
Habitat selection by the Cape clawless otter (*Aonyx capensis*) in rivers in the Western Cape Province, South Africa

Michael J. Somers* and Jan A. J. Nel

Department of Zoology, University of Stellenbosch, Matieland, South Africa

Abstract

We radio-tracked seven Cape clawless otters (*Aonyx capensis*) (Schinz, 1821) in two rivers in the Western Cape Province, South Africa, providing data on their habitat selection. Habitat type was investigated at a scale that enabled us to separate the effects of types of riparian vegetation, geomorphology and anthropogenic influences. Otters selected areas with boulders and/or reed beds, which provided high crab density and shelter. Direct observations showed that they used two foraging modes depending on the habitat selected. Otters could select open water within c. 8 m of the shore, dive and surface with or without prey. Otherwise hunting involved them moving into shallow water (c. 0.2 m deep), and walking along the substrate feeling for prey with their forefeet. Disturbed possible prey items were then caught with the forefeet.

Key words: African clawless otter, freshwater, habitat use, radio-tracking, resource use, telemetry

Résumé

Nous avons suivi par radio sept loutres sans griffes de la Province du Cap (*Aonyx capensis*) (Schinz, 1821) dans deux fleuves de la Province Occidentale du Cap, en Afrique du Sud, nous permettant de collectionner des données sur la sélection de l'habitat. Le genre d'habitat était étudié à un niveau qui nous a permis de distinguer entre les effets de différents genres de végétation riveraine, la géomorphologie et d'influences anthropogéniques. Les loutres ont choisi des locaux avec des blocs de roche et/ou des bancs de roseau, qui fournissent une forte densité de crabes et des

abris. Des observations directes montrent qu'ils se servent de deux modes de fourrage selon l'habitat choisi. Les loutres sélectionnent l'eau à environ 8 mètres du rivage, plongent et remontent avec ou sans la proie. Autrement, la chasse comprend un déplacement dans l'eau peu profonde (environ 20 cm), et une promenade sur le substrat, en cherchant la proie avec les pattes de devant. Une proie potentielle dérangée par ces investigations est alors attrapée avec les pattes de devant.

Introduction

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, Robertson & Kenward, 1993). Why an animal uses a particular habitat can be better understood by correlating use and movements to the acquisition of primary resources (e.g. food, shelter, mate and host) and the avoidance of sources of stress (e.g. predators, thermal extremes and dehydration) (Barbaresi, Gherardi & Vannini, 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, Green & Jefferies (1984), Kruuk *et al.* (1986) and Conroy & French (1987) show that for the European otter (*Lutra lutra*) the position of spraints is an unreliable indication of where otters spend their time. They may, however, be an indication of how the otters use the terrestrial habitat, which is important for

*Correspondence: Department of Zoology, University of Transkei, Private Bag X1, 5117 Umtata, South Africa.
E-mail: michael.somers@yahoo.com

semi-aquatic otters. Data from radiotelemetry would therefore compliment these data, giving a better understanding of how the otters use their habitat.

Only Arden-Clarke (1986) and Somers (2001) provide data on Cape clawless otters (*Aonyx capensis*) (Schinz, 1821) 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 (2001), in the present study area, showed that *A. capensis* ranges over distances as long as 54.1 km.

Aonyx capensis is a semi-aquatic predator, which occurs in Sub-Saharan Africa (Rowe-Rowe & Somers, 1998). In most areas crustaceans are their most important prey, but fish, frogs, insects, birds, reptiles, molluscs, dung (ungulate) and mammals are also eaten (Rowe-Rowe & Somers, 1998; Somers, 2000a). This is in contrast to most otters, which are mainly piscivorous (Estes, 1989).

Perrin & Carugati (2000) 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 correlate these with 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 correlate these with 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, Somers & Nel, 1998).

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, 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).

In this paper, we report on the habitat selection by seven *A. capensis*, as determined by radio-tracking. It is predicted that otters select some habitat types over others.

Material and 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 rocky and narrow, with a catchment of 420 km², including pristine conditions in the Jonkershoek Mountains, but then flows through agricultural, industrial and urban areas. The flow rate varies depending on rainfall, which is mostly in winter. It reaches the sea about 40 km from its source. It is disturbed for c. 90% of its length by agriculture, industry and the urban environment. For a detailed classification of the Eerste River see Eekhout, King & Wackernagel (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. The area down to c. 15 km below Bulshoek Dam is not intensively farmed, except for some cattle, with very little disturbance. For a detailed classification of the Olifants River see Harrison (1997) and Eekhout *et al.* (1997).

Seven otters (Table 1) were caught in standard carnivore traps (800 × 800 × 1400 mm) as described by van der Zee (1982). The traps were baited with either fish and/or fresh spraints from another area. The otters were anaesthetized with ketamine hydrochloride (Ketalar 50 mg ml⁻¹, Parke Davis, Retreat, USA). Radio transmitters [IMP/300/L, implantable transmitter, 40 g, 80 × 20 mm diameter cylinder (Telonics Inc., Mesa, AZ, U.S.A.)] were implanted by a veterinary surgeon into the otters' abdomen following the same procedures as described by McKenzie *et al.* (1990). A Telonics TR-4 receiver and a RA-2A antenna were then used to find their position.

Otter M1 died 4 months after the transmitter was implanted. There were skin punctures, which appeared to be a result of bites from another animal. On postmortem 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 carried out at times of usual otter activity and periodically on a 24-h basis. Most radio-tracking habitat use studies combine both active and nonactive data, which underestimates foraging habitat, with potentially important management and/or ecological consequences

Table 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 (subadult)	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

(Palomares & Delibes, 1992). We 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 10×42 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 1). Observations and radio-tracking were conducted from a vehicle and on foot. The otters were located by triangulation or tracking the path of increasing signal strength.

Following Durbin (1993), for the present analyses, the study areas were divided and numbered, 200 m stret-

ches of river, and drawn on 1 : 50,000 topographical maps and 1 : 10,000 orthophotographs. The position of the otters when active was continuously recorded on tape.

The surveys were carried out during the summers of 1995 and 1996. To prevent type II statistical errors the numbers of habitat variables were limited (Alldredge & Ratti, 1986). The variables decided on were those thought to be of importance to the otters. The importance was subjectively decided by reference to Durbin (1998) and to direct observations of the otters.

For each 200-m section, the areas or lengths of the various variables (Table 2) were estimated, and following

Table 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	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	$\ln [x/(100 - x)]$
Channel width	WIDT	Mean width	m	$\ln (x/\text{mean})$
Canalization	CANA	Length of bank	%L	$\ln [x/(100 - x)]$
Roads	ROAD	Minimum distance from road	m	$\ln (x/\text{mean})$
Buildings	BUIL	Minimum distance from building	m	$\ln (x/\text{mean})$

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

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 2).

Following Durbin (1993) and Kruuk *et al.* (1993) the mean width of each river section was calculated from two measurements at the upstream and downstream boundaries. This was made by direct measurement (narrow sections) or from the 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 orthophotographs, from which the length of canalized bank was also measured.

Analysis of data closely followed methods used by Durbin (1998) for *L. lutra*. Minor differences between this study and his in methods and the reasons for them are outlined below.

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 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 (L.S. Durbin, pers. comm.). The predicted values for each section were calculated as follows:

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

and

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

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 × 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:

$$PL(\text{deviation from uniform use of length}) = \ln(T/T^l)$$

and

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

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 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 2). Regressions between the preference indices with habitat variables were carried out 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 deter-

Table 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

mines 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 among 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 versus 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 (SE = 1.3, range = 2–110, $n = 178$) and of the Olifants River (including dams) was 182.8 m (SE = 12.07, range = 10–1250, $n = 270$). Excluding Bulshoek and Clanwilliam dams, the mean width of the Olifants River used by the radio-tracked otters was 50.1 m (SE = 2.01, range = 10–145, $n = 161$).

Two modes of hunting or foraging were recognized. In the first, the otters, selecting open water within *c.* 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 (*c.* 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).

In both rivers the second type of hunting, in shallow water, seemed more common than 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 (Somers, 2001).

Among the regressions using the index PL (correlated 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, SE = 0.1, range = 0.07–0.75; Mann–Whitney $U = 0$, $df = 13$, $P < 0.001$), and reeds (mean coefficient = 0.37, SE = 0.07, range = 0.08–0.66; Mann–Whitney $U = 0$, $df = 13$, $P < 0.001$) (Table 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). Except for otters M2 and F2 the others did not select for wide areas.

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, SE = 0.8, range = 0.03–0.057; Mann–Whitney $U = 0$, $df = 13$, $P < 0.001$), reeds (mean coefficient = 0.42, SE = 0.08, range = 0.14–0.76; Mann–Whitney $U = 0$, $df = 13$, $P < 0.001$) and overhanging vegetation (mean coefficient = 0.21, SE = 0.04, range = 0.07–0.35; Mann–Whitney $U = 0$, $df = 13$, $P < 0.001$). 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, SE = 0.04, range = –0.03–0.32; Mann–Whitney $U = 7$, $df = 13$, $P = 0.03$). Otters M2, F2 and F3 selected for wide areas.

Discussion

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 habitats with reed beds and boulders. When controlling for area the otters also selected areas with overhanging vegetation. Except for otters M2 and F2 the others did not select for wide areas. Otters M2 and F2 extensively used the dams while foraging (Somers, 2001). 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), 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 particle size may be of critical importance to otters. As crab size increases the amount of vegetable material in their diet increases (Raubenheimer, 1986; Hill & O'Kee, 1992). The reed beds may therefore be refugia for crabs and a source of food for the larger crabs. In addition, most freshwater fish species use submerged macrophytes in which to breed and

Table 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) PL													
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
(b) PA													
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

hide (Skelton, 1993). The otters therefore appear to be selecting habitats with high prey density.

This study offers an opportunity to compare the results with those where habitat selection was implied from the distribution and density of otter signs (Perrin & Carugati, 2000). The methods used by Perrin & Carugati (2000) 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 (2000) found that otters select, for time spent on land, and therefore in a terrestrial habitat, 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 (2000). The reason for this may be that although otters forage near anthropogenic disturbances they do not use these areas for sprinting 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 (2000). 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).

Acknowledgements

We thank WWF-SA, Mazda Wildlife Fund and the National Research Foundation for support. P. Chanin, H. Kruuk, D. Rowe-Rowe, B. Cook and M. Walters are thanked for commenting on this work.

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. *J. Wildl. Manage.* **50**, 157–165.
- 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. *J. Zool. (Lond.)* **209**, 201–211.
- BARBARESI, S., GHERARDI, F. & VANNINI, M. (1997) Movement patterns of river crabs (Decapoda, Potamoidea) in the field: predictable and unpredictable components. *J. Zool. (Lond.)* **242**, 247–259.
- BECK, M.W. (1995) Size-specific shelter limitation in stone crabs: a test of the demographic bottleneck hypothesis. *Ecology* **77**, 968–980.
- BUTLER, J.R.A. & DU TOIT, J.T. (1994) Diet and conservation of Cape clawless otters in eastern Zimbabwe. *S. Afr. J. Wildl. Res.* **24**, 41–47.
- CONROY, J.W.H. & FRENCH, D.D. (1987) The use of spraints to monitor populations of otters (*Lutra lutra* L.). *Symp. Zool. Soc. Lond.* No. 58, 247–262.
- DURBIN, L.S. (1993) *Food and habitat utilization of otters (Lutra Lutra L.) in a riparian habitat*. DPhil thesis, University of Aberdeen, Aberdeen.
- DURBIN, L.S. (1998) Habitat selection by five otters *Lutra lutra* in rivers of northern Scotland. *J. Zool. (Lond.)* **245**, 85–92.
- EEKHOUT, S., KING, J.M. & WACKERNAGEL, A. (1997) *Classification of South African river*, Vol. 1. Department of Environment Affairs and Tourism, Pretoria.
- ESTES, J.A. (1989) Adaptations for aquatic living by carnivores. In: *Carnivore Behavior, Ecology and Evolution* (Ed. J. 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, 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. *Mamm. Rev.* **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. *Trans. Roy. Soc. S. Afr.* **52**, 277–321.
- HILL, M.P. & O'KEEFE, 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. *S. Afr. J. Aquat. Sci.* **18**, 42–50.
- JOHNSON, D.H. (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology* **61**, 65–71.
- KRUUK, H., CONROY, J.W.H., GLIMMERVEEN, U. & OUWERKERK, E.J. (1986) The use spraints to survey populations of otter *Lutra lutra*. *Biol. Conserv.* **35**, 187–194.
- 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. *Symp. Zool. Soc. Lond.* No. 65, 171–191.
- 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. *Symp. Zool. Soc. Lond.* No. 71, 119–133.
- 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. BSc (Hons) thesis, University of Cape Town, Cape Town.
- McKENZIE, A.A., MELTZER, D.G.A., LE ROUX, P.G. & GOSS, R.A. (1990) Use of implantable radio transmitters in large African carnivores. *S. Afr. J. Wildl. Res.* **20**, 33–35.
- 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. *S. Afr. J. Wildl. Res.* **28**, 68–72.
- PALOMARES, F. & DELIBES, M. (1992) Data analysis design and potential bias in radio-tracking studies of animal habitat use. *Acta Oecol.* **13**, 221–226.
- PERRIN, M.R. & CARUGATI, C. (2000) Habitat use by the Cape clawless otter and the spotted-necked otter in the KwaZulu-Natal Drakensberg, South Africa. *S. Afr. J. Wildl. Res.* **30**, 103–113.
- RAÜBENHEIMER, C.D. (1986) *Aspects of the biology of the freshwater crab, Potamonautes sidneyi, with particular reference to general seasonality and female aggression*. MSc thesis, University of Natal, Durban.
- ROWE-ROWE, D.T. (1992) Survey of South African otters in freshwater habitat, using sign. *S. Afr. J. Wildl. Res.* **22**, 49–55.
- ROWE-ROWE, D.T. & SOMERS, M.J. (1998) Diet, foraging behaviour and coexistence of African otters and the water mongoose. *Symp. Zool. Soc. Lond.* No. 71, 215–227.
- 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. *Afr. Zool.* **35**, 261–268.
- SOMERS, M.J. (2000b) Foraging behaviour of Cape clawless otters (*Aonyx capensis*) in a marine habitat. *J. Zool. (Lond.)* **252**, 473–480.
- SOMERS, M.J. (2001) *Habitat utilization of Cape clawless otters Aonyx capensis*. PhD dissertation, University of Stellenbosch, Stellenbosch.
- SOMERS, M.J. & NEL, J.A.J. (1998) Dominance and population structure of freshwater crabs (*Potamonautes perlatus* Milne Edwards). *S. Afr. J. Zool.* **33**, 31–36.
- VERWOERD, D.J. (1987) Observations on the food and status of the Cape clawless otter *Aonyx capensis* at Betty's Bay, South Africa. *S. Afr. J. Zool.* **22**, 33–39.
- VAN DER ZEE, D. (1981) Prey of the Cape clawless otter (*Aonyx capensis*) in the Tsitsikama National Park, South Africa. *J. Zool. (Lond.)* **194**, 467–483.
- VAN DER ZEE, D. (1982) Density of Cape clawless otters *Aonyx capensis* (Schinz, 1821) in the Tsitsikama Coastal National Park. *S. Afr. J. Wildl. Res.* **12**, 8–12.

(Manuscript accepted 16 March 2004)