

Distribution and habitat choice of Cape clawless otters, *Aonyx capensis*, in South Africa

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Cape clawless otters, *Aonyx capensis*, are widely distributed in South Africa, as elsewhere on the continent. They occur in a wide variety of environments and most aquatic habitats, from freshwater lakes to the marine littoral, and even in episodic rivers in arid areas, provided freshwater sources are adequate and sufficient food is available. This animal is not much affected by turbid water as it locates prey by touch, and usually forages close to shores or banks. Evidence of presence in given localities and habitats, distributed over a large area of the Northern, Western, and Eastern Cape provinces, was deduced from signs (faecal deposits or distinctive tracks) on land. Accepting the inherent pitfalls of this approach we nevertheless feel using it is acceptable for a first approximation of habitat preferences over a large geographical area. Results point to areas with dense reed beds and a rocky substrate on banks being used most intensively, probably on account of a localized high food biomass.

Key words: African clawless otter, *Aonyx capensis*, habitat selection, river conservation.

INTRODUCTION

Knowledge of the distribution of African otters is derived from museum specimens, sightings (not always reliable where two or more species are sympatric) and on signs, e.g. distinctive tracks and spraints (faeces), or from diaries and expedition reports of earlier travellers. One species, the Eurasian otter (*Lutra lutra*), is allopatric to the others and occurs only in the Mahgreb, north of the Sahara. The other three are endemic to Africa; with the Cape clawless otter (*Aonyx capensis*) being the most widespread. Distributed over most of sub-Saharan Africa except for the Congo basin where it is replaced by the Congo clawless otter *A. congicus*, it occurs in landscapes ranging from semi-deserts, with <30 mm rainfall p.a. (J.A.J.N, unpubl. data), to evergreen tropical forests, and from the marine littoral to ≥3000 m a.s.l. (Rowe-Rowe & Somers 1998). Over this large geographical and ecological range it usually occurs in sympatry with the water mongoose (*Atilax paludinosus*), with which it shares part of its prey base (Purves *et al.* 1994; Rowe-Rowe & Somers 1998), and in some areas with the spotted-necked otter (*Lutra maculicollis*). The degree of spatial overlap with *A. congicus* is at present unresolved.

The broad geographical distributions of *A.*

capensis and *L. maculicollis* in South Africa have been described by Rowe-Rowe (1990), Rowe-Rowe & Somers (1998) and Skinner & Chimimba (2005). More detailed distributional data in the previously delineated provinces (prior to 1994) have been published by Rowe-Rowe (1978) (Natal), Stuart (1981) (Cape), Rautenbach (1982) (Transvaal), and Lynch (1983) (Orange Free State). However, some sight records may be misidentifications, and only limited numbers of skins reach museum collections: published records therefore may not be a true reflection of each species' distribution. Limited attention only has been given to physical and ecological factors affecting each species. *Aonyx capensis* often forages on its own but also can be gregarious, moving in small groups (Somers & Nel 2004a; Kruuk 2006). Their social structure is therefore much the same as that of *L. lutra* and North American river otters (*Lontra canadensis*) (Kruuk 2006).

Habitat usage by otters is usually deduced from occurrence of distinctive spraints, tracks, and resting places (see, e.g., Mason & Macdonald 1986) along riverbanks and lake- and seashores. Such signs, however, will lead to an unrepresentative picture as they cannot reliably indicate use of purely aquatic habitat (Kruuk *et al.* 1986; Conroy & French 1987) where the bulk of their prey is obtained. African otters, like all others, are semi-

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aquatic predators whose prey consists primarily of aquatic species such as fish, frogs and crabs with some insects and other taxa; *A. capensis* takes mainly crustaceans both in freshwater and marine habitats (Rowe-Rowe & Somers 1998; Somers 2000; Somers & Nel 2003). As otter occurrence reflects the suitability of the local habitat, variables other than food availability and bankside or shore characteristics also play a role, and presence of otter spraints or tracks should therefore be used with caution when assessing habitat use (Green *et al.* 1984; Kruuk *et al.* 1986; Conroy & French 1987), as this is an unreliable indication of where otters spend most of their time.

Habitat preferences of *A. capensis* have been analysed for montane habitats in the Drakensberg mountains of KwaZulu-Natal by Perrin & Carugati (2000), who compared sites indicated by otter signs on land with environmental characteristics. Otters there select undisturbed areas with rock cover and dense natural vegetation. Rowe-Rowe (1992) and Butler & Du Toit (1994) provided densities of spraints and resting places but did not correlate these to habitat variables. For the Cape south and southwest coasts, Van der Zee (1981), Arden-Clarke (1986), and Verwoerd (1987) again gave densities and distribution of signs of *A. capensis* without correlating these with habitat variables; along the coast *A. capensis* are active on land near dense vegetation, abundant food resources and fresh water. Similar to *L. lutra* on the coasts of Scotland and Portugal (Kruuk & Balharry 1990; Kruuk & Moorhouse 1991; Beja 1992, 1996), coastal *A. capensis* are dependent on freshwater sources (van Niekerk *et al.* 1998). These are used for drinking and as washing sites to remove salt from the fur and restore thermoinsulation (Kruuk & Balharry 1990; Kruuk 2006).

Tracking otters by radiotelemetry provide more robust data on habitat preference and use, as the time spent in the primary foraging habitat is documented. Arden-Clarke (1986) found differential use of habitats by coastal *A. capensis*, but did not document habitat variables. Somers (2001) and Somers & Nel (2004a,b) found that in two rivers in the southwestern Cape *A. capensis* move over 54 km and prefer areas with boulders and/or reed beds, which provide high crab densities and shelter. Where observed or radio-tracked, *A. capensis* forage mostly in open water within 8 m of the shore, or along riverbanks in shallow water where they walk and feel for prey with their forefeet. While radiotelemetry undoubtedly provides the best

analysis of habitat choice by otters, this method is impractical for large geographical areas due to logistical and time constraints. For such large-scale analyses spraint (and other signs) occurrence can provide a first and very useful approximation of the correlation between otter presence and habitat variables. Such data are crucial for determining limiting factors, a fundamental prerequisite for any conservation initiative (Kruuk *et al.* 1998; Kruuk 2006).

Otter distributions in relation to landscape or habitat features have been analysed on different scales, e.g. for *L. lutra* in Europe and France on a regional, country, and departmental scale, respectively (Robitaille & Laurence 2002), and for the southern river otter (*Lontra provocax*) in Chile on an inter-basin, habitat and within-habitat (lakes or rivers) scale (Thom *et al.* 1998; Aued *et al.* 2003). Our study on *A. capensis* involved between-habitat comparisons of occurrence based on signs. These habitats were situated in three provinces of South Africa (Northern Cape, Western Cape and Eastern Cape), involved several biomes (Fynbos, Succulent Karoo, Southern Savanna), extended from sea level to >1200 m a.s.l. and for rainfall regimes of <50 mm to >500 mm per annum. As *A. capensis* distribution is so extensive in Africa and involves such a diverse array of ecological conditions, we believe our analysis would help explain the local occurrence of this species, and therefore its possible geographical distribution, as some limiting factors are involved. In addition, increased aridity in parts of southern Africa (Hewitson *et al.* 2005) where any decline in precipitation will be amplified in the runoff (Schulze 2005) will inevitably lead to aquatic as well as riparian habitat deterioration and increased human usage of water sources, all factors that could negatively affect otter survival.

This paper documents the distribution of *A. capensis* in South Africa, from published accounts and based on results of our own fieldwork, and characteristics of the habitats used by otters, based on signs, in the Northern, Western and Eastern Cape provinces. We also discuss the environmental factors that could affect the occurrence of *A. capensis* in river systems, and along the South African seaboard.

METHODS

Data collection

Published and unpublished distributional records

Table 1. Factors and levels of each factor used in the habitat selection model for Cape clawless otters.

Habitat type	Shore	Current	Width (m)	Depth (m)	Bank 1 density	Bank 2 density	Reed presence	Land use	Water use	Pollution	Food
Estuary	Boulders	Static	<1	<0.5	Dense	Dense	Present	Natural	Boats	Agriculture	Crab
Lake	Stones	Sluggish	1-2	0.5-1	Sparse	Sparse	Absent	Grazing	Extraction	Domestic	Crab/frog
Marsh	Gravel	Slow	2-5	1-2	No record	No Record		Forestry	Livestock	Industrial	Fish
River	Soil	Fast	5-10	2-5				Crops	Recreation	None	Fish/frog
	Silt	Tidal	10-20	>5				Mixed agricultural	None	No record	Fish/crab
	Mixed	No record	20-40	No record				Urban	No record		Frog
	No record		>40					No record			Fish/crab/frog
			No Record								None
											No record

were used, with additional information from questionnaires to nature conservation bodies and farmers, requests in the press, and fieldwork during which records of sightings or more usually the distinctive sign (spoor and/or spraints) were collected. For correlating otter presence with habitat characteristics, surveys for otter sign, especially spraints, were conducted by ourselves and assistants between 1993 and 1996 at 248 localities distributed irregularly over the southern part of South Africa from 18°12'E to 29°30'E, and between 30°32'S and 34°46'S, and from sea level to ca 1200 m a.s.l. in the Northern, Western and Eastern Cape provinces. At each location sign were searched for on the banks of the water body. Habitats were assigned to a broad type (estuary, river, and marine – excluded from the present analysis owing to small sample size), and characteristics, some subjective, such as shore terrain (e.g. boulders, soil), water current flow (e.g. static, sluggish, slow, fast, tidal), width of water body (<1 m, 1-2 m, 2-5 m, 5-10 m, 10-20 m, 20-40 m, >40 m), water depth (<0.5 m, 0.5-1 m, 1-2 m, 2-5 m, >5m), vegetation density (sparse (e.g. grass, emergent, tall trees), dense (e.g. shrubs, reeds), reed presence, land use (e.g. natural, crops), water use (e.g. boats, extraction), pollution (agriculture, domestic, industrial, unpolluted) and food available (e.g. frog, crab) recorded. The main habitat variables for each section surveyed were recorded, as well as presence or absence of otter sign. These included spraints or spoor, here considered proof of otter presence. Survey length at most sites were the standard 600 m (Mason & Macdonald 1986) but in some cases were shorter; surveys were terminated when positive sign was found.

Diet of *A. capensis* was deduced from spraints analyses (see, e.g., Purves *et. al.* 1994; Somers & Purves 1996).

Data analysis

The STATISTICA (Statsoft, Inc. 2003) general linear model (GLM) module was used to build a model *with* otter presence (scat, spoor, sighting or any combination of these), scat presence and spoor presence as response variables. The independent factors and the levels of each factor used in the model are summarized in Table 1. Owing to the large design only main effects were included in the model. Results from both multivariate and univariate analyses were generated.

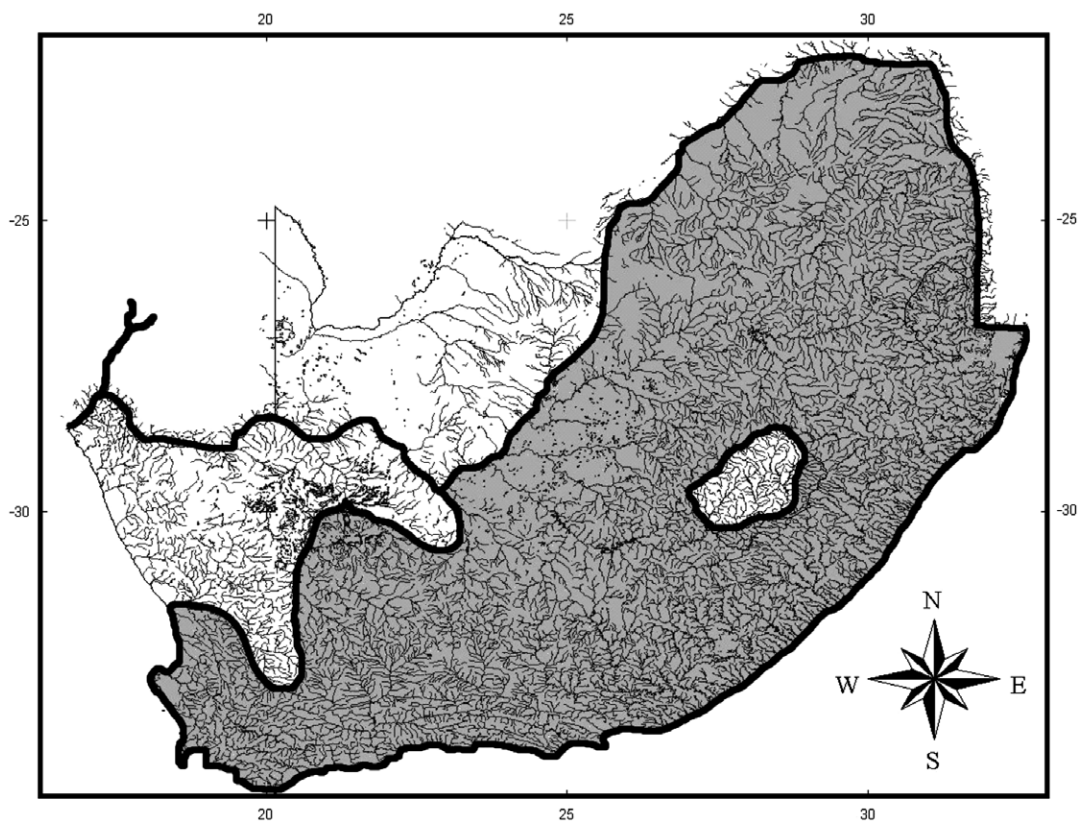


Fig. 1. The presently known distribution of the Cape clawless otter in South Africa. Distribution limits are indicated by the grey area enclosed by the solid line. The presence of the species to the mouth of the Gariep (= Orange) River, and up the Fish River and tributaries in Namibia is also shown.

RESULTS

Distribution

Figure 1 shows the distribution of *A. capensis* in South Africa, incorporating both perennial and episodic rivers and unoccupied terrestrial habitat in between; it should be noted, however, that this species makes frequent use of farm dams and temporary water bodies and can move long distances (>30 km) through sandy, waterless habitat (an individual tracked by spoor) and cross saddles in mountains between watersheds (a collared individual) (P. Lloyd, pers. comm. 1994; S. Hanekom, pers. comm. 1996). It occurs in all major drainage systems (following Davies *et al.* 1993), in both summer and winter rainfall regions, and between the 50 mm and 1250 mm isohyets; also in regions with between 1250 and 2000 mm evapotranspiration (Noble & Hemens 1978), and between <15 and >50% variability of rainfall (deviation from the normal annual). Occurrence of

A. capensis is therefore independent of local rainfall, but reflects overall precipitation in the catchment area of a particular river and its tributaries and the persistence of pools with adequate shelter and water such as in the Sak, Riet, Sout, Vis and Doring rivers in the arid interior, below the 250 mm isohyet. In episodic rivers such as these, and in particular the Hartbees River, a tributary of the Gariep (= Orange), variability in flow between 1700% and 9% of the annual average has been recorded; this river is situated between the 100 and 200 mm isohyets. Along the seaboard distribution is very localized for up to c. 250 km north of Cape Town, due to the scarcity of suitable freshwater sources in an otherwise very productive marine environment (Brown *et al.* 1991). Along the southwestern southern and eastern coast, at least up to the KwaZulu-Natal border, *A. capensis* is widespread along rocky shores; freshwater sources are varied and common.

Productivity

Productivity in rivers is low in the headwaters, increases in the middle reaches and peaks in the lower reaches (Day *et al.* 1986). This influences the prey biomass available to otters – the middle and lower reaches of most rivers usually have a higher prey biomass than the headwaters, unless other factors such as pollution from domestic, agricultural or industrial sources depresses productivity. Rivers arising in the mountain ranges forming the escarpment between the coastal pediment and inland plateau and high inland mountains follow this pattern: *A. capensis* is absent in the headwaters of, for example, the Olifants and Breede rivers in the Western Cape, the Gariiep River in the Maluti mountains in Lesotho, and scarce in the headwaters of the Caledon River in the Drakensberg (Purves & Sachse 1998). Conversely, *A. capensis* is absent from estuaries of large rivers subjected to extensive tidal flow, e.g. the Olifants, Berg and Breede rivers in the Western Cape Province, where salinity levels preclude permanent existence even if productivity levels are very high, unless where tributaries provide freshwater for drinking and cleansing fur. Where discharge into the sea is blocked by sand bars, as e.g. the Gariiep (Northern Cape) and Bot (Western Cape) rivers, increased salinity due to evaporation has the same effect. Subjectively basing otter density on spraint and spoor density indicates that industrial pollution negatively affects otter presence (see below), with agricultural pollution and urbanization, e.g. along the Eerste River in the Western Cape, also negatively affecting otter density (Somers & Nel 2004b).

Flow

Aonyx capensis occur in both perennial and episodic rivers such as the Sak and Doring rivers in the Northern Cape Province, and also the Fish and Leeuwen rivers in Namibia, provided large pools (the lower limit in size is unknown) persist (J.A.J.N. & M.J.S., unpubl. data). Chutter & Heath (1993) found that in the Letaba River in Mapumalanga Province interrupted flow did not have a long-term detrimental effect on invertebrate and fish species richness, provided that interruptions of <11 days occur in the case of invertebrates. They also found that pools with a sandy substrate act as important dry season refugia for many fish species during reduced flow; they suspect that such pools are maintained by seepage of water. This is presumably the case in many or all the

episodic rivers where *A. capensis* occurs. Otters move long distances between such pools in the Fish River in Namibia (M.G. Purves, pers. comm. 2000). The 24 major catchment areas, with contributions to the mean annual runoff that vary between 0.1 and 14.9% (Davies *et al.* 1993), all contain *A. capensis*. As these catchment areas include both perennial and episodic rivers silt loads vary considerably on both the long-term and the short-term, the latter due to episodic and often localized rainfall events.

Prey availability

Few data are available on the correlation between prey (primarily crab, *Potamonautes* spp.) and *A. capensis* density. However, these crabs are widespread throughout South Africa and provide the largest component of *A. capensis* diet in all river systems from which diets have been analysed (see e.g. Rowe-Rowe 1977; Ligthart *et al.* 1994; Purves *et al.* 1994; Somers & Purves 1996; Rowe-Rowe & Somers 1998).

Habitat characteristics

Otters were present at localities receiving <50 mm rainfall p.a. (e.g. Elandsfontein, Doring River, Northern Cape Province) to >500 mm p.a. (e.g. rivers in Jonkershoek near Stellenbosch, coastal forests in the southern Cape), and located from 0–>1200 m a.s.l. Of the 268 sites surveyed, 206 (76.86%) were located on riverbanks, 31 (11.56%) along the shores of lakes and dams, 17 (6.34%) along shores of estuaries, 9 (3.35%) along marshes and one on a canal (the latter was not included in the model). Signs were found at 150 (56%) of locations.

Univariate analyses

Univariate analysis showed that the depth of a water body is an important factor when spoor presence is the dependent variable ($F = 3.0$, d.f. = 5, $P = 0.01$). A post-hoc analysis using Fischer LSD showed that sign presence on banks where the water body has a depth of 1–2 m was significantly greater than where the depth was 2–5 m ($P = 0.03$), with the latter showing a poor association with spoor presence.

Current strength ($F = 2.8$, d.f. = 5, $P = 0.02$), water use ($F = 5.1$, d.f. = 5, $P < 0.001$), pollution ($F = 2.5$, d.f. = 4, $P = 0.04$) and food availability ($F = 3.3$, d.f. = 8, $P < 0.01$) were also important factors determining the presence of scats. Fast-flowing water bodies had significantly fewer scats

Table 2. Fischer LSD results for the effect of food presence on Cape clawless otter scat presence (significant results are indicated in bold).

	Crab	Fish/crab/frog	Fish	No record	Fish/crab	None	Crab/frog	Frog	Fish/frog
Crab									
Fish/crab/frog	0.547533								0.256907
Fish	0.005007	0.000321		0.001847	0.117365	0.001107	0.214470	0.004561	0.123714
No record	0.026186	0.001847	0.407341	0.407341	0.04822	0.551069	0.009824	0.488419	0.391107
Fish/crab	0.387306	0.117365	0.407341	0.184032	0.184032	0.208646	0.052098	0.936132	0.763580
None	0.005966	0.001107	0.044822	0.184032	0.031481	0.031481	0.638985	0.198123	0.569882
Crab/frog	0.631023	0.214470	0.551069	0.208646	0.638985	0.253178	0.010796	0.253178	0.218938
Frog	0.036244	0.004561	0.009824	0.936132	0.198123	0.253178	0.069064	0.069064	0.377657
Fish/frog	0.256907	0.123714	0.391107	0.763580	0.569882	0.218938	0.377657	0.731654	

on their banks than slow water bodies ($P < 0.01$) and those with no record of current strength ($P < 0.04$). Static water bodies also had fewer scats on their banks than slow flowing water bodies ($P < 0.01$). Compared with areas where water was not used, shores of open water bodies used for recreation, boating, and drinking by livestock had significantly fewer scats ($P = 0.02$, $P < 0.01$ and $P < 0.01$, respectively). Areas where boating took place also had fewer scats than those used for water extraction (pumping and irrigation) ($P = 0.02$). Fewer scats were also found in areas showing signs of agricultural pollution compared with those having no pollution ($P = 0.04$). The results of Fischer LSD for food as a factor determining scat presence is given in Table 2.

The food present was the only significant factor in the univariate model predicting otter presence ($F = 5.1$, d.f. = 5, $P < 0.0001$) (Fig. 2), at a given locality, with crabs being the most important food. Fischer LSD results are given in Table 3.

Multivariate analysis

Depth of the water body ($F = 1.8$, d.f. = 15, $P = 0.03$), water use or not ($F = 1.9$, d.f. = 15, $P = 0.02$) and available food ($F = 2.2$, d.f. = 24, $P = 0.001$) were all significant factors in the multivariate model.

DISCUSSION

As for all other otter species studied intensively (Kruuk 2006), food availability is the single most important factor determining otter presence in a given habitat: e.g. the degree of productivity directly affect numbers of *L. lutra* in northeast Scotland (Kruuk *et al.* 1993). Results from all studies so far suggest that where *A. capensis* co-occurs with *L. maculicollis* and *A. paludinosus*, differences in diet allow coexistence. Our results (see also Somers & Nel 2004b) indicate that the local presence of *A. capensis* indicated primarily by sign, is not affected by the width of a river or lake. As data on the distribution of this species in many African countries with large arid areas and episodic rivers (e.g. Somalia, Kenya, Mali and Niger) are deficient, our results suggest that *A. capensis* may have a more extensive distribution in such arid regions, usually considered too inhospitable for the survival of this species, than known at present. In such rivers the persistence of suitable pools would, however, be crucial. In this respect *A. capensis* parallels the local occurrence of *L. lutra* in semi-arid Morocco (Macdonald & Mason 1984;

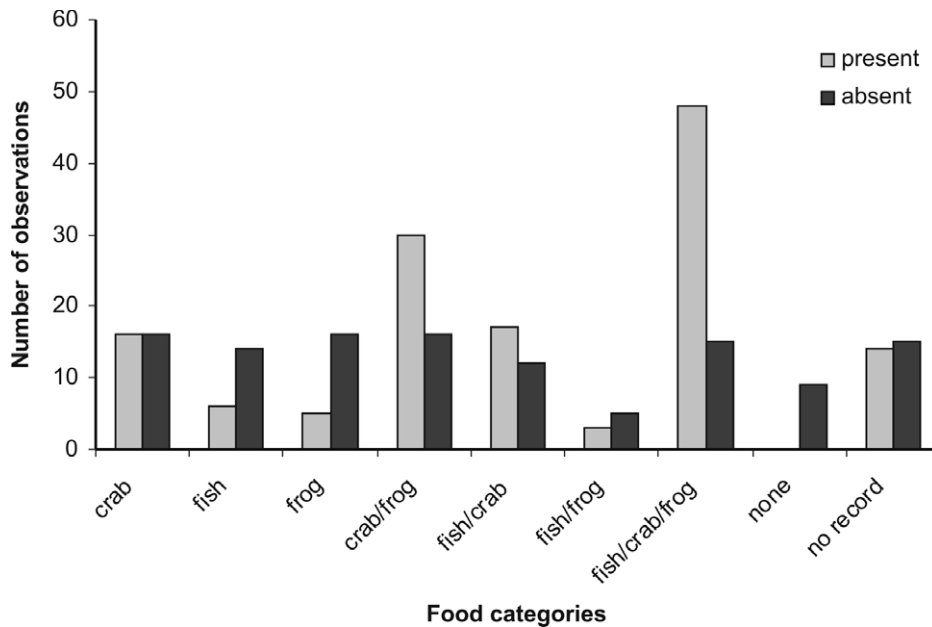


Fig. 2. Cape clawless otter presence as related to food availability.

Mason & Macdonald 1986). Given the wide prey spectrum of *A. capensis* (see, e.g., Rowe-Rowe & Somers 1998) such pools can be situated in a variety of substrates; while those in sand would contain a preponderance of fish, others in rocky areas would contain more crabs, or a mixture of potential prey species. With their wide food spectrum *A. capensis* can therefore 'switch' between prey taxa, i.e. show a functional response on a temporal or geographical level, a trait conducive to a wide geographical and ecological distribution. In addition, catching prey through touch to a large extent limits the constraining effect of turbidity; *A. capensis* therefore occurs in both clear and very turbid rivers. *Aonyx capensis* also readily passes through stretches of highly-polluted rivers to more pristine parts. The main limiting feature of the aquatic habitat therefore is food, while the necessary characteristics of the terrestrial habitat, when used for sprainting, resting and parturition, are adequate cover (Perrin & Carugati 2000), and, if the primary foraging habitat is marine, access to fresh water for drinking and cleansing the fur (Van der Zee 1982; Arden-Clarke 1986; van Niekerk *et al.* 1998; Kruuk & Balharry 1990). In this latter respect *A. capensis* parallels *L. lutra*, *L. canadensis* and possibly other primarily freshwater otter species foraging in the sea. *Aonyx capensis* also occurs over a wide altitudinal gradient. Although we have no data on the effect of altitude on *A. capensis*

density, a possible inverse relationship could exist between crab (and other prey) density and altitude, so that *A. capensis* density, in common with that of *L. lutra* (Ruiz-Olmo 1998) decreases with increasing altitude. This is to be expected, as the upper stretches of South African rivers, at higher altitudes, are less productive than lower down (Day *et al.* 1986).

As has been found for other otter species, e.g. *L. lutra* (Robitaille & Laurence 2002) *L. provocax* (Aued *et al.* 2003) important limiting factors are industrial pollution (although otters pass through such stretches of river without landing) and disturbance. Radio-telemetry studies have shown that *A. capensis* spends a greater part of its time in aquatic habitats containing reed beds and boulders, and areas with overhanging vegetation. The former offers prime breeding and shelter sites for crabs and fish, a ready source of food (Somers & Nelb 2004; Kruuk 2006). Such preference for a substrate mirrors that of *L. lutra*: Durbin (1998) found that they showed clear preferences for particular substrates such as riffles or gravel in Scotland. Refuge size is important for many aquatic organisms (Beck 1995) and crab density is low where a suitable substrate is absent, e.g. stretches of sand. Along the course of a particular river, therefore, food-rich and food-poor parts could alternate, with *A. capensis* spending less time in food-poor stretches and *vice versa*. Size

Table 3. Fischer LSD results for the effect of food presence on Cape clawless otter presence (significant results are indicated in bold).

	Crab	Fish/crab/frog	Fish	No record	Fish/crab	None	Crab/frog	Frog	Fish/frog
Crab	0.007150	0.007150	0.115572	1.000000	0.449699	0.003189	0.138037	0.036919	0.477095
Fish/crab/frog	0.115572	0.000072	0.000072	0.008458	0.079314	0.000003	0.203964	0.000005	0.021238
Fish	1.000000	0.008458	0.120194	0.120194	0.027676	0.093822	0.003429	0.655859	0.686755
No record	0.449699	0.079314	0.120194	0.456737	0.456737	0.003411	0.145678	0.039406	0.480005
Fish/crab	0.003189	0.000003	0.027676	0.456737	0.000659	0.000659	0.531579	0.006766	0.234941
None	0.138037	0.203964	0.003429	0.003411	0.531579	0.000079	0.000079	0.179774	0.083679
Crab/frog	0.036919	0.000005	0.003429	0.039406	0.006766	0.179774	0.000495	0.000495	0.104701
Frog	0.477095	0.021238	0.686755	0.480005	0.234941	0.083679	0.104701	0.458806	

distribution of the crab populations may be determined by the available refuges as supplied by different substrate particle size (Beck 1995; Somers & Nel 1998) – fewer, larger particle size equate with fewer but larger crabs (Somers & Nel 1998). As crabs grow they consume more vegetable matter (Raubenheimer 1986; Hill & O’Keeffe 1992) and therefore large crabs are more plentiful in reed beds, which also provides breeding sites and cover for fish (Skelton 1993). Where favourable characteristics (reed beds and boulders) are therefore absent, such stretches would be used less often and more as links to more productive parts. Our data do not, however, allow us to distinguish which habitats are preferred as quantitative comparisons were not attempted.

The most striking result of our survey is that water depth significantly affects the presence of otter signs in South African aquatic ecosystems, with shallow water being preferred as in all other otters (Kruuk 2006). This can perhaps be explained by results from work in the marine habitat where otters foraging at specific depths closer to the shore were more successful in capturing prey. Another habitat factor which affects presence of otter signs on land appears to be any utilization of water. As otters are shy animals this is to be expected due to higher levels of disturbance. In addition, although this does not apply to the present survey, crocodile presence has a limiting effect on *A. capensis* occurrence (Kruuk 2006).

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