

Foraging behaviour of Cape clawless otters (*Aonyx capensis*) in a marine habitat

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Abstract

The foraging behaviour of Cape clawless otters *Aonyx capensis* was investigated. Factors included: duration of dives, recovery times, processing times, hunting success, per cent time at the surface, and time foraging before each catch. Observations were made during the day on solitary adult *A. capensis* in a marine environment in False Bay, South Africa. There were significant differences in duration of unsuccessful dives, recovery times, and processing times as well as successful dives with various depths. *Aonyx capensis* prefer hunting at depths of 0.5–1.5 m. This is despite having a higher hunting success, catching larger, more energy-rich prey (fish), and shortest time foraging per catch, at depths of 1.5–2.5 m. Some of the data presented support the optimal breathing hypothesis, which predicts that both surface and dive times should increase for dives of greater depths. However, diving efficiency does not decrease with increasing depth, and percentage time at the surface does not increase with increasing depth. These are contrary to the optimal breathing hypothesis.

Key words: *Aonyx capensis*, diving behaviour, foraging, marine

INTRODUCTION

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

Our understanding of otter diving behaviour comes mainly from studies on Eurasian otters *Lutra lutra* (e.g. Kruuk, Wansink & Moorhouse, 1990; Nolet *et al.*, 1993; J. P. Watt, 1993), and sea otters *Enhydra lutris* (e.g. Kvitek & Oliver, 1988; Kvitek *et al.*, 1993; Ralls, Hatfield & Siniff, 1995). Although Rowe-Rowe (1977a) gave 16 dive times of Cape clawless otters *Aonyx 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 the diving behaviour of this species.

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 & Moorhouse, 1990; Kruuk, Wansink *et al.*, 1990; J. P. 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 diving organisms, the currencies could include maximizing the rate of energy intake, maximizing the rate of oxygen intake, minimizing 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 a successful dive to the start of the next dive), hunting success (HS, percentage of dives yielding prey), percentage time at surface, time preceding each catch, success or failure (capturing or not capturing prey) and whether to eat or reject a small prey.

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Owing to loss of energy in the water (Kruuk, Taylor & Mom, 1997) it would be expected that otters would always maximize the net rate of energy gain. Optimal foraging theory states that foraging strategies may involve decisions that maximize 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 *c.* 13.0 kg and males being larger than females (Skinner & Smithers, 1990). *Aonyx capensis* relies on sight for locating prey but also feels for prey that is hidden from view (Rowe-Rowe, 1977*b*). These otters dive directly to the bottom (Rowe-Rowe, 1977*b*) where they capture prey with their dextrous forefeet (Rowe-Rowe, 1977*b*; 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 the otters to catch crabs and frogs in freshwater, but do for fish (Rowe-Rowe, 1977*c*).

The otters use freshwater habitats extensively (Rowe-Rowe & Somers, 1998) but also use marine habitats for food (Van der Zee, 1981; Arden-Clarke, 1983; Verwoerd, 1987). However, they seem to use marine habitats only in the presence of freshwater (van Niekerk, Somers & Nel, 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 south-eastern coasts of South Africa. These are supplemented with octopus *Octopus granulatu* 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 paper is the first to present 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; (2) an indication of potential avenues for further research. This paper, 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); (4) compares diving behaviour of *A. capensis* with that of *L. lutra* in marine habitats. It is hypothesized that *A. capensis* maximize their diving success rate and that they dive at depths where they get most prey for least effort. It is predicted that because of differences in diet, there would be differences in the diving behaviour of *A. capensis* and *L. lutra*.

STUDY AREA AND 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 4 small, perennial, freshwater streams (*c.* 0.5–2 m wide and *c.* 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; winter, 13.2 °C (Clark, Bennett & Lamberth, 1996).

Observations using 10 × 40 binoculars were conducted on foot, during the day at low tide. As the age of individual *L. lutra* affects diving behaviour (J. P. Watt, 1993), diving data from adult *A. capensis* only were used. 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 seemed to be a high turnover of individuals over the 29-month study period. The longest time that 1 recognizable individual was observed in the area was 3 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), data from solitary otters only were used to compare diving

parameters at different depths. Group sizes were recorded for all sightings. Otters were located by walking transects along the 2-km shoreline in both directions (i.e. 4 km) ($n=106$), and scanning the sea and shore. 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 percentage of 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 (*c.* 150 mm for adults). Small prey were regarded as those < 50 mm, medium 50–100 mm and large > 100 mm (after Kvittek *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 them.

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

RESULTS

Two forms of hunting or foraging mode were recognized. 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 where the otter surfaced, or after the otter swam on the surface for a few metres. The most common foraging pattern seemed 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 *c.* 60°.

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.

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 *c.* 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, seeming 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 *c.* 2 m of the water while eating its prey. On one occasion, when the wind was 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. During six transects more than one individual or group was seen giving a total of 38 sightings of otters. Of the sightings of foraging otters, 69.4% were solitary otters, 21% of two otters and 10.5% of three otters.

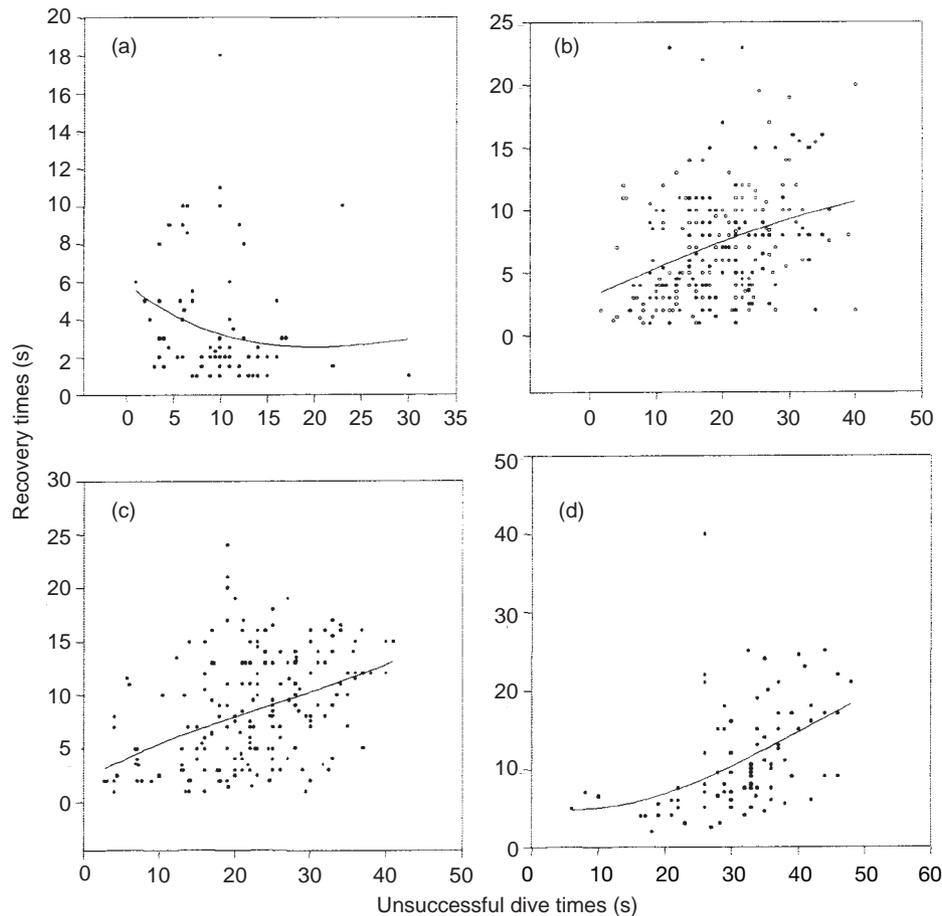
The otters tended to move along the coast while feeding (mean = 21.4 m/min, $n=5$, SE = 4.83, range 8.3–34.1). The furthest off shore an otter was estimated as hunting was 40 m, which was usually within the surf zone.

The mean duration of hunts of all groups observed, including solitary animals, was 75.3 min ($n=38$, SE = 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 1).

The mean dive time for all complete dives recorded was 21.0 s (Table 1). Unsuccessful dive times were not significantly longer than successful dive times at depths of 0.0–0.5 m (Mann–Whitney $U=184$, 101 d.f., $P=0.843$); 0.5–1.5 m (Mann–Whitney $U=1882$, 293 d.f., $P=0.803$) and 2.5–3.5 m (Mann–Whitney $U=428$, 105 d.f., $P=0.671$) but were for depths between 1.5–2.5 m (Mann–Whitney $U=7029$, 335 d.f., $P=0.015$). Combining all depths there was not a significant difference

Table 1. Diving behaviour of *A. capensis* at various depths: *n* = number of dives; UDT = unsuccessful dive time; SDT = successful dive time; PT = processing time; RT = recovery time

Depth (m)	<i>n</i>	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

**Fig. 1.** 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.

between unsuccessful and successful dive times (Mann–Whitney $U = 26133$, 837 d.f., $P = 0.464$) (Table 1).

Kruskal–Wallis one-way analysis of variance on ranks indicated that there were significant differences in recovery times ($H = 117.94$, 3 d.f., $P < 0.001$), processing times ($H = 9.61$, 3 d.f., $P = 0.022$), unsuccessful dive times ($H = 263.03$, 3 d.f., $P < 0.001$) and successful dive times ($H = 11.34$, 3 d.f., $P = 0.01$) with various depths (Table 1).

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 m ($r^2 = 0.10$, $P < 0.001$), 1.5–2.5 m ($r^2 = 0.16$, $P < 0.001$) and 2.5–3.5 m ($r = 0.21$, $P < 0.001$) (Fig. 1). Processing

time was longest after diving to 1.5–2.5 m depths (Table 1). Otters dived more frequently in water of < 1.5 m than would be expected on the basis of the area present (Fig. 2, $\chi^2 = 260$, 3 d.f., $P < 0.001$). As the furthest out an otter was estimated to hunt was 40 m, 80 ha was available to the otters along this 2-km stretch of coast.

Foraging efficiency at various depths is given in Table 2. HS was highest at a depth of between 1.5 and 2.5 m. Percentage of time at the surface was similar between depths (Table 2). Kruskal–Wallis one-way analysis of variance on ranks indicated that there were no significant differences in surface time before a successful dive ($H = 4.50$, 3 d.f., $P = 0.213$) with various depths (Table 2).

The otters were observed feeding mostly on fish

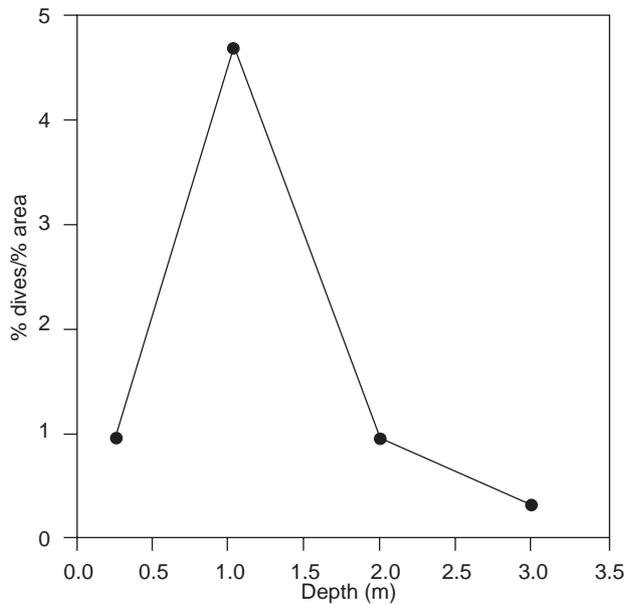


Fig. 2. The percentage of dives of Cape clawless otters *Anyx capensis* corrected for the percentage of the available area (within 40 m from the shore) at various depths. The depth figures are the medians of the depth ranges: 0.25 = 0.0–0.5 m; 1 = 0.5–1.5 m; 2 = 1.5–2.5 m; 3 = 2.5–3.5 m.

(50.0%), followed by crabs (27.8%), *J. lalandii* (11.1%) and abalone *Haliotis midae* (5.6%) (Fig. 3). 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 of where captured ($\chi^2 = 15.0$, 6 d.f., $P = 0.005$) (Table 3). The proportion of large prey (> 100 mm) also increased with depth (Table 3).

DISCUSSION

Despite *A. capensis* being primarily a crab eater the general swimming and diving behaviour are similar primarily to fish-eating otter species such as *L. lutra* (Conroy & Jenkins, 1986; Kruuk, 1995) and *L. canadensis* (Fish, 1994).

In the present study, the largest foraging group observed consisted of three individuals, which is fewer than found by Arden-Clarke (1983) who recorded three groups of four and one group of five ($n = 67$). 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%, respec-

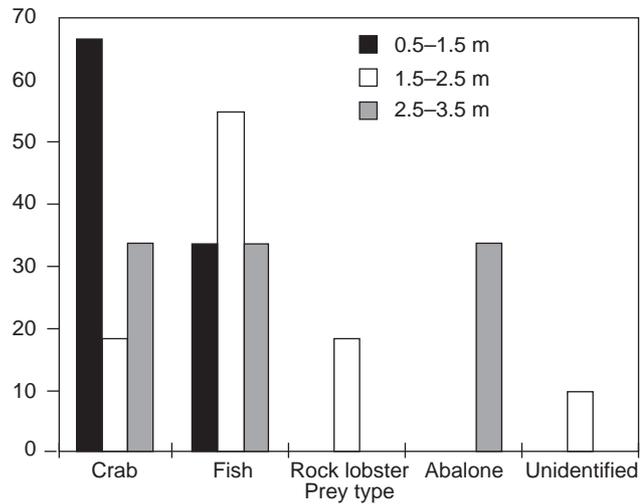


Fig. 3. Frequency of occurrence of different prey items obtained by Cape clawless otters *Anyx capensis* at different depths in False Bay, Western Cape, South Africa.

tively). These data suggest that marine *A. capensis* has a similar group structure to *L. lutra* (Kruuk, 1995) but further data, especially age and sex data, are needed to clarify this.

As expected from differences in metabolic rates and lung volume (Kooyman, 1989), Kruuk (1993) found a clear relationship between log mean body weight and log mean dive time for several diving mammals. 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 *c.* 26.5 s, which is longer than 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.

As at most depths in the present study, Arden-Clark (1983) found no significant differences between the

Table 2. Foraging efficiency of *A. 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 ($n = 5$)

Table 3. Frequency of occurrence (%) of prey sizes, as determined by direct observations, of *Aonyx capensis* at various depths in False Bay, South Africa

Prey size	Depth		
	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
<i>n</i>	12.0	22.0	8.0

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 may 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 continuing to dive 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 metres 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 than 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 the processing time as 30, 32 and 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 2) 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, Kruuk & Nel, 1994; Somers & Purves, 1996) than in the present study. Either the otters in the present study were selecting larger prey than 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, Wansink *et al.*, 1990) and 32.8% (Mull, West Scotland; J. P. Watt, 1993). These success rates for *L. lutra*, although very different, are rather closer to the 4.1–12.8% (Table 2)

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 *E. lutris*. As results seem to vary between habitats, this may apply to *A. capensis* as well. Kruuk, Wansink *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 it 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, scat analysis by Arden-Clarke (1983) and Rowe-Rowe (1977c) for the same study area as Rowe-Rowe (1977a), gave crustaceans as 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. The otters therefore seem 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 *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; J. 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, Taylor *et al.*, 1997), they may need a higher success rate to minimize 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. J. P. 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 between 32.2% and 70.9%. *Aonyx capensis* in the present study has a per cent time at the surface varying between 35.9% and 39.4% (Table 2), with no trend with depth.

Although a very imprecise measure, the technique used to determine prey size (i.e. comparing with head-width (*c.* 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. 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 faeces of *A. capensis* inhabiting the study area.

Fish were the most common prey, followed by crabs, although the species of both could be seldom 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.

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 of 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 > c. 4 m.

Optimum foraging theory predicts that *A. capensis* will forage at the depth that maximizes net rate of food intake, 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 the otters 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. 3 & Table 3) 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).

Data on diet at various depths (Fig. 3 & Table 3) 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. 3) also emphasize the importance of rock lobsters *J. lalandii* in the diets of these carnivores, indicating the need for more continued stringent measures for the conservation management of *J. lalandii*. Rock lobsters and abalone 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.*, 1997) can slow the population growth of prey species. It is therefore highly recommended that for the conservation management of *A. capensis*, *J. lalandii* and *H. midae*, 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.

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