeet. They occasionally submerged their heads, presumably looking for food.

After a successful dive the otters ate their prey while in the water, either in an upright position or lying on their back. The prey items were held with the forefeet, sometimes submerged. When a wave approached, the otter would briefly submerge its head until the wave passed. When large prey items of *ca* 150 mm or more were caught, an otter would head directly to the shore with the prey in its mouth, land, and then eat the prey. On 21 occasions the landing behaviour was clearly observed. The otter approached the shore, appearing vigilant by occasionally lifting its head and looking around. The otter would then wait for a wave surge to

lift it onto the shore, which consisted of boulders in the present study area. The otter usually lay down on a boulder within *ca* 2 m of the water while eating its prey. On one occasion, when the wind was very strong, an otter took shelter between boulders. On 43% of the landings they had a prey item with them. They defaecated on 57% of landings. Fifty seven per cent of landings were at freshwater streams, while for another 38% they moved up into a freshwater stream and were not seen again.

Otters were seen on 30.2% ($n = 32$) of the 106 transects along the 2 km of coast of the study area. Two groups were seen during six transects giving a total of 38 groups sighted. Sixty eight per cent of groups sighted foraging consisted of solitary otters (Fig. 6.1).

*Aonyx capensis* tended to move along the coast while feeding (mean = 21.4 m per min, $n = 5$, S.E. = 4.83, range = 8.3-34.1). The furthest off shore an otter was estimated hunting was 40 m, which was usually within the surf zone.

The mean duration of hunts of all groups observed, including solitary animals, was 75.3 min ($n = 38$, S.E. = 5.9, range = 5-181 min).

The durations of two hunts where the start and end were observed were 66 and 181 min. In total 848 dives of solitary, foraging adults were observed (Table 6.1).

The mean dive time for all complete dives recorded was 21.0 s ($n = 848$, S.E. = 0.3, range = 1.0-48.0). Mean successful dive time was 21.0 s ($n = 64$, S.E. = 1.5, range = 5.4-48) while unsuccessful dives also lasted a mean of 21.0 s ($n = 774$, S.E. = 0.3, range = 1.0-46.0). Unsuccessful dive times were not significantly longer then successful dive times at depths of 0.0-0.5 m (Mann-Whitney $U = 184$, d.f. = 101, $P = 0.843$); 0.5-1.5 m (Mann-Whitney $U = 1882$, d.f. = 293, $P = 0.803$) and 2.5-3.5 m (Mann-Whitney $U = 428$; d.f. = 105, $P = 0.671$) but were for depths between 1.5-2.5 m (Mann-Whitney $U = 7029$, d.f. = 335, $P = 0.015$).
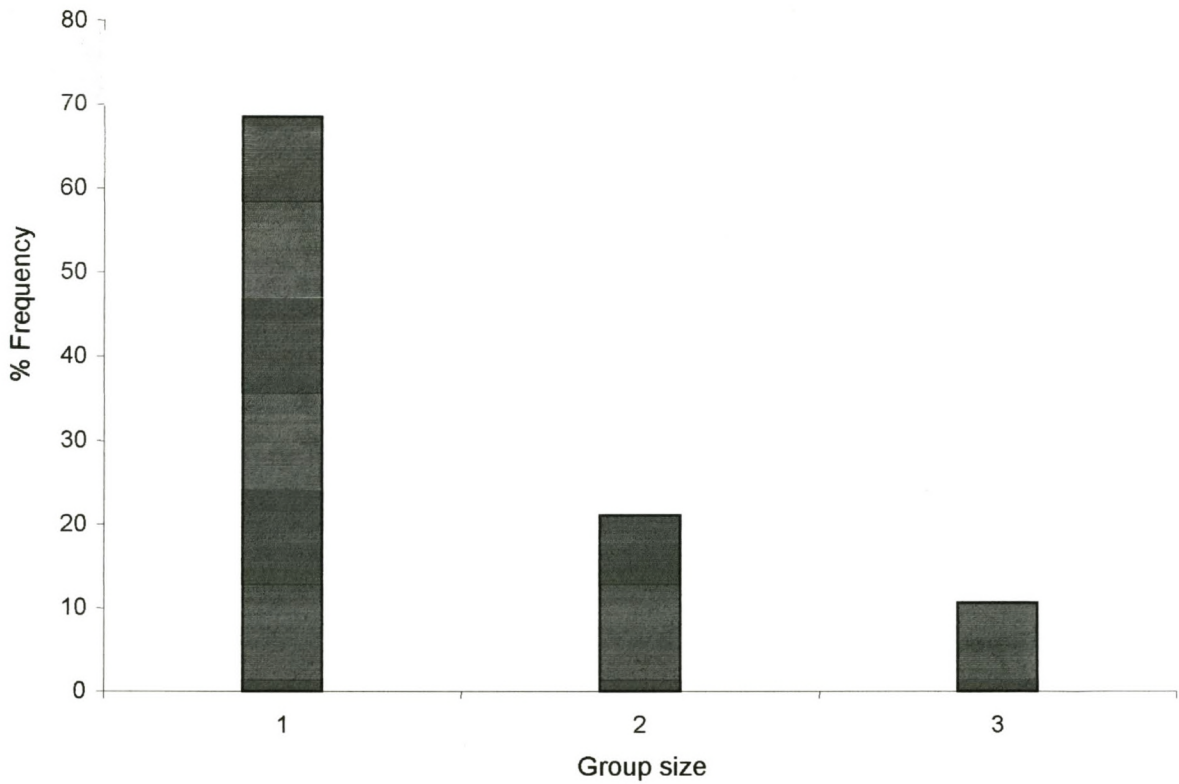
**Fig. 6.1.** The percentage frequency distribution of group size classes of Cape clawless otters *Aonyx capensis* seen in False Bay from 26 April 1994 to 2 October 1996 (*n* = 38 sightings).

**Table 6.1.** Diving behaviour of Cape clawless otters *Aonyx capensis* at various depths: *n* = number of dives; UDT = unsuccessful dive time; SDT = successful dive time; PT = processing time; RT = recovery time.

| Depth (m) | *n* | UDT ± SE (s) | SDT ± SE (s) | PT ± SE (s) | RT ± SE (s) |
|---|---|---|---|---|---|
| 0.0-0.5 | 102 | 9.9±0.5 | 10.0±1.4 | 10.6±2.3 | 3.6±0.3 |
| 0.5-1.5 | 298 | 19.3±0.4 | 22.3±3.5 | 58.2±12.1 | 7.3±0.3 |
| 1.5-2.5 | 344 | 22.8±0.5 | 19.4±1.7 | 153.1±40.4 | 8.5±0.3 |
| 2.5-3.5 | 104 | 31.5±0.8 | 31.5±3.9 | 43.5±12.0 | 11.3±0.7 |
| 0.0-3.5 | 848 | 21.0±0.3 | 21.0±1.5 | 109.6±24.5 | 7.8±0.2 |

Combining all depths there was not a significant difference between unsuccessful and successful dive times (Mann-Whitney $U = 26133$, d.f. $= 837$, $P = 0.464$) (Table 6.1). Mean recovery time was 7.8 s ($n = 764$, S.E. $= 0.2$, range $= 1.0$–$40.0$) and mean processing time was 109.6 s ($n = 82$, S.E. $= 24.5$).

As expected, recovery time increased with the preceding unsuccessful dive time for all depths combined ($r^2 = 0.24$, $P < 0.001$).

Recovery time, however, did not increase with the preceding unsuccessful dive time at 0.0–0.5 m ($r^2 = 0.05$, $P = 0.216$) but did for 0.5–1.5 ($r^2 = 0.10$, $P < 0.001$), 1.5–2.5 ($r^2 = 0.16$, $P < 0.001$) 2.5–3.5 m ($r^2 = 0.21$, $P < 0.001$) (Fig. 6.2). Processing time was longest after diving to 1.5-2.5 m depths (Table 6.1).

Otters dived more frequently in water of less then 1.5 m than would be expected on the basis of the area present (Fig. 6.3, $\chi^2 = 260$, d.f. $= 3$, $P < 0.001$) (Table 6.2). As the furthest out an otter was estimated hunting was 40 m, 80 ha was available to the otters along this 2-km stretch of coast.

Foraging efficiency at various depths are given in Table 6.3. HS was highest at a depth of between 1.5–2.5 m. Per cent time at the surface was similar between depths (Table 6.3). Kruskal-Wallis one way analysis of variance on ranks indicated that there were no significant differences in surface time before a successful dive ($H = 4.50$, d.f. $= 3$, $P = 0.213$) with various depths (Table 6.3).

Kruskal-Wallis one way analysis of variance on ranks indicated that there were significant differences in recovery times ($H = 117.94$, d.f. $= 3$, $P < 0.001$), processing times ($H = 9.61$, d.f. $= 3$, $P = 0.022$), unsuccessful dive times ($H = 263.03$, d.f. $= 3$, $P < 0.001$) and successful dive times ($H = 11.34$, df $= 3$, p $= 0.01$) with various depths (Table 6.1).
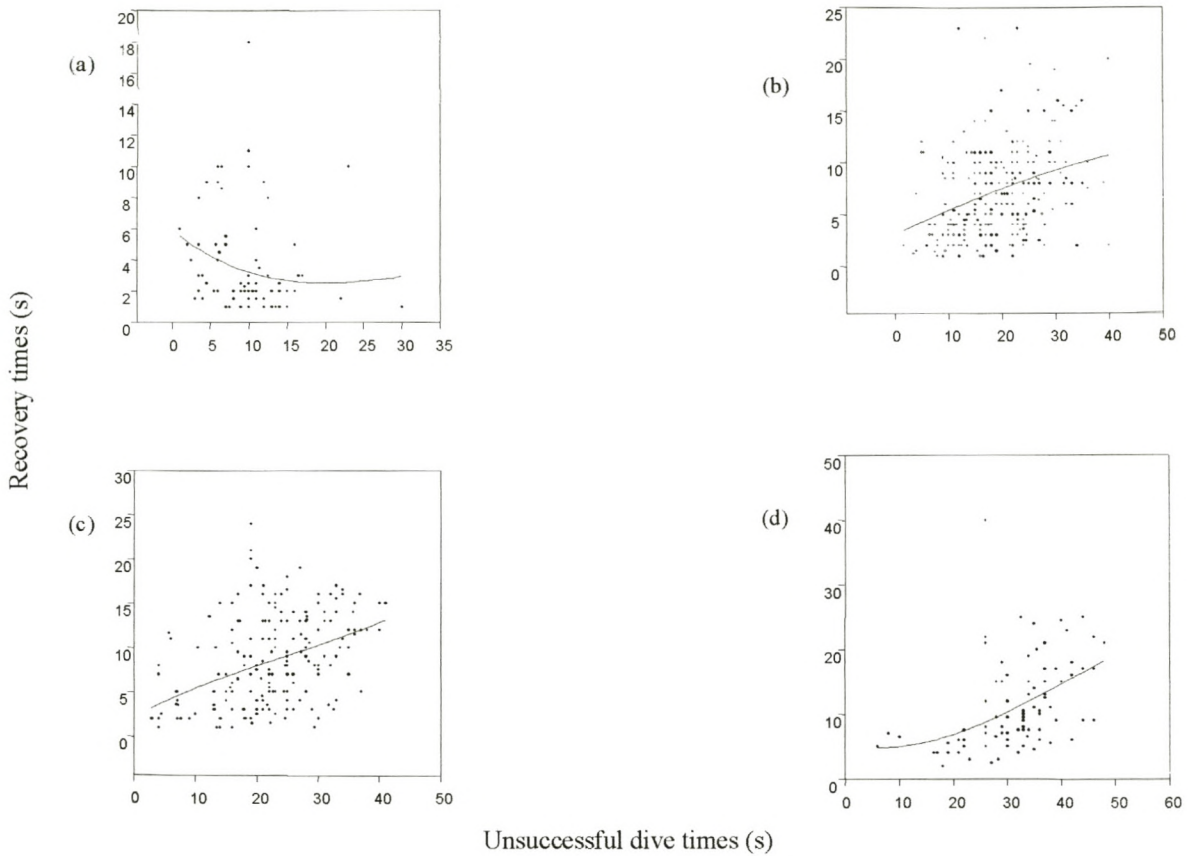
**Fig. 6.2.** Relationship between recovery times and preceding unsuccessful dive times of Cape clawless otters *Aonyx capensis* in False Bay, South Africa. (a) 0.0–0.5 m, (b) 0.5–1.5 m, (c) 1.5–2.5 m, (d) 2.5–3.5 m.
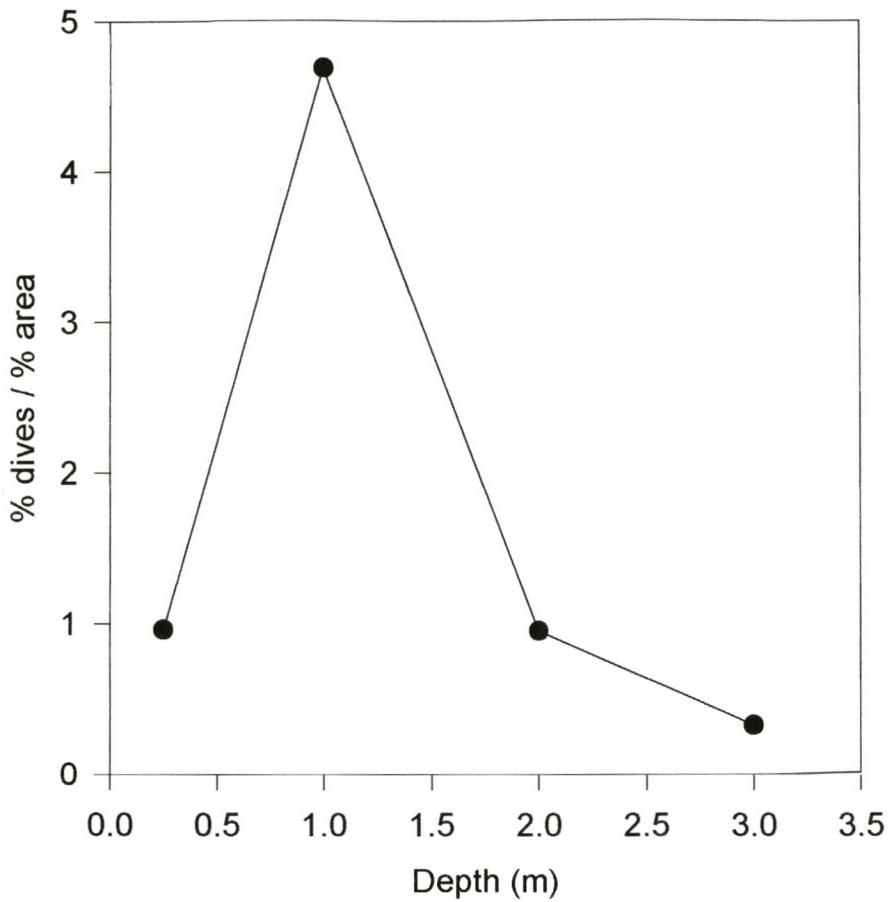
**Fig. 6.3.** The percentage of dives of Cape clawless otters *Aonyx capensis* corrected for the percentage of the available area (within 40 m from the shore) at various depths. (The depth figures are the medians of the depth ranges, 0.25 = 0.0-0.5 m, 1 = 0.5-1.5 m, 2 = 1.5-2.5 m, 3 = 2.5-3.5 m).

**Table 6.2.** Area per depth-class within 40 m from the shore of Cape clawless otters *Aonyx capensis*, and number of dives in each.

| Depth (m) | Area (ha) | Area (%) | No dives observed | No dives expected |
|---|---|---|---|---|
| 0.0-1.5 | 16.0 | 20.0 | 400 | 170 |
| (0-0.5) | (10.0) | (12.5) | (102) | (106) |
| (0.5-1.5) | (6.0) | (7.5) | (298) | (64) |
| 1.5-2.5 | 34.0 | 42.5 | 344 | 360 |
| 2.5-3.5 | 30.0 | 37.5 | 104 | 318 |

**Table 6.3.** Foraging efficiency of Cape clawless otters *Aonyx capensis* in various depths.

| Depth (m) | Hunting success (% of dives yielding prey) | % time at surface | Time foraging before each catch (s) |
|---|---|---|---|
| 0.0-0.5 | 4.1 | 39.4 | 92.5 (*n* = 2) |
| 0.5-1.5 | 5.0 | 37.6 | 221.0 (*n* = 11) |
| 1.5-2.5 | 12.8 | 37.3 | 71.8 (*n* = 16) |
| 2.5-3.5 | 8.2 | 35.9 | 280.5 (*n* = 5) |

*Aonyx capensis* were observed feeding mostly on fish
(50.0%) followed by crabs (27.8%), *J. lalandii* (11.1%) and
abalone *Haliotis midae* (5.6%) (Fig. 6.4). On two occasions crabs
were identified as *C. punctatus*. It was not possible to identify
the species of fish caught.

Prey size varied significantly with depth where captured ($\chi^2$
= 15.0, d.f. = 6, *P* = 0.005) (Table 6.4). The proportion of large
prey (> 100 mm) also increased with depth (Table 6.4).

## DISCUSSION

Despite *A. capensis* being primarily a crab eater the general
swimming and diving behaviour are similar to primarily fish
eating otter species. The foraging pattern of 'swim-fishing' is
as described for *L. lutra* (Kruuk 1995). The undulatory swimming
mode described here is similar to that of *L. canadensis* (Fish
1994) and the 'porpoiseing' has been previously described for *L.
lutra* (Conroy & Jenkins 1986).

In the present study, the largest foraging group observed
consisted of three individuals, which is less than found by
Arden-Clarke (1983) who recorded three groups of four and one
group of five (*n* = 76). The percentage of individuals (64.2%),
twosomes (17.9%) and threesomes (11.9%) were similar to those
found in the present study (i.e. 68.4, 21.1 & 10.5%
respectively). These data suggest that marine *A. capensis* has a
similar group structure to *L. lutra* (Kruuk 1995) but further
data, especially age sex data, are needed to clarify this.
As expected on the basis of differences in metabolic rates and
lung volume (Kooyman 1989), Kruuk (1993) found that there is a
clear relationship between log mean body weight and log mean dive
time for a number of diving mammals.
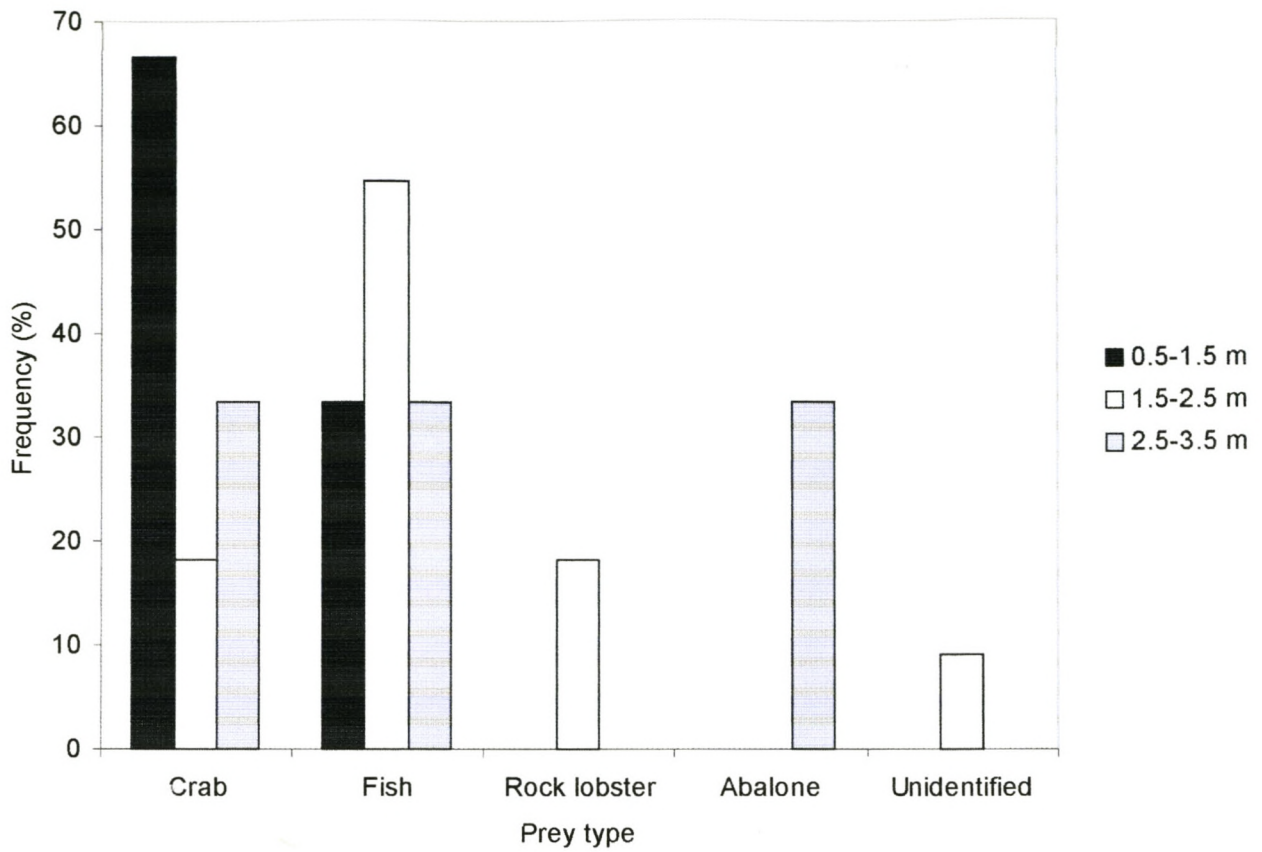
**Fig. 6.4.** Frequency of occurrence of food items obtained by Cape clawless otters *Aonyx capensis* at different depths in False Bay, Western Cape Province, South Africa.

**Table 6.4.** Frequency occurrence (%) of prey sizes, as determined by direct observations, of Cape clawless otters *Aonyx capensis* at various depths in False Bay, South Africa

| Prey size | 0.5–1.5 m | 1.5–2.5 m | 2.5–3.5 m |
|---|---|---|---|
| Small (< 50 mm) | 50.0 | 0.0 | 25.0 |
| Medium (50–100 mm) | 16.7 | 36.4 | 0.0 |
| Large (> 100 mm) | 33.3 | 54.5 | 75.0 |
| Unidentified | 0.0 | 9.1 | 0.0 |
| *n* | 12 | 22 | 8 |

The data in the multi-species comparison of Kruuk (1993) are best expressed with the polynomial:

$$Y = 2.6 - 0.83x + 0.05x^2 + 0.02x^3 \quad (r^2 = 0.96)$$

which predicts a mean dive time for a 13.0 kg *A. capensis* to be about 26.5 s, longer then that found in this study (21.0 s).Others have also found dive times of *A. capensis* to be lower than that expected. Arden-Clarke (1983) gave successful dive times of solitary males as 19.8 s ($n = 15$) and unsuccessful dive times as 23.6 s ($n = 11$). These are similar to those of the present study at 1.5-2.5 m depths. Verwoerd (1987) gave two mean dive times for *A. capensis* of 4.75 s ($n = 8$, range = 3-13 s), and 8.6 s ($n = 6$, range = 8-16 s), but did not give depths or success of these dives. Although not directly comparable with the marine environment, Rowe-Rowe (1977b) gave mean freshwater diving time (depth = 1.5 m) as 17.4 s ($n = 6$, range = 8-26), in KwaZulu-Natal Province, South Africa.

Kruuk & Hewson (1978) recorded mean times of successful dives of *L. lutra* in a marine habitat to be 15.9 s, and 24.8 s for unsuccessful dives - a significant difference. Kruuk & Moorhouse (1990) recorded a mean recovery time of 3.7 s for depths of < 1 m. Other mean diving times for *L. lutra* are 23.1 s (West Scotland; Kruuk & Hewson 1978), 20.1 s (Shetland, Conroy & Jenkins 1986), 23.3 s (Shetland; Nolet *et al.* 1993), and 22.7 s (Mull, West Scotland; Watt 1993).

As at most depths in the present study, Arden-Clarke (1983) found no significant differences between the duration of unsuccessful and successful dives. One reason for this may be that the otters continue searching for better prey until oxygen stores need to be replenished, even after catching a prey item. A second possibility could be that they have a constant giving up time owing to a trade-off between saving energy, if the dive is not successful in a given time, and keeping on diving in the hope of eventually getting prey (but expending much energy if unsuccessful). This could be related to food availability. A

third possibility is that during every dive the animals investigate only one prey-hiding place, and come up regardless of success. The third possibility is unlikely as bubbles can sometimes be seen coming up over a few meters while the otter forages at the bottom. There is, however, no other evidence for any of these possibilities. This similarity in duration of successful and unsuccessful dives differs from *L. lutra*, where successful dive times are significantly shorter then unsuccessful dive times (Kruuk & Hewson 1978).

Arden-Clarke (1983) recorded processing times of 42.5 s (*n* = 21) for unidentified prey, which is less than that of the present study (153.1 s) for depths of 1.5-2.5 m, but closer to that found (10-58 s) at other depths. For three "relatively large" crabs Arden-Clarke (1983) recorded processing time as 30, 32 & 180 s, while six large fish required processing times of 180-900 s (mean = 555 s).

The hunting success recorded in the present study (4.1-12.8%; Table 6.3) is in contrast to that recorded by Arden-Clarke (1983) who gave hunting success in Tsitsikama National Park as 62.3% (*n* = 53). Rowe-Rowe (1977a) recorded hunting success in freshwater to be 62.2% (*n* = 37). In freshwater systems *A. capensis* have been shown to eat much smaller prey of 23.5-28.5 mm (mean carapace width of *P. perlatus*) (Purves *et al.* 1994; Somers & Purves 1996 (Chapter 7)) than in the present study. Either the otters in the present study were selecting larger prey then along the Tsitsikama coast, or there was only larger prey available. In any case, the larger prey selected may have enabled *A. capensis* to have a lower success rate and still meet their energy needs.

Hunting success rates in *L. lutra* vary between areas e.g. 19.2% (West Scotland; Kruuk & Hewson 1978), 23.0% and 25.0% (Shetland; Kruuk *et al.* 1990) and 32.8% (Mull, West Scotland; Watt 1993). These success rates for *L. lutra*, although very different, are rather closer to the 4.1-12.8% (Table 6.3) found for *A. capensis* in the present study than that found for *A. capensis* by Arden-Clarke (1983).

Ostfeld (1991) suggested that hunting success is a useful means of comparing forage strategies and habitat characteristics in sea otters. As results appear to vary between habitats, this may apply to *A. capensis* as well. Kruuk *et al.* (1990), however, caution that hunting success may merely measure the likelihood that a predator will initiate a hunt after observing a situation with a potential for a capture (Kruuk 1972), and is therefore not a suitable unit of prey-capturing effort.

The question arises as to why *A. capensis* foraging in False Bay have a much lower hunting success than in Tsitsikama National Park and in KwaZulu-Natal. Although not directly comparable, spraint analysis by Arden-Clarke (1983) and Rowe-Rowe (1977c) for the same study area as Rowe-Rowe (1977a), gave crustaceans to be the most important prey. The lower hunting success in False Bay may therefore be explained by the higher percentage of high energy food (fish) eaten compared to Tsitsikama National Park and KwaZulu-Natal where a higher percentage of low energy food (crustaceans) are eaten. *Aonyx capensis* therefore appear to be able to switch prey and change foraging behaviour to accommodate availability of prey of various energy values. Prey switching has been shown in *E. lutris* (Ostfeld 1982) which prefer food species of high energy intake/unit foraging time but replace depleted dietary items with those of the next highest rank. Poor hunting success rates in *E. lutris* also drive them to hunt for different prey species (Ostfeld 1982).

As animals relatively seldom focus on feeding to the exclusion of other factors such as avoiding predators or finding mates (Perry & Pianka 1997) behaviour may not be optimal. Phylogenetic history may have 'won' over local behavioural adaptations (Perry & Pianka 1997). *Aonyx capensis*, however, seem to be able to adapt their foraging behaviour to different habitats (i.e. they can vary hunting success in different habitats).

As *A. capensis* in the present study ate a lower percentage (50%) of energy-rich fish than marine *L. lutra* (50-100% occurrence) (Kruuk & Moorhouse 1990; Clode & Macdonald 1995; Watt

1995), it would be expected to require a higher hunting success to compensate. However, as *L. lutra* hunt in colder water than *A. capensis,* which is energetically highly costly (Kruuk *et al. 19*97), they may need a higher success rate to minimise time in the water.

Time taken for each catch could be used as a measure of diving efficiency. The results presented here showed no significant trend with depth.

A low per cent time at the surface indicates efficient hunting behaviour. Watt (1993) recorded a per cent time at the surface for adult *L. lutra* of 29.8 – 43.5% increasing with depth. Nolet *et al.* (1993) gave per cent time at the surface to vary between 32.2 and 70.9%. *Aonyx capensis* in the present study has a per cent time at the surface, varying between 35.9–39.4% (Table 6.3), with no trend with depth.

Although a very imprecise measure, the technique used to determine prey size (i.e. comparing with head-width (*ca* 150 mm) of an adult otter) did provide some indication of the prey sizes eaten by the otters. These data also provide a comparison for more detailed faecal analyses (Somers, in prep). The data are also sufficient to show the differences in prey type, relative quantities and sizes of prey. Although only a small sample size was obtained, the results show that composition of the diet in False Bay was similar to that found elsewhere along the South African coast in marine habitats (Tayler 1970; Van der Zee 1981; Arden-Clarke 1983; Verwoerd 1987), except that *O. granulatus* was not observed as a prey item, but *H. midae* was. Remains of *O. granulatus* have, however, been found in the spraints of *A. capensis* inhabiting the study area (Somers 2000) (Chapter 6).

Fish were the most common prey, followed by crabs, although the species of both could seldom be identified. *Jasus lalandii* were not seen to be caught in shallow waters (0.0–1.5 m) and deeper waters (2.5–3.5 m), while *H. midae* were only seen to be caught in the deeper (2.5-3.5 m) waters. *Aonyx capensis* are generally regarded as crab specialists in freshwater habitats (Rowe-Rowe 1977c), having broadened bunodont molars for crushing

the exoskeletons of invertebrate prey (Rowe-Rowe 1977b). Their manual dexterity further enables them to feel for and capture prey under stones and in crevices (Rowe-Rowe 1977a), possibly facilitating capture of crabs, and probably *J. lalandii* as well.

The data presented above support Kramer's (1988) optimal breathing hypothesis in that surface times as well as dive times increase with dives of greater depths. The percentage time at the surface, however, does not increase with depth. Time taken for each catch also does not decrease with depth as would be expected.

The results indicate that, as predicted, significant differences existed in diving behaviour with various depths. It is often assumed that divers switch to anaerobic respiration on reaching the aerobic dive limit (Carbone & Houston 1996). It is also argued that the upturn commonly observed in the relationship between recovery time and dive time may be associated with a shift to anaerobic respiration (Kramer 1988). This was not observed with the otters in the present study, perhaps because they did not dive to depths of more than *ca* 4 m.

Optimum foraging theory predicts that *A. capensis* will forage at the depth that optimises food intake per unit effort, or of some other measure of foraging efficiency. Here I have shown that they are diving more at a depth shallower than where they are catching the most prey, the largest prey and the most energy-rich prey (i.e. fish). One possibility for deviations from the predicted trends is that *A. capensis* are avoiding predators such as great white sharks *Carcharodon carcharias*, an inshore species that eats sea mammals such as seals and small dolphins (Smith & Heemstra 1986) and possibly otters. Selecting for a depth range of 0.5-1.5 m may be locally optimal, and could therefore be different in other systems or areas.

The results (Fig. 6.4 and Table 6.4) show that when the otters dived at increasing depths their response was to vary prey size in a way which both qualitatively (increasing prey size with increasing depth) and quantitatively is as predicted by the marginal value theorem. This assumes a gradual depletion of

resources (Krebs & Kacelnik 1991). If no depletion occurs, the explanation of a load-distance (prey-size depth in the present situation) effect may lie in the energy cost or time cost of transporting different sized loads (Krebs & Kacelnik 1991). The marginal value theorem would therefore still explain the load-size distance relationship, but in a modified way (Krebs & Kacelnik 1991).

The data on diet at various depths (Fig. 6.4 and Table 6.4) suggests that the marginal value theorem provides a satisfactory account of foraging by adult *A. capensis*. This, however, is only the beginning as the data show only the outcome of behaviour and not the mechanisms by which the outcome was achieved (Krebs & Kacelnik 1991). The results do show that the assumptions about currency and constraints incorporated into the marginal value theorem are helpful in explaining the behaviour of otters (Krebs & Kacelnik 1991). A full analysis of the fitness consequences would be needed to separate out the consequences of all variables. This could clearly not be done using the present data, but opens up ideas for future research.

In broad discussions on conservation of southern African aquatic ecosystems (Branch & Branch 1981; Davies & Day 1998), little or no mention is made of either *A. capensis* or the often sympatric spotted-necked otter *L. maculicollis*. This is despite them being top predators in aquatic systems. The results obtained (Fig. 6.4) also emphasise the importance of *J. lalandii* in the diets of these carnivores, indicating the need for more continued stringent conservation measures for the conservation management of *J. lalandii*. *Jasus lalandii* and *H. midae* are intensively exploited in the study area by recreational and commercial fisheries. It is also known that otters (Kvitek & Oliver 1992) and other mustelids (Klemola *et al. 19*97) can slow the population growth of prey species. It is therefore highly recommended that for the conservation management of *A. capensis, H. midae* and *J. lalandii*, further data be collected to determine the ecological interactions between the three species. We need to bring together

decisions made by foraging otters and community and population processes.

## REFERENCES

ARDEN-CLARKE, C.H.G. 1983. Population density and social organisation of the Cape clawless otter, *Aonyx capensis* Schinz, in the Tsitsikama Coastal National Park. M.Sc. thesis, University of Pretoria, Pretoria, South Africa.

ARDEN-CLARKE, C.H.G. 1986. Population density, home range size and spatial organization of the Cape clawless otter, *Aonyx capensis*, in a marine habitat. *Journal of Zoology, London* **209**: 201-211.

ATKINS, G.R. 1970. Thermal structure and salinity of False Bay. *Transactions of the Royal Society of South Africa* **34**: 11-128.

BRANCH, G. & BRANCH, M. 1981. *The living shores of southern Africa*. C. Struik, Cape Town.

CARBONE, C. & HOUSTON, A.I. 1996. The optimal allocation of time over the dive cycle: an approach based on aerobic and anaerobic respiration. *Animal Behaviour* **51**: 1247-1255.

CHARNOV, E.L. 1976. Optimal foraging: the marginal value theorem. *Theoretical Population Biology* **9**: 129-136.

CLARK, B.M., BENNETT, B.A. & LAMBERTH, S.J. 1996. Temporal variations in surf zone fish assemblages from False Bay, South Africa. *Marine Ecology Progress Series* **131**: 35-47.

CLODE, D. & MACDONALD. D.W. 1995. Evidence for food competition between mink (*Mustela vision*) and otter (*Lutra lutra*) on Scottish islands. *Journal Zoology, London* **237**: 435-444.

CONROY, J.W.H. & JENKINS, D. 1986. Ecology of otters in northern Scotland. VI. Diving times and hunting success of otters (*Lutra lutra*) at Dinnet, Aberdeenshire and in Yell Sound, Shetland. *Journal of Zoology, London* **209**: 341-346.

DAVIES, B.R. & DAY, J.A. 1998. *Vanishing waters*. University of Cape Town Press, Cape Town.

EMLEN, J.M. 1966. The role of time and energy in food preference. *American Naturalist* **100**: 611-617.

FISH, F.E. 1994. Association of propulsive swimming mode with behavior in river otters (*Lutra canadensis*). *Journal of Mammalogy* **75**: 989-997.

HOUSTON, A.I. & MCNAMARA. J.M. 1985. A general theory of central place foraging for single-prey loaders. *Theoretical Population Biology* **28**: 233-262.

KLEMOLA, T., KOIVULA, M., KORPIMÄKI, E. & KAINORRDAHL, K. 1997. Small mustelid predation slows population growth of *Microtus* voles: a predator reduction experiment. *Journal of Animal Ecology* **66**: 607-614.

KOOYMAN, G.L. 1989. *Diverse divers*. Springer Verlag, Berlin.

KRAMER, D.L. 1988. The behavioral ecology of air breathing by aquatic animals. *Canadian Journal of Zoology* **66**: 89-94.

KREBS, J.R. & KACELNIK, A. 1991. Decision making. In: *Behavioural ecology an evolutionary approach*, (eds) J.R. Krebs, & N.B. Davies, 3rd edn, Blackwell Scientific Publications, Oxford.

KRUUK, H. 1972. *The spotted hyena*. University of Chicago Press, Chicago.

KRUUK, H. 1993. The diving behaviour of the platypus (*Ornithorhynchus anatinus*) in waters with different trophic status. *Journal of Applied Ecology* **30**: 592-598.

KRUUK, H. 1995. *Wild otters: predation and populations*. Oxford University Press, Oxford.

KRUUK, H. & HEWSON, R. 1978. Spacing and foraging of otters (*Lutra lutra*) in a marine habitat. *Journal of Zoology, London* **185**: 205-212.

KRUUK, H. & MOORHOUSE, A. 1990. Seasonal and spatial differences in food selection by otters (*Lutra lutra*) in Shetland. *Journal of Zoology, London* **221**: 621-637.

KRUUK, H., TAYLOR, P.T. & MOM, G.A.T. 1997. Body temperature and foraging behaviour of the Eurasian otter (*Lutra lutra*), in relation to water temperature. *Journal of Zoology, London* **241**: 689-697.

KRUUK, H., WANSINK, D. & MOORHOUSE, A. 1990. Feeding patches and diving success of otters, *Lutra lutra*, in Shetland. *Oikos* **57**: 68-72.

KVITEK, R.G. & OLIVER, J.S. 1988. Sea otter foraging habits and effects on prey populations and communities in soft-bottom environments. In: *The community ecology of sea otters,* (eds) G.R. VanBlaricom & J.A. Estes, Springer-Verlag, Berlin.

KVITEK, R.G. & OLIVER, J.S. 1992. Influence of sea otters on soft-bottom prey communities in southeast Alaska. *Marine Ecology Progress Series* **82**: 103-113.

KVITEK, R.G., BOWLBY, C.E. & STAEDLER, M. 1993. Diet and foraging behavior of sea otters in Southeast Alaska. *Marine Mammal Science* **9**: 168-181.

MACARTHUR, R.H. & PIANKA, E.R. 1966. On optimal use of a patchy environment. *American Naturalist* **100**: 603-609.

NOLET, B.A., WANSINK, D.E.H. & KRUUK, H. 1993. Diving of otters (*Lutra lutra*) in a marine habitat: use of depths by a single-prey loader. *Journal of Animal Ecology* **62**: 22-32.

OSTFELD, R.S. 1991. Measuring diving success of otters. *Oikos* **60**: 258-260.

PERRY, G. & PIANKA, E.R. 1997. Animal foraging: past, present and future. *Trends in Ecology and Evolution* **12**: 360-364.

PURVES, M.G., KRUUK, H. & NEL, J.A.J. 1994. Crabs *Potamonautes perlatus* in the diet of the otter *Aonyx capensis* and water mongoose *Atilax paludinosus* in a freshwater habitat in South Africa. *Zeitschrift für Säugetierkunde* **59**: 332-341.

RALLS, K., HATFIELD, B.B. & SINIFF, D.B. 1995. Foraging patterns of California sea otters as indicated by telemetry. *Canadian Journal of Zoology* **73**: 523-531.

ROWE-ROWE, D.T. 1977a. Variation in the predatory behaviour of the clawless otter. *Lammergeyer* **23**: 22-27.

ROWE-ROWE, D.T. 1977b. Prey capture and feeding behaviour of South African otters. *Lammergeyer* **23**: 13-21.

ROWE-ROWE, D.T. 1977c. Food ecology of otters in Natal, South Africa. *Oikos* **28**: 210-219.

ROWE-ROWE, D.T. & SOMERS, M.J. 1998. Diet, foraging behaviour and coexistence of African otters and the water mongoose. *Symposia of the Zoological Society of London* No. 71: 215-227.

SCHULZE, B.R. 1965. *Climate of South Africa, Part 8, General Survey*. Weather Bureau, Pretoria.

SIEGEL, S. 1956. *Nonparametric Statistics for the behavioural sciences*. McGraw-Hill, New York.

SKINNER, J.D. & SMITHERS, R.H.N. 1990. *The mammals of the Southern African subregion*. University of Pretoria, Pretoria.

SMITH, M.M. & HEEMSTRA, P.C. 1986. *Smiths' sea fishes*. Macmillan, Johannesburg.

SOMERS, M.J. 2000. Seasonal variation in the diet of Cape clawless otters (*Aonyx capensis*) in a marine habitat. *African Zoology* **35**: 261-268.

SOMERS, M.J. & PURVES, M.G. 1996. Trophic overlap between three syntopic semi-aquatic carnivores: Cape clawless otter, spotted-necked otter, and water mongoose. *African Journal of Ecology* **34**: 158-166.

SPARGO, P.E. 1991. False Bay, South Africa – an historic and scientific overview. *Transactions of the Royal Society of South Africa* **47**: 363-375.

TAYLER, C. 1970. The elusive otter. *The Eastern Cape Naturalist* **39**: 20-23.

VAN DER ZEE, D. 1979. Food and status of the Cape clawless otter *Aonyx capensis* Schinz, in the Tsitsikama Coastal National Park, South Africa. M.Sc. thesis, University of Pretoria, Pretoria, South Africa.

VAN DER ZEE, D. 1981. Prey of the Cape clawless otter (*Aonyx capensis*) in the Tsitsikama National Park, South Africa. *Journal of Zoology, London* **194**: 467-483.

VAN NIEKERK, C.H., SOMERS, M.J. & NEL, J.A.J. 1998. Freshwater availability and distribution of Cape clawless otter spraints and resting places along the south-west coast of South Africa. *South African Journal of Wildlife Research* **28**: 68-72.

VERWOERD, D.J. 1987. Observations on the food and status of the Cape clawless otter *Aonyx capensis* at Betty's Bay, South Africa. *South African Journal of Zoology* **22**: 33-39.

WATT, J.P. 1993. Ontogeny of hunting behaviour of otters (*Lutra lutra* L.) in a marine environment. *Symposia of the Zoological Society of London* No. 65: 87-104.

WATT, J. 1995. Seasonal and area-related variations in the diet of otters *Lutra lutra* on Mull. *Journal of Zoology, London* **237**: 179-194.

# CHAPTER 7*

# TROPHIC OVERLAP BETWEEN THREE SYNTOPIC SEMI-AQUATIC CARNIVORES: CAPE CLAWLESS OTTER (*AONYX CAPENSIS*), SPOTTED-NECKED OTTER (*LUTRA MACULICOLLIS*), AND WATER MONGOOSE (*ATILAX PALUDINOSUS*).

## INTRODUCTION

Cape clawless otters *Aonyx capensis* (Schinz), spotted-necked otters *Lutra maculicollis* (Lichtenstein), and water mongooses *Atilax paludinosus* (Cuvier), coexist throughout much of their geographic ranges (Rowe-Rowe 1991), feed on many of the same foods, (Rowe-Rowe 1977a; Skinner & Smithers 1990) and use similar habitats (Skinner & Smithers 1990). Interspecific competition can therefore occur, but the extent and nature of this is largely unknown. Rowe-Rowe (1977a) compared the diet of the three carnivores where they coexist in KwaZulu-Natal, South Africa, but no other comparative data on factors affecting their coexistence are available.

Both *A. capensis* and *A. paludinosus* are widely distributed in southern Africa (Skinner & Smithers 1990), but the geographical range of *L. maculicollis* appears to be shrinking (Stuart 1985; Nel & Somers unpublished data). Applicable ecological information is therefore essential for successful conservation measures. During a drought between 1990 and 1993 a large part of the

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Bushmans River system dried up and suitable habitat, especially for the two otter species, was much reduced. This forced the three carnivores to coexist in restricted areas. It allowed observation and quantification of the way in which they shared food resources under conditions of enforced competition.

I report here on the food of *A. capensis*, *L. maculicollis* and *A. paludinosus* in the Bushmans River, Eastern Cape Province, South Africa, as indicated by the composition of their scats. This study quantifies sizes of crabs *Potamonautes perlatus* (Milne Edwards) eaten by the three carnivores, using length of eyestalks found in the faeces (Purves *et al.* 1994). The sizes of the fish *Tilapia sparrmanii* (Smith) eaten is also quantified, using the diameter of eye-lenses in the faeces (Kruuk & Goudswaard 1990).

## Ecological background of the three species

*Aonyx capensis* weigh between 10 and 16 kg, with males being larger than females. Prey of *A. capensis* have been documented in marine habitats by Van der Zee (1981); Arden-Clarke (1983) and Verwoerd (1987). Crustaceans have been shown to be the most common prey of *A. capensis* freshwater ecosystems, supplemented with lesser amounts of frogs, fishes, and aquatic insects (Turnbull-Kemp 1960; Rowe-Rowe 1977a; Kruuk & Goudswaard 1990; Butler & du Toit 1994; Ligthart *et al.* 1994; Purves *et al.* 1994). Birds, reptiles, molluscs, dung (ungulate) and mammals are all minor items, seldom eaten. In freshwater habitats *A. capensis* are active mainly during late afternoon, early evening, and early morning (Rowe-Rowe 1978; unpublished radio-tracking data). In marine habitats they are mainly nocturnal (Arden-Clarke 1983).

*Lutra maculicollis* have a total length of less than 1 m and weight of about 4.5 kg for males and 3.5 kg for females (Skinner & Smithers 1990). No published data are available on *L. maculicollis* prey in the Eastern Cape Province. Present information indicates cichlid fish (*Haplochromis* spp.) to be the most common prey of *L. maculicollis* in Lake Muhazi, Rwanda (Lejeune 1990) and in Lake Victoria, Tanzania (Procter 1963;

Kruuk & Goudswaard 1990), while in KwaZulu-Natal, South
Africa, crabs (*Potamonautes* spp.) and fish appear to be the most
common prey (Rowe-Rowe 1977a). Birds, frogs, insects, and
molluscs are also taken (Rowe-Rowe 1977a; Kruuk & Goudswaard
1990; Lejeune 1990). Although not based on radio telemetry, *L.
maculicollis* are reported to be mainly diurnal (Procter 1963;
Kruuk & Goudswaard 1990), with activity peaking in the morning
and late afternoon (Rowe-Rowe 1978). *Lutra maculicollis* do not
occur in marine habitats (Skinner & Smithers 1990).

Male and female *A. paludinosus* have mean lengths of 878 and
848 mm respectively, and the mean weight for both sexes is 3.4 kg
(Skinner & Smithers 1990). Crabs appear to be the most common
prey of *A. paludinosus* in most areas with mammals, birds,
reptiles, fish, frogs, molluscs, insects, diplopods, isopods, and
fruit also being taken (Rowe-Rowe 1977a; Smithers & Wilson 1979;
du Toit 1980; Whitfield & Blaber 1980; Louw & Nel 1986; Baker
1989; Purves *et al.* 1994). *Atilax paludinosus* are nocturnal
(Maddock & Perrin 1993), and hunt mainly along the edges of water
(Rowe-Rowe 1978) but may fully immerse themselves when catching
food (Baker 1989).

## MATERIALS & METHODS

Scats were collected during September, October, and November
1993, along a 3-km stretch of the Bushmans River running through
and south of Alicedale (33° 19' S, 26° 05' E), Eastern Cape
Province, South Africa. The average width of the river was *ca* 8
m. Depth varied between 20 mm (riffles and reed beds) and 1.5 m
(pools). Water level rose by about 0.5 m during rain in October.
The vegetation is classified as subtropical transitional thicket.
Structurally the plant communities are dominated by evergreen
sclerophyllous shrubs and succulents (Cowling 1984). Annual
rainfall for the area is *ca* 450 mm (Kopke 1988).

Sixty-six *A. capensis*, 79 *L. maculicollis*, and 31 *A.
paludinosus* scats were collected. Identification of otter scats

in the field was based on their characteristic odour. The species origin was based on locality of deposition and size (Rowe-Rowe 1992) and the presence of otter tracks. Identification of *A. paludinosus* scats was based on locality and characteristic banded hairs in them. When the species origin was not clear the scats were not collected.

The scats were air-dried, teased apart and prey remains identified using a stereomicroscope (**X** 10 - 100 magnification). Prey items were sorted into the following categories: mammal, bird, reptile, frog, fish, crab, insect, unidentified material, and non-food such as soil and leaves. The presence of mammal remains in the scats was determined from hair and bones, crabs and insects from carapaces, fish from bones and scales, reptiles and frogs from bones, and birds from feathers.

The presence of each prey category in each scat was scored. Scores for each category were added and expressed as a percentage of the total number of scores of all categories, yielding relative percentage frequency. This method has been shown to closely approximate the proportions of different items actually consumed by otters (Erlinge 1968; Rowe-Rowe 1977a).

For each scat the dominant prey type was also determined by volumetric analysis of prey items. For that analysis, in a scat consisting mainly of crab remains, crab would be the dominant prey type and the other prey items in the scat would be ignored. The different dominant prey items were then added up and expressed as percentage of the total number of scats (Kruuk *et al.* 1994; Purves *et al.* 1994).

Crabs (*n* = 33, mean carapace width = 22.3 mm, S.D. = 8.1 mm, range = 8.6-49.7 mm) were collected from reed beds in the river by searching under stones and in grass. Crabs (*n* = 10, mean carapace width = 50.5 mm, S.D. = 12.3 mm, range = 29.9-69.1 mm) were also caught in pools in funnel traps baited with dead fish. The maximum carapace widths of these crabs were measured with calipers and eyestalk lengths were measured with an ocular ruler in a stereomicroscope. A regression was calculated for carapace

width and eyestalk lengths (Purves *et al.* 1994). There was a
linear relationship for which

C = -11.94+7.90*E, where C = carapace width (mm) and E = eyestalk
length (mm). The correlation was significant ($r$ = 0.996, $n$ = 50,
S.E. = 6.09%). Lengths of eyestalks in the scats of all three
species were measured. The equation was then used to determine
size of crabs taken by the three predators.

Fish were caught in funnel traps to determine species
present. I identified river goby *Glossogobius callidus* (Smith),
goldie barb *Barbus pallidus* (Greenwood), and banded tilapia *T.
sparrmanii*. Other fish species known to occur at the study site
are moggel *Labeo umbratus* (Smith) and largemouth bass *Micropterus
salmoides* (Lacepède) (P. Skelton pers. comm. 1993). Scales were
removed from each fish species and mounted on slides.

Scales from *Labeo umbratus* were provided by the J.L.B. Smith
Institute of Ichthyology, Grahamstown and *Micropterus salmoides*
from reference material of the Department of Zoology, University
of Stellenbosch. Fish scales found in the scats of the three
carnivores were compared with the mounted specimens.

The only fish species found in the scats was *T. sparrmanii*. A
regression using eye-lens diameter and fish fork length was
calculated, as has been done for cichlids in Lake Victoria (Kruuk
& Goudswaard 1990). The eye-lenses were air dried with the scats
before they were measured. There was a linear relationship for
which F = 11.75+43.84*E, where F = fish fork length (mm) and E =
eye-lens diameter (mm). The correlation was significant ($r$ =
0.988, $n$ = 87, S.E. = 3.51%). Eye-lenses from the scats were then
measured and the size of fishes preyed upon by the three
predators was determined.

## RESULTS

### Faecal analysis

The relative percentage occurrence and dominant category of prey items recorded in scats of *A. capensis*, *L. maculicollis* and *A. paludinosus* are shown in Tables 7.1-7.3. Crab remains were of *P. perlatus,* the only freshwater crab in the Bushmans River (Barnard 1950). Fish remains in all scats were from *T. sparrmanii*, insect remains represented Coleoptera and Odonata, while mammals and frogs were unidentified.

### Size of crabs and fish

The crabs which *A. paludinosus* and *L. maculicollis* ate were of similar sizes (Mann-Whitney *U* test, *P* = 0.082, two-tailed for this and all subsequent Mann-Whitney *U* tests) (Table 7.4), but significantly larger than the crabs eaten by *A. capensis* (Mann-Whitney *U* test, *P* < 0.001, for both tests) (Table 7.4). The size distribution of crabs eaten by the three carnivores differed with *A. capensis* taking a wider range than the other two species (Table 7.5).

The fish which *A. paludinosus* and *A. capensis* ate were of similar size (Mann-Whitney *U* test, *P* = 0.056) (Table 7.6), and both ate significantly smaller fish than did *L. maculicollis* (Mann-Whitney *U* test, *P* = 0.048); (Mann-Whitney *U* test, *P* < 0.001) (Table 7.6).

## DISCUSSION

Although it is not clear how many individuals of each species were present, frequent sightings of *A. capensis* and abundant tracks of *L. maculicollis* and *A. paludinosus* indicated that there were many individuals of all three carnivores. These data were collected over a short period from a small sample of scats.

**Table 7.1.** Prey items recorded in 66 *Aonyx capensis* scats collected from the Bushmans River from September to November 1993, as percentage occurrence, relative frequency occurrence, and percentage of scats dominated by a prey.

| | Observed | % Freq. | Rel. % Freq. | % Dominance |
|---|---|---|---|---|
| Crab | 66 | 100 | 50.8 | 95.5 |
| Insect (total) | 25 | 37.9 | 19.2 | |
|     Odonata | 14 | 21.2 | 10.8 | |
|     Coleoptera | 2 | 3.0 | 1.5 | |
| Fish | 23 | 36.4 | 17.7 | 4.6 |
| Frog | 12 | 18.2 | 9.2 | |
| Spider | 2 | 3.0 | 1.5 | |
| Unidentified | 2 | 3.0 | 1.5 | |
| Non-food (soil leaves) | 9 | 13.6 | ____ | |

**Table 7.2.** Prey items recorded in 79 *Lutra maculicollis* scats collected from the Bushmans River from September to November 1993, as percentage occurrence, relative frequency occurrence, and percentage of scats dominated by a prey.

| | Observed | % Freq. | Rel. % Freq. | % Dominance |
|---|---|---|---|---|
| Fish | 64 | 81.0 | 46.7 | 53.2 |
| Crab | 52 | 65.8 | 38.0 | 44.3 |
| Frog | 11 | 13.9 | 8.0 | 2.5 |
| Unidentified | 4 | 5.6 | 2.9 | |
| Insect (total) | 3 | 3.8 | 2.2 | |
| Odonata | 1 | 1.3 | 0.7 | |
| Bird | 2 | 2.5 | 1.5 | |
| Mammal | 1 | 1.3 | 0.7 | |
| Non-food (soil leaves) | 1 | 1.3 | ____ | |

**Table 7.3.** Prey items recorded in 31 *Atilax paludinosus* scats collected from the Bushmans River from September to November, as percentage occurrence, relative frequency occurrence, and percentage of scats dominated by a prey.

|  | Observed | % Freq. | Rel. % Freq. | % Dominance |
|---|---|---|---|---|
| Insect | 25 | 80.7 | 28.4 | 12.9 |
| Crab | 23 | 74.2 | 26.1 | 42.0 |
| Mammal | 13 | 41.9 | 14.8 | 16.2 |
| Frog | 12 | 38.7 | 13.6 | 3.2 |
| Bird | 6 | 19.4 | 6.8 | 12.9 |
| Lizard | 4 | 12.9 | 4.5 | 3.2 |
| Fish | 3 | 9.7 | 3.4 | 3.2 |
| Unidentified | 2 | 6.5 | 2.3 | 3.2 |
| Non-food (soil leaves) | 2 | 6.5 | ____ | |

**Table 7.4.** The size of crabs eaten by *Aonyx capensis*, *Lutra maculicollis* and *Atilax paludinosus* in the Bushmans River.

|            | *Aonyx*    | *Lutra*   | *Atilax*    |
|------------|------------|-----------|-------------|
| *n*        | 1365       | 91        | 64          |
| Mean (mm)  | 23.5       | 27.3      | 25.0        |
| S.D.       | 10.0       | 8.6       | 6.6         |
| Range      | 3.1-65.5   | 8.6-44.2  | 10.2-41.0   |

**Table 7.5.** The size distribution of crabs *Potamonautes perlatus* eaten by *Aonyx capensis*, *Lutra maculicollis*, *Atilax paludinosus* in the Bushmans River.

| Size of crabs (mm) | Aonyx (%) (n = 1365) | Lutra (%) (n = 91) | Atilax (%) (n = 64) |
|---|---|---|---|
| 0-4 | 0.2 | 0 | 0 |
| 5-9 | 4.4 | 1.1 | 0 |
| 10-14 | 12.5 | 4.4 | 6.25 |
| 15-19 | 20.8 | 15.4 | 7.8 |
| 20-24 | 24.8 | 15.4 | 34.3 |
| 25-29 | 15.2 | 24.2 | 34.3 |
| 30-34 | 8.1 | 16.5 | 7.8 |
| 35-39 | 6.2 | 13.2 | 4.7 |
| 40-44 | 4.1 | 9.9 | 4.7 |
| 45-49 | 1.3 | 0 | 0 |
| 50-54 | 1.8 | 0 | 0 |
| 55-59 | 0.4 | 0 | 0 |
| 60-65 | 0.1 | 0 | 0 |
| 66-70 | 0.2 | 0 | 0 |

**Table 7.6.** The size of fish eaten by *Aonyx capensis*, *Lutra maculicollis* and *Atilax paludinosus* in the Bushmans River.

|  | *Aonyx* | *Lutra* | *Atilax* |
|---|---|---|---|
| *n* | 60 | 205 | 8 |
| Mean (mm) | 20.5 | 28.0 | 24.7 |
| S.D. | 4.0 | 7.2 | 5.7 |
| range | 12.8-30.5 | 9.6-52.9 | 20.9-38.5 |

They are, however, sufficient to show the degree of overlap in prey types between the three carnivores, and the differences in relative quantities and sizes of prey, especially for crabs and fish.

The results show that even during enforced cohabitation in a relatively small range during drought conditions there is separation of diets in these three carnivores. The differences in prey species selection are similar to those reported by Rowe-Rowe (1977a) for the three species where they coexist in rivers in KwaZulu-Natal, suggesting little or no resource shift in response to drought conditions.

Crabs were the main prey of *A. capensis* and *A. paludinosus*, whereas *L. maculicollis* took fish and crabs in similar proportions. *Atilax paludinosus*, however, used a wider range of terrestrial prey than did the two otter species.

The hunting behaviour of the predators may have influenced the selection of prey. Both otter species actively dive in search of prey (Rowe-Rowe 1977b), while *A. paludinosus* occupy a wider range of habitats and only immerse their heads once prey have been sighted (Rowe-Rowe 1978; Baker 1989), usually in shallow water. The more frequent occurrence of aquatic prey in the diet of the two otter species suggests that their foraging is mostly restricted to the river, whereas *A. paludinosus* were the only predators taking terrestrial prey in significant proportions.

Another factor that would further aid dietary segregation, although only over a short period, is that the carnivores utilized different sizes of prey. Although the differences between the means were not very great, the crabs eaten by *L. maculicollis* and *A. paludinosus* were significantly larger than those taken by *A. capensis*. *Aonyx capensis* ate a wide range of crab sizes, including specimens much larger than those taken by the other two carnivores. This could be related to differences in feeding behaviour of the predators, as well as to differences in foraging behaviour of the crabs (Hill & O'Keeffe 1992). The relationship between the predators and the size of crabs they prey upon, is therefore complex. Local differences such as the

depth of the river, substratum type, availability of alternative prey, seasonal floods, or the density of the predators, probably all interact to determine which section of the crab population is available to a specific predator species at a specific time. In the Olifants River, Western Cape Province, *A. capensis* ate smaller crabs than *A. paludinosus* (Purves *et al.* 1994).

*Aonyx capensis* are generally regarded as crab specialists in freshwater habitats (Rowe-Rowe 1977a), having broadened bunodont molars for crushing the exoskeletons of invertebrate prey. Their manual dexterity further enables them to feel for and capture prey under stones and in crevices (Rowe-Rowe 1977a), possibly facilitating capture of all sizes of crabs. In contrast, *L. maculicollis* are not as well adapted for the capture and consumption of crabs and even avoid larger crabs (> 50 mm) when available (Rowe-Rowe 1977b). In Lakes Victoria and Muhazi, where fish are particularly abundant, *L. maculicollis* are virtually entirely piscivorous (Kruuk & Goudswaard 1990; Lejeune 1990), whereas in KwaZulu-Natal, where fish faunas are impoverished, Rowe-Rowe (1977a) found that they ate almost equal amounts of crab and fish. Larger crabs would be more visible than smaller specimens, especially in a river with a high turbidity, such as the Bushmans River during this study. The size distribution of crabs eaten by the three predators, also suggests that there is no obvious selection for energetically more rewarding large crabs above smaller specimens (Table 7.5).

*Lutra maculicollis* preyed on fish more often and ate larger fish than did the other two predators, reflecting their piscivorous adaptations. *Aonyx capensis* and *A. paludinosus* took similar sized fish, although this was not a major prey type of *A. paludinosus*. All the fish eaten were *T. sparrmanii*, which was also the species eaten most often (81 %) by *A. capensis* in the Olifants River, Western Cape (Purves *et al.* 1994). Similar to the rivers in KwaZulu-Natal, the fish fauna of the Bushmans River may not be rich enough to sustain *L. maculicollis*, and crabs, therefore, form an important complimentary part of their diet.

*Tilapia sparrmanii* are exotic to the Olifants and Bushmans Rivers (Skelton 1993), indicating a possible improvement in the availability of food for otters, in these areas, as a result of human interference.

The results show the importance of crabs in the diets of these three carnivores, emphasizing, for the conservation management of otters and *A. paludinosus*, the need for more information about factors limiting crab numbers.

## REFERENCES

ARDEN-CLARKE, C.H.G. 1983. Population density and social organization of the Cape clawless otter, *Aonyx capensis* Schinz, in the Tsitsikama Coastal National Park. M.Sc. thesis, University of Pretoria, Pretoria, South Africa.

BAKER, C.M. 1989. Feeding habits of the water mongoose (*Atilax paludinosus*). *Zeitschrift für Säugetierkunde* **54**: 31-39.

BARNARD, K.H. 1950. Descriptive catalogue of South African Decapod Crustacea (crabs and shrimps). *Annals of the South African Museum* **38**: 179-194.

BUTLER, J.R.A. 1994. Cape clawless otter conservation and a trout river in Zimbabwe: a case study. *Oryx* **28**: 276-282.

TURNBULL-KEMP, P.ST.J. 1960. Quantitative estimations of populations of river crab, *Potamon (Potamonautes) perlatus* (M. Edw.), in Rhodesian trout streams. *Nature, London* **185**: 481.

BUTLER, J.R.A. & DU TOIT, J.T. 1994. Diet and conservation of Cape clawless otters in eastern Zimbabwe. *South African Journal of Wildlife Research* **24**: 41-47.

COWLING, R.M. 1984. A syntaxonomic and synecological study in the Humansdorp region of the fynbos biome. *Bothalia* **15**: 175-227.

DU TOIT, C.F. 1980. The yellow mongoose *Cynictis penicillata* and other small carnivores in the Mountain Zebra National Park. *Koedoe* **23**: 179-184.

ERLINGE, S. .1968. Food studies on captive otters *Lutra lutra* L.. *Oikos* **19**: 259-270.

HILL, M.P. & O'KEEFFE, J.H. 1992. Some aspects of the ecology of the freshwater crab (*Potamonautes perlatus* Milne Edwards) in the upper reaches of the Buffalo River, eastern Cape Province, South Africa. *South African Journal of Aquatic Sciences* **18**: 42-50.

KOPKE, D. 1988. The climate of the eastern Cape. In: *Towards an environmental plan for the eastern Cape,* (eds) M.N. Bruton & F.W. Gess, Rhodes University, Grahamstown.

KRUUK, H. & GOUDSWAARD, P.C. 1990. Effects of changes in fish populations in Lake Victoria on the food of otters (*Lutra maculicollis* Schinz and *Aonyx capensis* Lichtenstein). *African Journal of Ecology* **28**: 322-329.

KRUUK, H., KANCHANASAKA, B., O'SULLIVAN, S. & WANGHONGSA, S. 1994. Niche separation in three sympatric otters *Lutra perspicillata, L. lutra* and *Aonyx cinerea* in Huai Kha Khaeng, Thailand. *Biological Conservation* **69**: 115-120.

LEJEUNE, A. 1990. Ecologie alimentaire de la loutre (*Hydrictis maculicollis*) au lac Muhazi. *Mammalia* **54**: 33-45.

LIGTHART, M.F., NEL, J.A.J. & AVENANT, N.L. 1994. Diet of Cape clawless otters in part of the Breede River system. *South African Journal of Wildlife Research* **24**: 38-39.

LOUW, C.J. & NEL, J.A.J. 1986. Diets of coastal and inland-dwelling water mongoose. *South African Journal of Wildlife Research* **16**: 153-156.

MADDOCK, A.H. & PERRIN, M.R. 1993. Spatial and temporal ecology of an assemblage of viverrids in Natal, South Africa. *Journal of Zoology, London* **229**: 227-287.

PROCTER, J. 1963. A contribution to the natural history of the spotted-necked otter (*Lutra maculicollis* Lichtenstein) in Tanganyika. *East African Wildlife Journal* **1**: 93-102.

PURVES, M.G., KRUUK, H. & NEL, J.A.J. 1994. Crabs *Potamonautes perlatus* in the diet of the otter *Aonyx capensis* and water mongoose *Atilax paludinosus* in a freshwater habitat in South Africa. *Zeitschrift für Säugetierkunde* **59**: 332-341.

ROWE-ROWE, D.T. .1977a. Food ecology of otters in Natal, South Africa. *Oikos* **28**: 210-219.

ROWE-ROWE, D.T. 1977b Prey capture and feeding behaviour of South African otters. *Lammergeyer* **23**: 13-21.

ROWE-ROWE, D.T. 1978. The small carnivores of Natal. *Lammergeyer* **25**: 1-48.

ROWE-ROWE. D.T. 1991. Status of otters in Africa. *Habitat* **6**: 15-20.

ROWE-ROWE, D.T. 1992. Survey of South African otters in freshwater habitat, using sign. *South African Journal of Wildlife Research* **22**: 49-55.

SKELTON, P.H. 1993. A *complete guide to the freshwater fishes of southern Africa*. Southern Book Publishers, Halfway House.

SKINNER, J.D. & SMITHERS, R.H.N. 1990. *The mammals of the southern African subregion*. University of Pretoria, Pretoria.

SMITHERS, R.H.N. & WILSON, V.J. 1979. Check list and atlas of the mammals of Zimbabwe Rhodesia. *Museum Memoirs of the National Museums and Monuments of Rhodesia* **9**: 1-147.

STUART, C.T. 1985. The status of two endangered carnivores occurring in the Cape province, South Africa, *Felis serval* and *Lutra maculicollis*. *Biological Conservation* **32**: 375-382.

TURNBULL-KEMP, P.St J. 1960. Quantitative estimations of populations of river crab, *Potamon (Potamonautes) perlatus* (M. Edw.), in Rhodesian trout streams. *Nature, London* **185**: 481.

VAN DER ZEE, D. 1981 Prey of the Cape clawless otter (*Aonyx capensis*) in the Tsitsikama National Park. South Africa. *Journal of Zoology, London* **194**: 467-483.

VERWOERD, D.J. 1987. Observations on the food and status of the Cape clawless otter *Aonyx capensis* at Betty's Bay, South Africa. *South African Journal of Zoology* **22**: 33-39.

WHITFIELD, A.K. & BLABER, S.J.M. 1980. The diet of *Atilax paludinosus* (water mongoose) at St Lucia, South Africa. *Mammalia* **44**: 315-318.

# CHAPTER 8

# CONCLUSION AND CONSERVATION MANAGEMENT CONSIDERATIONS

Of the 13 species of otter worldwide most if not all are to a greater or lesser extent, or in part of their distributional range, subject to habitat changes brought about by man. Most have their main distribution in freshwater ecosystems and with the burgeoning human population and increased use of finite freshwater resources pressure on most species can only increase. In addition, apart from a few species, e.g. European otter *Lutra lutra*, the North American river otter *Lutra canadensis* and the sea otter *Enhydra lutris*, knowledge of the ecology and behaviour, and conservation status of most species is limited. The Cape clawless otter *Aonyx capensis* is widespread in sub-Saharan Africa and inhabit both freshwater and marine ecosystems, but apart from a few studies in southern Africa are largely unknown. As a top predator in freshwater ecosystems it was initially thought to be a good indicator species but as will be shown below are widespread and can tolerate altered habitats and human disturbance, so it probably cannot fulfil this role.

The rationale and aims for the present study was to expand our knowledge on some aspects of the ecology and behaviour of *A. capensis*, and especially to obtain data on habitat use, and relation between prey availability and prey eaten (aspects not previously addressed in a quantitative fashion) of *A. capensis* in the southwestern Western Cape Province. In addition, data on the same aspects in a marine habitat were also obtained; the otters enjoy a wide distribution along the southern and eastern seaboards of South Africa, and marine habitats can therefore possibly function as an important stronghold for the species.

This study therefore tested several hypotheses regarding various aspects of habitat use by *A. capensis,* in various

habitats. The hypotheses, namely that *A. capensis* do not select any prey types, prey sizes or habitat type were tested. Habitat types used were investigated at a scale that enabled separating the effects of types of riparian vegetation, geomorphology and anthropogenic influences. Aspects of the resource dispersion hypothesis and optimal foraging theory were also tested. This was done in both the marine and freshwater environments.

Prey availability (as apposed to density) is notoriously difficult to quantify. For otters, as for other carnivores, this entails sampling prey at the times and in the habitats, where foraging takes place. Activity of *A. capensis* were deduced from radio-tracking data, as were habitats most often used. Freshwater crabs have been shown in all previous as well as the present study to be the main prey species. On account of the habitats frequented by otters, sampling of crabs by hand was not always possible, and other methods, e.g. – by trapping them in traps, had to be used. Results from the two rivers indicated that hand sampling was more accurate, as traps were selective for size; small crabs were excluded.

While crabs were the most important prey in all seasons fish was the second most important in both the rivers, and during all seasons. The percentage occurrence of prey of *A. capensis* in both rivers showed an increase in the amount of crab in summer and a corresponding decrease in the number of fish eaten. The seasonal fluctuation in crabs and fish found in the spraints (faeces), corresponded with the expected frequencies as determined from trapping. The results obtained are also consistent with those of previous studies (see Rowe-Rowe & Somers 1998 for review), but for those of Rowe-Rowe (1977a) and Purves & Sachse (1998), where frogs were found to be the second most common prey type. These two studies were, however, done at middle to high altitudes (1060-1650 m.a.s.l.) where fish faunas are poor (Rowe-Rowe & Somers 1998). The importance of different secondary prey found in the various studies is probably related to local prey availability (Rowe-Rowe & Somers 1998).

Optimal foraging theory can be used to account for the types and sizes of prey items taken by predators (Krebs & Kacelnik 1991). One possible hypothesis to explain why several types of prey are eaten, apart from the main prey (for which *A. capensis* is anatomically (long vibrissae, prehensile toes) and behaviourally (foraging mode, degree of sociality, habitat choice) adapted) is that the times taken to search for the most profitable prey type influences choice. If it takes a long time to find and catch a more profitable prey item (such as a fish), an otter might be able to obtain a higher overall rate of energy intake per unit time by eating something less profitable, e.g. crabs. The same may apply to sizes of prey eaten. The size of crabs in the present and in other studies, were relatively small compared to what was available. Otters may find small crabs more "profitable" because these are more easily located, caught, and eaten than larger crabs (i.e. a higher encounter rate, and lower handling time) and this is what they are adapted to catching.

Butler & du Toit (1994) speculated that the low densities of *A. capensis* in Zimbabwe is probably a reflection of the low numbers of crabs in certain water bodies. If this holds true elsewhere a rapidly decreasing quality and quantity of fresh water in Africa (Davies & Day 1998) indicates that the fate of many aquatic biological communities is uncertain. More detailed long-term data are therefore needed to determine the relationships between *A. capensis* and their main and secondary prey.

### Home range use

What is a home range, and what is it used for? The classical definition of Burt (1943) still holds good: that a home range is that area about an animal's established home which is traversed by an animal in its normal activities of food-gathering, mating, and caring for young. This study has found that total home range length of the seven radio-tracked otters varied from 4.9 to 54.1 km and core home range length from 0.2 to 9.8 km. Total surface area of water used ranged from 4.9 to 1062.5 ha, and the core area used from 1.1 to 138.9 ha.

As home range used by some of the otters were large, conservation areas for otters would need to be extremely large, even including whole river systems.

The spatial organization found i.e. home ranges of males overlap, possibly forming male group ranges, while those of males overlap those of several females, with the females being possibly territorial, is common in mustelids (Powell 1979). If, as this study suggests, females have exclusive home ranges, they are probably density dependent. Habitat loss, i.e. less available food and shelter, will therefore directly affect total otter population size. The results presented here suggest that submerged macrophytes are important habitat types for otters, because it is here that their main food source (crabs) is located. With increasing silting up of rivers (Davies & Day 1998), such habitat types are at risk through increased flooding (Colloty *et al.* 2000).

### Activity and effects of distance

Except for the otters moving through Stellenbosch, human activity did not appear to affect otter movements. This, and evidence from studies on other species such as *L. lutra* (e.g. Durbin 1993), suggests that "disturbance" *per se* should not be afforded high priority in conservation programmes, unless this affects habitat structure or pollution levels.

The otters studied were typically active from dawn for 2.6 h, and moved a mean of 0.9 km. They were also typically active from sunset for a mean of 2.3 h, moving a mean of 1.3 km. They were found to select for areas with boulders and/or reed beds, areas with widely dispersed reed beds will have otters ranging over greater distances. As pointed out above, reed beds are where prey density (and probably availability) is highest, and where otters were found to spend most of their time foraging. Boulder substrate is also a habitat rich in crabs (as apposed to e.g. a sandy substrate) so habitat "selection" reflects prey densities more than anything else.

*Aonyx capensis* cause losses to trout farms and domestic fowl and are therefore caught and either relocated or killed. The results obtained showed that there will probably be other otters in the area and the problem will not be solved by killing or translocations.

### Otters in the sea

Of the three species of sub-Saharan otters (*A. capensis*, Congo clawless otter *Aonyx congica*, spotted-necked otter *Lutra maculicollis*) *A. capensis* is the only one thus far documented as using the marine seaboard, in South Africa as well as in Guinea-Bissau (Bijago archipelago). Considering the extent, and often pristine condition of stretches of the coast, the marine habitat is an important one for *A. capensis*.

The most common prey species during all seasons was Cape rock crab *Plagusia chabrus*. Diversity of prey was lowest in winter, increasing from spring through to autumn, probably because prey were more easily caught in the cold water, enabling the otters to be more selective with regards prey types eaten. Foraging behaviour data obtained support the optimal breathing hypothesis, which predicts that both surface and dive times should increase for dives of greater depths. However, diving efficiency did not decrease with increasing depth, nor did percentage time at the surface increase with increasing depth.

For *A. capensis* in the sea a combination of direct observation and spraint analysis would give a more complete description of diet. For example, in the present study soft prey such as abalone were not represented in the spraints, yet observations indicated that they were eaten. On the other hand, crab and fish species data were not available from direct observations, but were from spraint analyses. The general seasonal shift in diet composition, from fish being more important in autumn and winter to crustaceans being more important in summer and spring suggests a mechanism akin to that operating in freshwater: changes in the mortality of the prey. As the water gets warmer fish are less easily caught.

By foraging in both marine and freshwater habitats *Aonyx capensis* demonstrates an ability to successfully exploit different types of aquatic environments while also being capable of exploiting different kinds of prey in each. Because of this ability otters can be regarded as opportunist predators, able to exploit a wide variety of habitats. This augurs well for their continued existence in a variety of habitats. They, however, do exhibit a degree of anatomical specialisation, being primarily adapted to feed on crustaceans, but are able to make use of other suitable prey, such as slow-moving fishes.

The results on diet emphasised, for the conservation management of otters, the need for more information about factors limiting prey populations. In the sea this is the commercially exploited (Branch & Branch 1981) and ecologically important (van Zyl *et al.* 1998 and references therein) Cape rock lobster *Jasus lalandii*. The role of otters in the sea is also at present practically unknown and poorly understood, and deserves further study. It is also not possible, with the limited data available, to assess the impact of *A. capensis* on prey populations in the marine environment. Detailed data on the prey populations need to be gathered, but such data are, however, difficult to collect in the rough surf zones of False Bay and other areas of southern Africa's coast.

### Competition with sympatric species in the same feeding guild

How *A. capensis* use freshwater habitats in the presence of potential competitors, e.g. *L. maculicollis* and water mongooses *Atilax paludinosus*, was highlighted by investigating their trophic overlap during enforced cohabitation in a relatively small range during drought conditions. As the three species exploit the same class of environmental resources in a similar way they could be called a "guild" (Root 1967). This would have important influences on the way they utilise resources. Though the species' diets overlap, competition forces each member of the guild to adopt a distinct food niche. The analysis of trophic overlap showed that even during enforced cohabitation in a

relatively small range during drought conditions, there was separation of diets of *A. capensis, L. maculicollis* and *A. paludinosus*. This predicted that coexistence of similar species is only possible if intraspecific competition is greater then interspecific competition (Lotka 1925; MacArthur & Levins 1967). Since many species do compete with each other and still manage to coexist (Creel & Creel 1996), another explanation is necessary (Durant 1998). Models show that resource partitioning (MacArthur & Levins 1967), fluctuating environments (Chesson & Huntly 1989) and spatial heterogeneity (Hanski 1994; Durant 1998) can promote coexistence (Schoener 1974). *Aonyx capensis, L. maculicollis* and *A. paludinosus* may therefore be able to coexist as a result of resource partitioning, primarily as far as prey resources and sizes are concerned.

The hunting behaviour of the three coexisting predators may also influence the selection of prey. Both otter species actively dive in search of prey (Rowe-Rowe 1977b), while *A. paludinosus* also use terrestrial habitats to a much larger extent and only immerse their heads once prey have been sighted (Rowe-Rowe 1978; Baker 1989), usually in shallow water. The more frequent occurrence of aquatic prey in the diet of the two otter species therefore suggests that their foraging is mostly restricted to the river, whereas *A. paludinosus* also take terrestrial prey in significant proportions.

Another factor that would further aid dietary segregation, although only over a short period, is the utilization of different sizes of prey. Although the differences between the means were not very great, the crabs eaten by *L. maculicollis* and *A. paludinosus* were significantly larger than those taken by *A. capensis*. *Aonyx capensis* ate a wide range of crab sizes, including specimens much larger than those taken by the other two carnivores. This could be related to differences in feeding behaviour of the predators, as well as to differences in foraging behaviour of the crabs (Hill & O'Keeffe 1992). The relationship between the three sympatric predators and the sizes of crabs they prey upon, is therefore complex. Local differences such as the

depth of the river, substratum type, availability of
alternative prey, seasonal floods, or the density of the
predators, probably all interact to determine which section of
the crab population is available to a specific predator species
at a specific time.

## Conservation management consideration

Conservation management practices can be divided into
protecting species in their natural habitat, breeding them in
captivity, and reintroducing them back into the wild. Each of
these different spheres of intervention relies on behavioural and
ecological information (Caro 1998). The present study provided
much ecological and behavioural data necessary when planning
conservation management of *A. capensis*. The environment is dynamic
which dictates that different management strategies will have to
be applied at different times. No specific instructions as to the
management of otters in the rivers can, therefore, be given.
Rather the implications of the results of this study should be
used wisely with the specific conditions in mind.

In South Africa, and elsewhere in Africa, freshwater habitats
are under serious and increasing threat (Davies & Day 1998). In
South Africa, e.g., at best, with the slowest estimated
population growth and the smallest demand for water, fresh water
supplies will no longer be able to meet demand some time between
2020 (use of all surface water) and 2040 (use of surface and
ground water). At worst, with the highest population growth and
water demand, supplies will be fully committed some time between
2003 and 2015 (Davies & Day 1998). As almost all of the water
used in South Africa comes from rivers (Davies & Day 1998), the
potential impact on *A. capensis* habitat is of immediate and great
concern. For example, water extraction would mean lowering of
water levels and therefore a decreased food supply. Elsewhere in
Africa and the world, rapidly expanding human populations and
accelerated water extraction for industry and agriculture, yields
an equally dismal scenario (see Tilman *et al.* 2001).

In broad discussions on conservation of southern African aquatic ecosystems (Branch & Branch 1981; Davies & Day 1998), little or no mention is made of otters. This happens despite them being top predators and therefore subject to the accumulative affects of organisms lower in the food chain. Besides being at or near the top of the food chain, otters possess characteristics that should make them good biological indicators. They rely both on aquatic and terrestrial habitats, which exposes them to disturbance of either or both habitats (double jeopardy), and they feed on a variety of prey and have been shown to be sensitive to pollution and habitat destruction (Mason & Macdonald 1986). However, it is difficult to estimate otter densities, the only accurate methods probably being the use of radio tracking combined with radionuclide recovery (Knaus *et al.* 1983; Kruuk *et al.* (1993), or through extensive microsatellite genotyping of faeces collected throughout an area (Kohn & Wayne 1997). Second, because fresh water crabs tolerate eutrophic areas so do *A. capensis*. Therefore, although seemingly in possession of many characteristics expected for acting a biological indicators otters fail in this respect. But this does not negate the need for more information on them. They also have a great potential as an ecotourism attraction.

## REFERENCES

BAKER, C.M. 1989. Feeding habits of the water mongoose (*Atilax paludinosus*). *Zeitschrift für Säugetierkunde* **54**: 31-39.

BRANCH, G. & BRANCH, M. 1981. *The living shores of southern Africa*. C. Struik, Cape Town.

BURT, W.H. 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* **24**: 346-352.

BUTLER, J.R.A. & DU TOIT, J.T. 1994. Diet and conservation of Cape clawless otters in eastern Zimbabwe. *South African Journal of Wildlife Research* **24**: 41-47.

CARO, T. 1998. *Behavioral ecology and conservation biology*. Oxford University Press, New York.

CHESSON, P. & HUNTLY, N. 1989. Short-term instabilities and long-term community dynamics. *Trends in Ecology and Evolution* **4**: 293-299.

COLLOTY, B.M., ADAMS, J.B. & BATE, G.C. 2000. The use of a botanical importance rating to assess changes in the flora of the Swartkops Estuary over time. *Water SA* **26**: 171-180.

CREEL, S. & CREEL, N.M. 1996. Limitation of African wild dogs by competition with larger carnivores. *Conservation Biology* **10**: 526-538.

DAVIES, B.R. & DAY, J.A. 1998. *Vanishing waters*. University of Cape Town Press, Cape Town.

DURANT, S.M. 1998. Competition refuges and coexistence: an example from Serengeti carnivores. *Journal of Animal Ecology* **67**: 370-386.

DURBIN, L.S. 1993. Food and Habitat Utilization of Otters (*Lutra Lutra L.*) in a Riparian Habitat. D. Phil. thesis, University of Aberdeen, Aberdeen, Scotland.

HANSKI, I. 1994. Spatial scale, patchiness and population dynamics on land. *Philosophical Transactions of the Royal Society, London, B.* **343**: 19-25

HILL, M.P. & O'KEEFFE, J.H. 1992. Some aspects of the ecology of the freshwater crab (*Potamonautes perlatus* Milne Edwards) in the upper reaches of the Buffalo River, eastern Cape Province, South Africa. *South African Journal of Aquatic Science* **18**: 42-50.

KNAUS, R.M., KINLER, N. & LINSCOMBE, R.G. 1983. Estimating river otter populations: the feasibility of $^{65}$Zn to label feces. *Wildlife Society Bulletin* **11**: 375-377.

KOHN, M.H. & WAYNE, R.K. 1997. Facts from feces revisited. *Trends in Ecology and Evolution* **12**: 223-227.

KREBS, J.R. & KACELNIK, A. 1991. Decision making. In: *Behavioural ecology an evolutionary approach*, (eds) J.R. Krebs, & N.B. Davies, Blackwell Scientific Publications, Oxford.

KRUUK, H. & CONROY, J.W.H. 1991. Mortality of otters (*Lutra lutra*) in Shetland. *Journal of Applied Ecology* **28**: 83-94.

KRUUK, H., CONROY, J.W.H. & MOORHOUSE, A. 1991. Recruitment to a population of otters (*Lutra lutra*) in Shetland, in relation to fish abundance. *Journal of Applied Ecology* **28**: 95-101.

KRUUK, H., CARSS, D.N., CONROY, J.W.H. & DURBIN, L. 1993. Otter (*Lutra lutra* L.) numbers and fish productivity in rivers in north-east Scotland. *Symposia of the Zoological Society of London* No. 65: 171-191.

KRUUK, H., KANCHANASAKA, B., O'SULLIVAN, S. & WANGHONGSA, S. 1994. Niche separation in three sympatric otters *Lutra perspicillata, L. lutra* and *Aonyx cinerea* in Huai Kha Khaeng, Thailand. *Biological Conservation* **69**: 115-120.

MACARTHUR, R.H. & LEVINS, R. 1967. Competition, habitat selection and character displacement in a patchy environment. *Proceedings of the National Academy of Science USA* **51**: 1207-1210.

MASON, C.F. & MACDONALD, S.M. 1986. *Otters: ecology and conservation*. Cambridge University Press, Cambridge.

POWELL, R.A. 1979. Mustelid spacing patterns: variations on a theme by *Mustela. Zeitschrift für Tierpsychologie* **50**: 153-163.

PURVES, M.G. & SACHSE, B. 1998. *The utilization of freshwater crabs by co-existing otter* (Aonyx capensis *Schinz) and water mongoose* (Atilax paludinosus *Cuvier) in the Drakensberg, South Africa*. Unpublished report, University of Stellenbosch, Stellenbosch.

ROOT, R.B. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. *Ecological Monographs* **37**: 317-350.

ROWE-ROWE, D.T. & SOMERS, M.J. 1998. Diet, foraging behaviour and coexistence of African otters and the water mongoose. *Symposia of the Zoological Society of London* No. 71: 215-227.

ROWE-ROWE, D.T. 1977a. Food ecology of otters in Natal, South Africa. *Oikos* **28**: 210-219.

ROWE-ROWE, D.T. 1977b. Prey capture and feeding behaviour of South African otters. *Lammergeyer* **23**: 13-21.

ROWE-ROWE, D.T. 1978. The small carnivores of Natal. *Lammergeyer* **25**: 1-48.

SCHOENER, T.W. 1974. Resource partitioning in ecological communities. *Science* **185**: 27-39.

TILMAN, D., FARGIONE, J., WOLFF, B., D'ANTONIO, C., DOBSON, A., HOWARTH, R., SCHINDLER, D., SCHLESINGER, W.H., SIMBERLOFF, D. & SWACKHAMER, D. 2001. Forecasting agriculturally driven global environmental change. *Science* **292**: 281-284.

VAN DER ZEE, D. 1981. Prey of the Cape clawless otter (*Aonyx capensis*) in the Tsitsikama National Park, South Africa. *Journal of African Zoology* **194**: 467-483.

VAN ZYL, R.F., MAYFIELD, S., PULFRISH, A. & GRIFFITHS, C.L. 1998. Predation by West coast rock lobster (*Jasus lalandii*) on two species of winkle (*Oxystele sinensis* and *Turbo cidaris*). *South African Journal of Zoology* **33**: 203-209.