Z. Säugetierkunde 59 (1994) 332–341
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ISSN 0044-3468

Crabs *Potamonautes perlatus* in the diet of Otter *Aonyx capensis* and Water mongoose *Atilax paludinosus* in a freshwater habitat in South Africa

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Receipt of Ms. 23. 3. 1994
Acceptance of Ms. 22. 6. 1994

Abstract

Studied the feeding ecology of sympatric Cape clawless otter and water mongoose at the Olifants River, Cape Province. Crab was an important prey in the diet of both species and faecal analysis was used to determine the extent of dietary overlap. Mean crab size taken by water mongoose was larger than that taken by otters. Fish was the second most important prey in the diet of otters, whereas terrestrial prey comprised a major part of the diet of the water mongoose. Different foraging patterns of the predators and habitat selection by crabs of different sizes could explain the observed variation.

Introduction

Over most of their range in southern Africa the two species of otter – Cape clawless *Aonyx capensis* and spotted-necked *Lutra maculicollis* – coexist with the water mongoose *Atilax paludinosus*. They share the same habitat, albeit that the otters are more aquatic and the water mongoose ranges more often away from water; they show temporal overlap in activity; and some prey items are common to two or all three species (Skinner and Smithers 1990). *Atilax paludinosus* is the most widespread, followed by *A. capensis; L. maculicollis* has a more easterly distribution and unlike the others does not utilize marine habitats.

Both otter species have been little studied. Rowe-Rowe (1977a, b) documented their feeding behaviour in captivity and under natural conditions in Natal, while van der Zee (1981, 1982), Arden-Clarke (1986) and Verwoerd (1987) reported on the food, status, population density and spatial organization of *A. capensis* in marine habitats. Baker (1989) compared the feeding habits of *A. paludinosus* in the wild and in captivity and Maddock and Perrin (1993) reported on their role in an assemblage of viverrids.

Freshwater crabs *Potamonautes* spp. (Family Potamonidae) contributed the major portion of the diet of *A. capensis* in Natal (Rowe-Rowe 1977a), in Lake Victoria (Kruuk and Goudswaard 1990) and in various rivers in the SW Cape (unpubl. data). Du Toit (1980), Louw and Nel (1986), Rowe-Rowe (1977a) and Baker (1989) found crab to be important prey of *A. paludinosus* in freshwater habitats, while Whitfield and Blaber (1980), Louw and Nel (1986), and MacDonald and Nel (1986) found crustaceans of importance in the diet of water mongooses in estuarine and in marine habitats.

Crabs constitute the highest macroinvertebrate biomass in some South African rivers (Hill and O'Keeffe 1992), as do crayfish in some rivers in Italy (Gherardi et al. 1989) and high crab densities have also been recorded in trout streams in Zimbabwe (Turnbull-Kemp 1960). Crustaceans can, therefore, either seasonally or year-round provide an important food base for both otters and water mongoose.

This study discusses the utilization of this resource by sympatric *A. capensis* and *A. paludinosus*. It reports on their diet, the use of crabs and seasonal changes in diet in a

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freshwater habitat, and it discusses differences in foraging patterns underlining the observed variation.

Study area

The study was conducted along a 5 km stretch of the Olifants River ca. 8 km downstream from the Bulshoek Dam (31° 58′ S; 18° 45′ E), some 100 m above sea level and ca. 32 km north and downstream of Clanwilliam. Here the river is slow-flowing with marshlands, reeds or grassy verges, oxbows, large basins and with rapids or rocky pools up to 6 m deep. Vegetation on the banks were mainly grasses and sedges e.g. *Paspalum* sp., *Juncus* sp. and *Prionium* sp. *Sesbania punicea* trees formed thickets right up to the river edge in some places.

Average rainfall at the dam site is 265 mm p.a. (1981–1991), while the total rainfall for 1991 was 275 mm (Weather Bureau, in lit.). There is a rise of approximately 2–3 m in the water level at the study site during June and July, when rainfall is at its peak and the sluices of the Bulshoek Dam are opened. The minimum and maximum air temperatures vary from 19–34 °C in January (summer) to 9–19 °C in July (winter).

The fish species in the study area are mostly exotic, e.g. smallmouth bass *Micropterus dolomieu*, or translocated species, e.g. banded tilapia *Tilapia sparrmanii*, while indigenous species (e.g. *Barbus capensis, B. serra* and *Labeo seeberi*), of which most are endemic, are rare. Juvenile fish (2–8 cm in length) were more abundant during the summer, with a rapid decline in numbers from May/June onwards (Swiegers, pers. comm.).

Material and methods

Collection and analysis of scats

Aonyx scats were usually found < 10 m from the water edge, often in exposed areas. Flat rocks were commonly used for collective sprainting, which probably had a communicatory function (Kruuk 1992), as in the European otter. Such latrines were often used repeatedly over several visits to the study area. Individual scats were also scattered around in areas ranging from flat rocks to grassy banks. The mean diameter of the scats collected (when measurable) was 22.2 mm (SD = 3.63, range = 15.3–30.0, n = 50). No otter scats were found in September.

Atilax scats were also deposited at latrines as well as singly on different substrates, but usually in areas with vegetational cover, often > 10 m from the water edge. The mean diameter was 15.8 mm (SD = 2.2, range = 13.0–20.0, n = 23). No water mongoose scats were collected in April.

Both Cape clawless otter *Aonyx capensis* and water mongoose *Atilax paludinosus* scats were collected during February and November (summer), April (autumn), June (winter) and September (spring) 1991, from latrines as well as individual defecation sites. Otter scats were identified and distinguished from water mongoose scats by size, form, smell and the absence of banded hair as found in water mongoose scats. Only relatively fresh (unbleached) and intact scats were collected; those not positively identified were rejected. Scats were placed separately in paper bags and labelled with the species name, date and site of collection.

Air-dried scats were teased apart and all crab eyestalks, intact or broken, extracted. Other diagnostic prey remains, e.g. fish scales and bones were also removed. Fish were identified using scale characteristics and frogs were identified from skeletal remains.

Crabs were identified as *Potamonautes perlatus* (Milne Edwards). A total of 66 crabs of varying sizes (mean carapace width = 31.6 mm, SD = 13.8, range = 8.5–60.1 mm) were trapped or collected by hand in the study area. Both eyestalks of each crab were measured with an occular ruler in a stereo microscope. The length (L) of an eyestalk was taken as the longest axis from anterior to posterior when viewed from the lateral side. There was no consistent difference in the length of the two eyestalks of individual crabs and it was assumed that they were the same length.

The maximum width of the carapace was measured with calipers and correlated with the eyestalk length. There was a clear numerical linear relationship (Fig. 1), for which

$$C = 8.33E - 11.48 \quad (1)$$

In this C = carapace width (mm) and E = eyestalk length (mm). The correlation was highly significant ($r^2 = 0.99$, $p < 0.001$).

The crabs were also weighed, and regressions of wet weight (dependant variable) and eyestalk length (independent variable) were calculated. A log-linear relationship was found

$$\log W = -0.72 + 0.319E \quad (2)$$

where W = wet weight (g) and E = eyestalk length (mm); ($r^2 = 0.96$, $p < 0.001$).

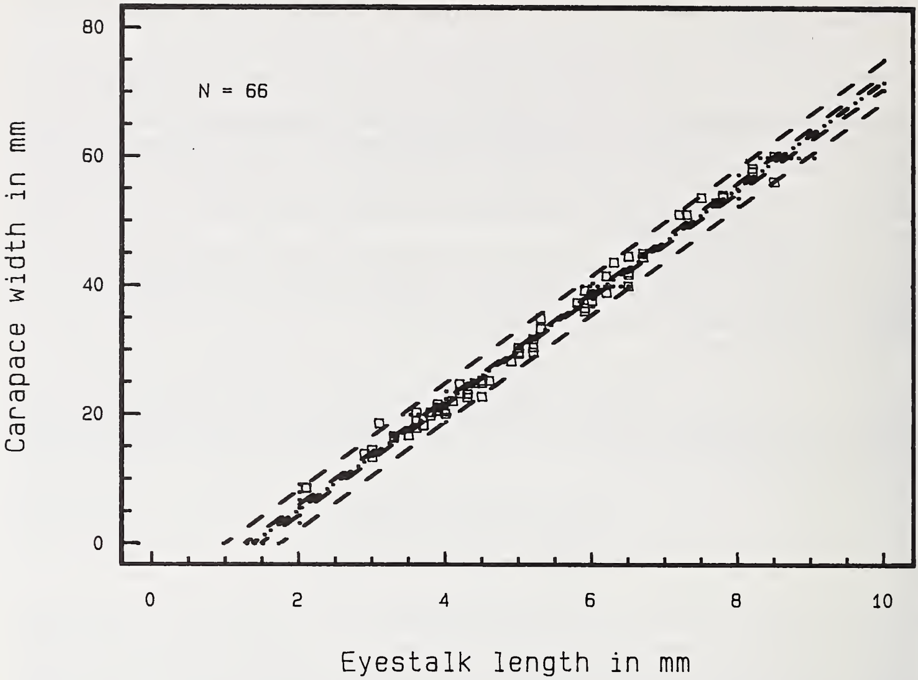

Fig. 1. The relationship between carapace width and eyestalk length in the freshwater crab *Potamonautes perlatus* ($r^2 = 0.988$, $P < 0.001$, $n = 66$, slope = 8.33)

Quantification of data

Prey remains found in scats were expressed as relative percentage of occurrence, calculated by totalling all the occurrences of all the prey items and expressing the actual occurrence of each prey item as a percentage of the total. For each scat dominance of prey type was also found 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 this scat would be ignored. The different dominant prey items were than totalled and expressed as a percentage of the total number of scats.

The maximum number of crabs potentially represented by the eyestalks in each scat was taken as the number of eyestalks found, i.e. each eyestalk represented a crab. Half of the number of eyestalks found in each scat was taken as indicating the minimum number of crabs in that scat, implying that a pair of eyestalks represented a crab.

Results

Diet composition

The proportions of prey remains from scat collections at different times of year is shown in figure 2. In both predators, crabs were the most abundant prey at all times, and especially in February. From then until November this proportion in the diet decreases. At all times the diet of *Atilax* was more varied than that of *Aonyx*, with slightly fewer crabs, and also fewer fish, but more terrestrial prey such as rodents and insects. A similar picture emerges from the analyses of scats by estimated bulk of prey remains (Fig. 3).

In total 70 % of the otter scats analysed were dominated by crab and 13.1 % by fish (Tab. 1). *Tilapia sparrmanii* was by far the dominant fish species (85 % occurrence) recorded, with smallmouth bass *Micropterus dolomieu* being the only other fish preyed

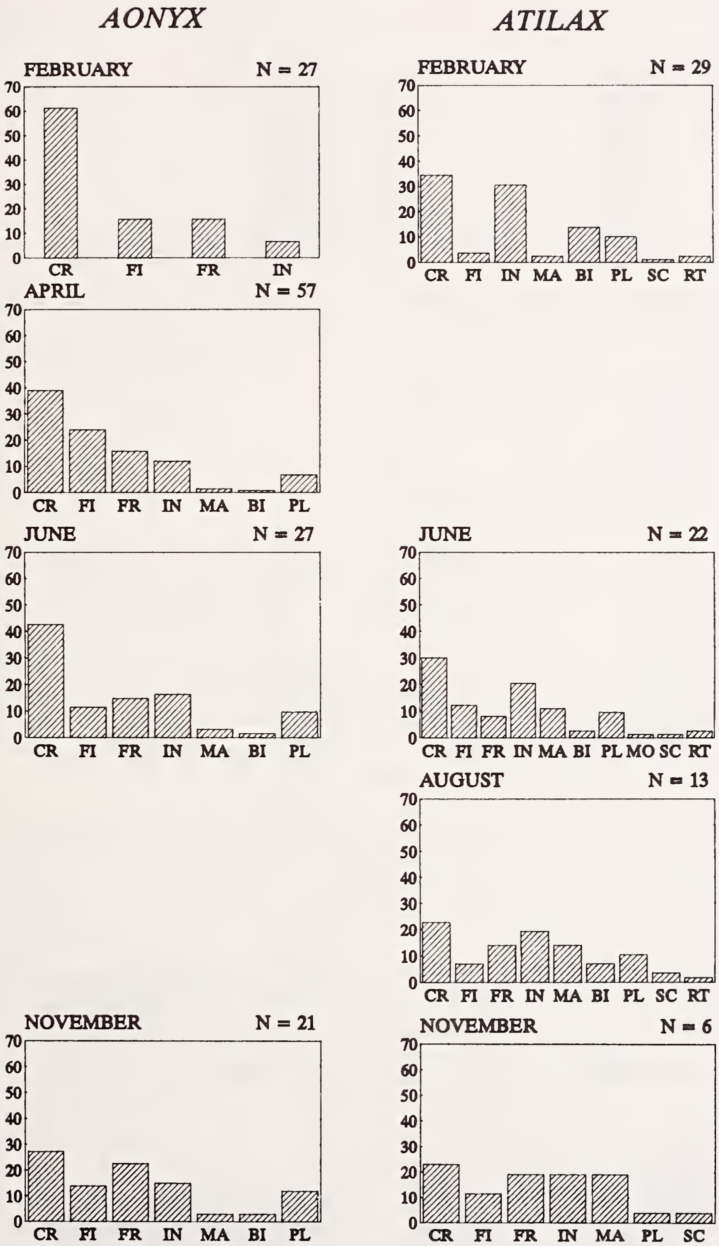

Fig. 2. Relative percentage of occurrence showing seasonal variation of different prey items in the diets of *Aonyx capensis* and *Atilax paludinosus*. (CR = crab, FI = fish, FR = frog, IN = insect, MA = small mammal, BI = bird, PL = plant, MO = mollusc, SC = scorpion, RT = reptile). N = number of scats

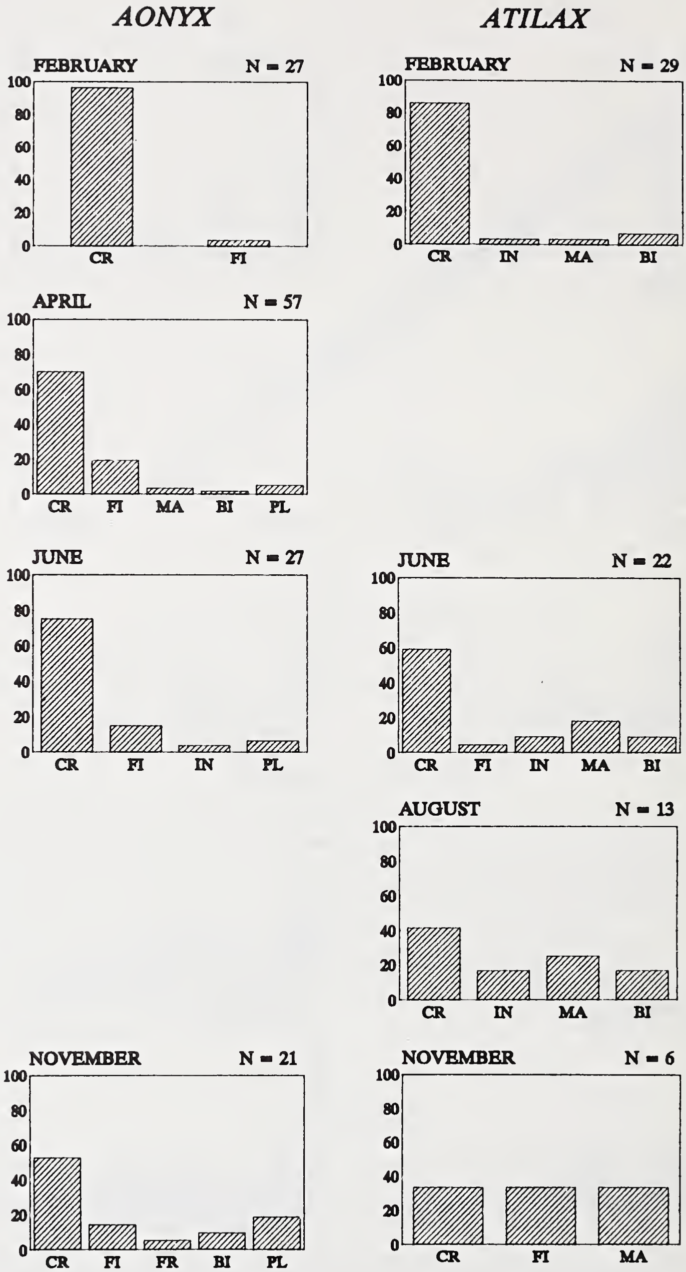

Fig. 3. Percentage dominance of occurrence showing seasonal variation of different prey items in the diets of *Aonyx capensis* and *Atilax paludinosus*. N = number of scats

upon. No remains of indigenous fish species were recorded. The frogs were *Strongylopus grayii* and *Rana fuscigula*. A variety of insect taxa were represented, but only those with a volumetric contribution of > 5 % (suggesting deliberate ingestion) were taken into consideration. These included: Odonata-Aeschnidae nymphs (dragonflies), which were the volumetric dominant insect prey, Coleoptera-Dytiscidae and Scarabaeidae (beetles), Hymenoptera-Formicidae (ants) and Orthoptera-Acrididae (grasshoppers). A small number of spiders (Subclass Arachnida) also occurred. *Otomys saundersiae* was the only small mammal that could be identified from *A. capensis* scats.

Table 1. **Summary of prey items recorded in 132 *Aonyx capensis* scats**

Item	Occurrence	Relative %	% Dominance
Crab	123	40.1	73.5
Fish	57	18.6	14.4
Frog	52	16.9	0.8
Insect	42	13.7	0.8
Plant	23	7.5	6.7
Mammal	6	1.9	1.5
Bird	4	1.3	2.3

Table 2. **Summary of prey items recorded in 70 *Atilax paludinosus* scats**

Item	Occurrence	Relative %	% Dominance
Crab	68	29.0	65.7
Fish	19	8.1	4.3
Frog	19	8.1	0
Insect	55	23.6	7.1
Plant	22	9.3	0
Mammal	23	9.9	14.3
Bird	17	7.2	8.6
Reptile	5	2.1	0
Miscellaneous	6	2.7	0

In 65.7 % of scats of *A. paludinosus* crab was the dominant food (Tab. 2). *Atilax* preyed on a greater variety of insects than *Aonyx*. Coleoptera (beetles) were the most abundant insects found in the diet of *Atilax*. Orthopteran (grasshoppers, locusts and crickets), Lepidopteran (moths and butterflies) and Isopteran (Termites) remains were also identified. Odonata nymphs were less important than in the diet of otters. Mammal prey that could be identified were *O. saundersiae* and *Aethomys namaquensis*.

Size of crabs eaten

Some 1860 eyestalks found in *Aonyx* scats were undamaged enough to be measured. Using equation (1), carapace widths could be calculated (Fig. 4a). The size of crabs varied from a minimum carapace width of 4.3 mm to a maximum of 61.0 mm (mean carapace width = 28.5 mm, SD = 8.88). Of the eyestalks extracted 75 % represented crabs with carapace widths of 15–35 mm (Fig. 4a).

Some scats contained only small crabs; e.g. 27 eyestalks found in one scat all represented crabs with carapace widths < 30 mm. Others consisted of only larger sized crabs, e.g. 6 eyestalks found in one scat represented crabs all with carapace width > 30 mm. Very few (1.7 %) crabs found in the scats had a carapace width > 45 mm.

In the *Atilax* scats analysed 85 eyestalks were found, representing crab sizes ranging from a minimum carapace width of 9.3 mm to a maximum of 47.7 mm (mean carapace width = 29.4 mm, SD = 9.16). Most (62 %) of the crabs had a carapace width of 15–35 mm (Fig. 4b). A significant difference ($p < 0.001$) was found between the sizes of crab preyed upon by otters and water mongoose (Mann-Whitney Test, T = 6494). *Atilax* ate more larger sized crabs, although none of the remains in their diet represented crabs as large as those eaten by *Aonyx*. The distribution of crab-sizes eaten by *Atilax* was bi-modal. The average wet weight of crabs taken was 8.33 g (range: 0.27–74.73 g) for *Aonyx capensis* and 8.98 g (range: 0.75–35.3 g) for *Atilax paludinosus*.

The foraging behaviour of two groups of otters, active at dawn, were observed during February. One group comprised four individuals and the other two. Only crabs were seen to be eaten. The 30 crabs taken were all caught by the otters diving and all were eaten in the

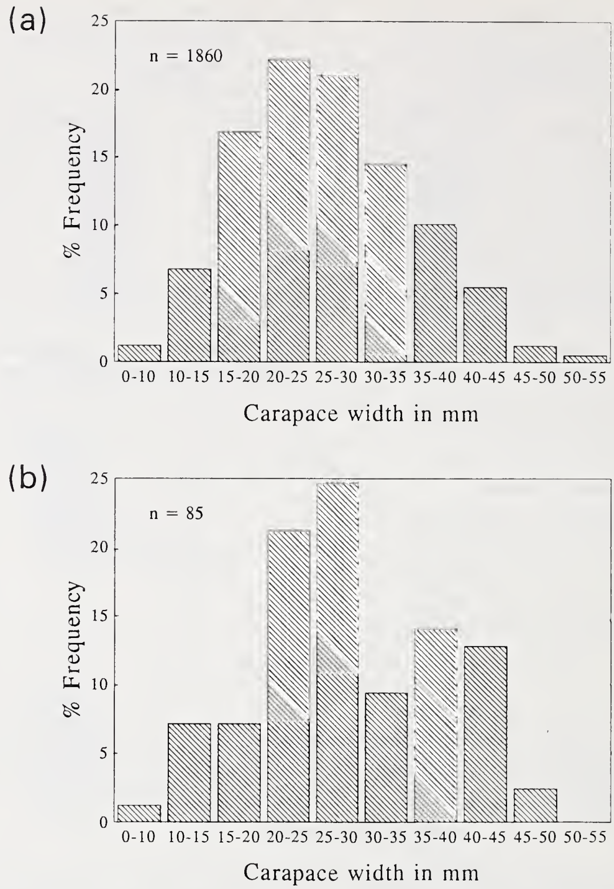

Fig. 4. Frequency of different sizes of crabs, as deducted from the length of eyestalks extracted from the scats of (a) *Aonyx capensis* and (b) *Atilax paludinosus*

water. Larger crabs were eaten with the otter lying on its back and the pincers being fed into the mouth first. Crab catching was concentrated in grassy areas where the depth of the water was <1 m. No observations were made on the foraging behaviour of water mongoose.

Discussion

Although the diets of both *Aonyx* and *Atilax* varied during different seasons, crab remained the single most important prey type for both, and both often ate rather small sized crabs. On average, *Atilax* took larger crabs than *Aonyx*.

Atilax occupies a wider range of habitats than *Aonyx* (Rowe-Rowe 1978; Whitfield and Blaber 1980; Stuart 1981; Skinner and Smithers 1990), it is more mobile on land and wanders greater distances away from water (Rautenbach and Nel 1978). Although there is considerable dietary overlap, terrestrial prey seem to be of more importance in the diet of *Atilax* and the hunting of aquatic prey could be restricted to the shallows (Rautenbach and Nel 1978).

In a marine habitat Louw and Nel (1986) found virtually no dietary overlap between the two species, with *Atilax* concentrating on shore crabs and other terrestrial species, while *Aonyx* took mainly benthic prey. Thus there was a degree of spatial as well as food segregation between the two sympatric species, with *A. paludinosus* foraging along the water edge intertidally and *A. capensis* foraging in the sea itself. Rowe-Rowe (1977a) found a dietary overlap of 65 % between the two species in a freshwater habitat. Both species seem to have much the same activity regimen, being mostly nocturnal and crepuscular (Rowe-Rowe 1978; Maddock and Perrin 1993; own observations).

Predatory and feeding behaviour have been described for the clawless otter (Rowe-Rowe 1977b) and water mongoose (Baker 1989). *Aonyx* swims underwater, turning the head from side to side and often feeling under stones for prey with the fore-feet (Rowe-Rowe 1977b). Rowe-Rowe (1977b) also found that captured crabs were held with both fore-feet and eaten in the water and that the whole crab was eaten. Our observations in the field confirmed this.

Baker (1989) found that *Atilax* sighted crabs when swimming or when walking past water. Their feet were then used in feeling for the crabs, but their heads were not immersed. Once the crabs had been located, however, they ducked their heads under water and caught the crabs in the mouth (Baker 1989). Crabs were taken from the water and eaten on land, and in large specimens parts of the carapace were often discarded (Baker 1989). Empty carapaces, with intact eyestalks, were often seen near the Olifants River and if these were discarded *Atilax* prey, there might be a degree of bias in the sizes of crabs represented in the scats. However some birds e.g. Giant and Pied kingfishers, are also known to prey on crabs and could have been responsible for the empty carapaces.

A difference in size of crab eaten by the two species could be expected, because of the difference in feeding behaviour of the two predators, and differences in movement patterns between small and larger crabs (Hill and O'Keeffe 1992). Smaller crabs were more often found in the grassy verges and muddy banks of the river and in secluded pools away from the main flow. Larger crabs appeared to prefer deeper water. Based on the differences in foraging areas of the otter and mongoose, and therefore availability of different sized crabs, one would expect *Aonyx* to consume larger crabs than *Atilax*. Similarly, the disparity in body size (ca. 3 kg for *Atilax*, 10–12 kg for *Aonyx*) favours *Aonyx* taking larger crabs. However our results do not bear out this prediction.

In Israel Gherardi and Micheli (1989) found larger crabs straying up to 40 m away from the water at night, while the smaller ones hid under rocks and in crevices at this time and did not venture out of the water as often. In the Jonkershoek valley near Stellenbosch large crabs are also occasionally seen venturing far (up to >500 m) away from the Eerste River. If the same applies to the crabs in the Olifants River, *Atilax* would more readily encounter such crabs as they forage not only along the water edge, but also further afield. This could explain why the average size of crabs found in their diet was larger than that found in the diet of otters.

Atilax utilized a wider range of prey, of which about 45 % was terrestrial. This and the fact that tracks of *Atilax* were often concentrated along the side of the river and at shallows and pools away from the main flow, indicates that they do not forage in water as much as *Aonyx*.

In Thailand the SE Asian small clawed otter *Aonyx cinerea* and the crab eating mongoose *Herpestes urva* occur sympatrically. Both species feed on freshwater crabs *Potamon smithianus*. Here it was found that the mongoose took significantly smaller crabs than the otter (Kruuk et al. 1994 and unpubl. obs.). In contrast to the situation in South Africa the size disparity between these two species is much smaller with *A. cinerea* weighing 5 kg, *H. urva* 3.4 kg. Both are nocturnal and solitary (MacDonald 1984) or occur in small groups (*A. cinerea* – pers. obs.). Ewer (1973) mentions that *H. urva* feeds largely on similar prey as *Atilax paludinosus*, i.e. frogs and Crustacea.

Thus overlap in resource utilization between crab-eating otters and mongooses does not appear to be confined to Africa. However, despite the high proportion of crab in the diet of these various species, there is no evidence to suggest that actual competition occurs. To investigate that important question, further information is required about possible limiting roles of the different prey species in the lives of these carnivores.

Acknowledgements

We thank the Foundation for Research Development and the University of Stellenbosch for providing funds for fieldwork, and travel funds for H. K.; P. R. Swiegers for field assistance; B. Sachse for her help in analyzing scats and assisting in various other ways; H. Huysamen for permission to work on his farm; E. van Dijk for identifying anuran remains; H. Geertsema for identifying insect remains and I. Cordes for translating the German summary.

Zusammenfassung

Krabben, Potamonautes perlatus, in der Nahrung von Kapfingerotter, Aonyx capensis, und Wassermanguste, Atilax paludinosus, in einem Süßwasserhabitat in Südafrika

Die Nahrungsökologie zweier syntoper Arten, Kapfingerotter und Wassermanguste, wurde am Olifants-Fluß in der Kapprovinz, Südafrika, untersucht. Süßwasserkrabben waren ein wichtiger Bestandteil in der Nahrung beider Arten. Anhand von Kotanalysen wurde ermittelt, in welchem Maße sich die Nahrungsspektren überschneiden. Wassermangusten ernähren sich von durchschnittlich größeren Krabben als Otter. Nach Krabben war Fisch der zweitwichtigste Bestandteil der Nahrung der Otter, während terrestrische Tiere einen größeren Teil der Nahrung von Wassermangusten ausmachen. Unterschiede in der Ernährungsweise der beiden Raubtierarten und in der Wahl von Krabben verschiedener Größe können die gefundenen Unterschiede erklären.

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