

Aonyx capensis. By Serge Larivière

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***Aonyx* (Lesson, 1827)**

Aonyx Lesson, 1827:157. Type species *Aonyx delalandi* Lesson (= *Lutra capensis* Schinz).

Anahyster Murray, 1860:157. Type species *Anahyster calabaricus* Murray (= *Lutra capensis* Schinz).

Paraonyx Hinton, 1921:195. Type species *Paraonyx philippi* Hinton.

CONTEXT AND CONTENT. Order Carnivora, family Mustelidae, subfamily Lutrinae. The genus *Aonyx* is monophyletic and phylogenetically linked to the New World otters (*Lontra*—van Zyll de Jong 1987), with *Paraonyx* recognized as a valid subgenus (Ellerman et al. 1953). Exactly which species should be included in the genus *Aonyx* is not resolved. For example, the Asian small-clawed otter (*Amblonyx cinerea*) is often included in the genus *Aonyx* (Chanin 1985; Foster-Turley et al. 1990), but recent phylogenetic analyses suggest that the generic distinction between *Aonyx* and *Amblonyx* is not warranted (Koepli and Wayne 1998). Within *Aonyx*, the Congo clawless otter (*A. congicus*) is often considered under *A. capensis* (Davis 1978). However, Wozencraft (1993) recognizes 2 species: *A. capensis* and *A. congicus*.

***Aonyx capensis* (Schinz, 1821)**

Cape Clawless Otter

Lutra capensis Schinz, 1821:214. Type locality “Cape of Good Hope.”

Lutra inunguis Cuvier, 1823:247. Type locality “Cape of Good Hope.”

Aonyx delalandi Lesson, 1827:157. Type locality “Cape of Good Hope.”

CONTEXT AND CONTENT. Generic context given above. *Aonyx capensis* is monotypic.

DIAGNOSIS. The Cape clawless otter can be differentiated from the sympatric spotted-necked otter (*Lutra maculicollis*) by its larger size (ca. 12–18 kg), greater length (ca. 950 mm), paler color, lack of spotted markings on neck and throat, long vibrissae, lack of webbing on feet, and lack of claws on toes (Roberts 1951; Rowe-Rowe 1978a, 1985). The water mongoose (*Atilax paludinosus*) is gray to reddish-brown as opposed to the dark brown dorsum and creamy white underparts of *A. capensis* (Turnbull-Kemp 1960a). The Congo clawless otter (*A. congicus*) is similar in color, but smaller in size and more slender, especially in the head and neck region (Kingdon 1997). Furthermore, the 2 *Aonyx* species are sympatric only in Rwanda and Uganda, where they do not share the same habitats (Baranga 1995; Rowe-Rowe 1986, 1995).

GENERAL CHARACTERS. The Cape clawless otter (Fig. 1) is the largest of the Old World otters (Turnbull-Kemp 1960a) and the 3rd largest of all otters (Estes 1991) after the giant otter (*Pteronura brasiliensis*) and the sea otter (*Enhydra lutris*). Body is massive and the tail is stout (Turnbull-Kemp 1960a). Upper lips, sides of face, neck, throat, belly, and edge of ears are white (Skinner and Smithers 1990). Eyes and ears are small and rounded (Dorst and Dandelot 1970; Eyre 1963). Vibrissae are white to gray and occur on both upper and lower jaw (Tayler 1970).

Coat is dense and lustrous. Guard hairs reach 25 mm in mid-back, but are shorter (ca. 10 mm) on head and tail (Skinner and Smithers 1990). Underfur is white to off-white in color, hairs are wrinkled and much finer than guard hairs. Skin is thick (Skinner and Smithers 1990).

Toes are clawless, except for digits 2, 3, and 4 of hind feet, which bear small grooming claws (Davis 1978). Hind feet are par-

tially webbed, but front feet are not (Skinner and Smithers 1990). *A. capensis* has the least interdigital webbing of all otters (Davis 1978). Undersides of feet are hairless, and thumb is opposable (Rowe-Rowe 1978a).

Average measurements (mm), with parenthetical ranges of 7 males and 2 females, respectively, from the Cape province in South Africa (Stuart 1981), are as follows: length of head and body, 829 (762–880), 733 (730–736); length of tail, 487 (465–515), 500 (495–515); length of hind foot, 152 (130–170), 135 (130–139); length of ear, 31 (23–35), 28 (28–29). In the Cape Province, mean body mass (kg), with parenthetical ranges of 7 males and 3 females, is 15.1 (11.5–21.0) and 12.9 (10.6–14.2), respectively (Stuart 1981). Mean body mass (kg) and parenthetical ranges and sample sizes of adult males and females, are: 12.3 (10.0–15.4, 9) and 14.3 (12.3–16.3, 2) in Zimbabwe (Smithers 1983) and 13.7 (10.0–17.8, 13) and 11.9 (11.0–13.0, 3) in Tsitsikama National Park (Skinner and Smithers 1990). One male and 1 female from Natal weighed 16.4 and 11.8 kg, respectively (Rowe-Rowe 1978b).

Skull (Fig. 2) is massive, and brain is large relative to body (Sheppey and Bernard 1984). Cranium is broad and flattened, broadest at ears and tapering sharply at interparietal constriction. Eye orbits are relatively small; rostrum is broad and short; zygomatic arches are thin and lightly built. A small sagittal crest is present (Skinner and Smithers 1990). Greatest length of skulls (mm) and parenthetical ranges for 7 male and 2 females, respectively, from Cape Province, South Africa, averaged 138 (134–144) and 131 (128–134—Stuart 1981). Mean skull measurements (mm) and parenthetical ranges for 3 adult males and 3 adult females, respectively, from South Africa are: greatest length of skull, 133.5 (131.5–136), 130.9 (125–134); basilar length, 120.3 (118–122), 118.3 (112–122); zygomatic breadth, 98.8 (95.5–101.5), 92.7 (91–96); mastoid breadth, 96.7 (92.5–99.7), 90.6 (86–93.5); interorbital constriction, 32.9 (31.7–34.8), 29.3 (28.5–30.5); intertemporal constriction, 28.5 (27–30), 27.5 (26.5–28—Roberts 1951).

DISTRIBUTION. The Cape clawless otter occurs from South Africa northward to Ethiopia in the east and Senegal in the west (Fig. 3). The Cape clawless otter is common in Guinea, Kenya, Liberia, Malawi, Mozambique, Senegal, South Africa, Tanzania, Zaire, Zambia, and Zimbabwe; rare in Angola, Benin, Botswana, Burkina Faso, Chad, Guinea-Bissau, Ivory Coast, Sierra Leone, Swaziland, and Uganda; and very rare in Central African Republic, Ethiopia, Ghana, Lesotho, Namibia, Niger, Nigeria, and Rwanda (Avenant 1997; Crawford-Cabral 1989; Pringle 1977; Rowe-Rowe 1990a, 1990b; Smithers 1966). *A. capensis* is absent from the central African rainforest region of the Congo basin where *A. congicus* occurs. The status of the Cape clawless otter in Gambia, Mali,



FIG. 1. Adult *Aonyx capensis*. Photograph courtesy of Michael J. Somers.



FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Aonyx capensis* from Kenya (female, Royal Ontario Museum 38431). Greatest length of cranium is 128.5 mm.

Sudan, and Togo is unknown (Rowe-Rowe 1990a, 1990b, 1995). Both species of *Aonyx* are sympatric in Rwanda and Uganda (Rowe-Rowe 1986).

FOSSIL RECORD. The earliest known species of otter, *Potamotherium valetoni*, occurred in the upper Oligocene of Europe (Savage 1957; van Zyll de Jong 1972). "*Lutra*" *hessica* appears in the European Pliocene (van Zyll de Jong 1972) and is possibly the 1st member of the genus *Aonyx* (Pohle 1919). In the Upper Pliocene of Europe, "*Lutra*" *bavarti* is recorded and is also considered a member of the genus *Aonyx* based on the M1 which is broadened as in recent *Aonyx* (van Zyll de Jong 1972). In the Upper Pliocene of China, "*Lutra*" *aonychooides* shows many similarities with the recent *Aonyx* (Teilhard de Chardin and Leroy 1945; van Zyll de Jong 1972). *A. capensis* is 1st recorded from the Pleistocene at Swartklip, Florisbab, and Gamble's sites (Hopwood and Hollyfield 1954; Savage 1978), and fossils have been found in northern, southern, and eastern Africa in sites away from the coast (Savage 1978).

In Africa, the history of the Lutrinae is not well known. The Lutrinae probably reached Africa in the Pliocene, but most of the

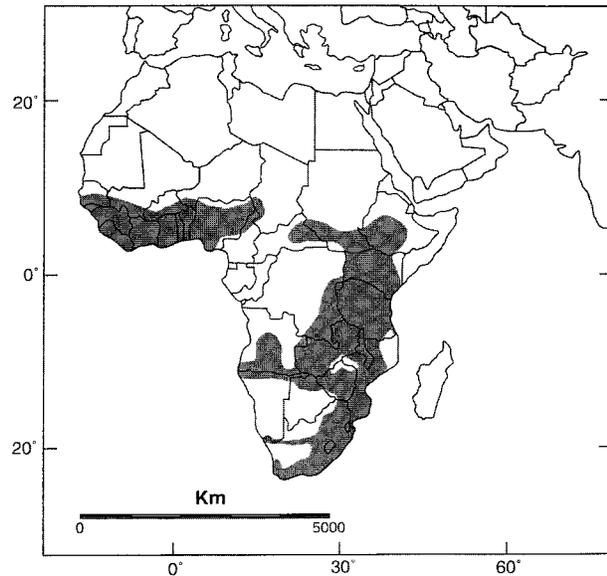


FIG. 3. Distribution of *Aonyx capensis* in Africa; modified from Rowe-Rowe (1990b, 1995) and Rowe-Rowe and Somers (1998).

ancestral forms cannot be linked to current forms. Based on the specialization of the dentition for crushing instead of shearing, *A. capensis* is probably more recent than its sympatric counterpart *L. maculicollis* (van Zyll de Jong 1972). *Aonyx* and *Amblonyx* probably diverged from the Eurasian otter (*Lutra lutra*) about 6.3–8.0 million years ago, and diverged from each other 5 million years ago (Koepfli and Wayne 1998).

FORM AND FUNCTION. *Aonyx capensis* is a specialist for feeding on crabs (Rowe-Rowe 1986). Its large molars, powerful jaws, and lack of cutting teeth are well adapted for crushing crustacean carapaces and skull bones of large fish (Rowe-Rowe 1977a). In Africa, molariform teeth of *A. capensis* vary geographically with the size of molluscs and crustaceans (Davis 1978).

Aonyx capensis has dexterous forefeet, which can also detect prey by touch (Kingdon 1977). Rough skin on palms and fingers enables Cape clawless otters to grasp slippery fish and frogs securely (Smithers 1971). Long vibrissae are used to detect movement of prey in murky water (Rowe-Rowe 1977b). Food passage for *A. capensis* is ca. 3 h (van der Zee 1982).

Males have a well-developed baculum. Prepuce is pendulous, not haired, and anterior to scrotum (Estes 1991). Although prepuce protrudes well beyond ventral hair, body of penis lies completely sheathed under the skin (Davis 1978). Females possess 2 pairs of abdominal mammae (Roberts 1951).

Cape clawless otters possess a pair of anal glands which may serve for scent-marking (Smithers 1971). Scats of *Aonyx capensis* can be differentiated from those of *Lutra maculicollis* by their greater diameter: scats of *A. capensis* average (\pm SD) 25.5 \pm 2.4 mm ($n = 185$), whereas scats of *L. maculicollis* average (\pm SD) 14.6 \pm 2.1 mm ($n = 85$ —Rowe-Rowe 1992).

ONTOGENY AND REPRODUCTION. Copulation may occur during December (Verwoerd 1987), but births have been reported in most months, with a possible peak during the dry season south of the equator (Rowe-Rowe 1978a, 1978b). In KwaZulu-Natal, South Africa, parturition occurs at the end of August (Rowe-Rowe 1978b), which coincides with the start of the rainy season in this summer rainfall area. Along the coast of South Africa, where the rainy season is in winter, parturition occurs from December to February (Verwoerd 1987).

Gestation is 63 days, and litter size is 1–3 (Rowe-Rowe 1978a). Young are born with pale, smoky-gray, woolly fur (Kingdon 1997; Rowe-Rowe 1985). Two young otters (sex unknown) <1 week old weighed 260 g each (Rowe-Rowe 1978b), whereas a pair of 14-day-old cubs (sex unknown) weighed 700 and 1,400 g, respectively (Chanin 1985). Between 8 and 16 weeks of age, Cape clawless otter cubs gain weight at a rate of 330 g per week (Chanin 1985).

Eye opening occurs after 16–30 days, after which cubs venture outside of the den (Chanin 1985; Smithers 1971). Weaning occurs at 45–60 days (Harris 1968). Young become independent and reach sexual maturity after 1 year (Verwoerd 1987).

ECOLOGY. Although most populations occur in freshwater, some populations may occupy the sea coast (Rowe-Rowe 1990b; Shortridge 1934). Unlike true marine mammals, Cape clawless otters must drink freshwater and, accordingly, live near springs or rivers (Tayler 1970; van Niekerk et al. 1998). Cape clawless otters are found in major river systems, many minor water courses, and also in many nonperennial streams and small reservoirs (Stuart 1981). *A. capensis* makes extensive use of reed-beds (*Phragmites* and *Typha*) and prefers shallow over deep water (Rowe-Rowe 1977a; Stuart 1981).

In freshwater habitats, diet of the Cape clawless otter comprises primarily crabs (*Potamonautes*), frogs, insects, and fish (Butler 1994; Donnelly and Grobler 1976; Kruuk and Goudswaard 1990; Lighthart et al. 1994; Purves et al. 1994; Rowe-Rowe 1977a; Somers and Purves 1996; Turnbull-Kemp 1960b). Although crabs dominate the diet in all localities (42–65% relative occurrence), percentage of other items in diet varies locally or seasonally, and depends on prey availability (Rowe-Rowe and Somers 1998). Typically, *A. capensis* consumes more fish during winter (10–30% occurrence) than in summer (0–10%—Rowe-Rowe 1977a). Fish consumed by Cape clawless otters include *Amphilius uranoscopus*, *Anguilla bengalensis*, *Barbus anoplus*, *B. natalensis*, *Lepomis macrochirus*, *Micropterus dolomieu*, *M. punctatus*, *M. salmoides*, *Salmo trutta*, and *Tilapia sparrmanii* (Purves et al. 1994; Rowe-Rowe 1977a). In Zimbabwe, introduced rainbow trout (*Oncorhynchus mykiss*) composed only 1% of the diet (Butler and du Toit 1994), and in KwaZulu-Natal, most introduced trout that were eaten (88%) were <200 mm in length (Rowe-Rowe 1977a).

In coastal waters of the Cape province, *A. capensis* captured 50% fish ($n = 64$ successful dives), 28% crabs, 11% Cape rock lobsters (*Jasus lalandii*), and 6% abalone (*Haliotis midae*—Somers 2000). In a marine habitat in Tsitsikama Coastal National Park, South Africa, the diet of *A. capensis* consists mostly of red rock crab (*Plagusia chabrus*), brown rock crab (*Cyclograpsus punctatus*), Cape rock lobster, octopus (*Octopus granulatus*), frogs (*Xenopus*), and fish (Rowe-Rowe 1977a, 1985; van der Zee 1981; Verwoerd 1987). In Betty's Bay, South Africa, the Cape clawless otter ate mostly fish (59% of biomass consumed), crustaceans (24%), and octopus (15%—Verwoerd 1987). Although *A. capensis* at Betty's Bay consumes more fish and lobster and fewer crabs, the foraging behavior of Cape clawless otters in both locations was similar (Verwoerd 1987).

Predation on waterfowl is rare (Rowe-Rowe 1978a), but in winter, Cape clawless otters may kill domestic ducks, geese, coots, or swans (Rowe-Rowe 1978b; Stuart 1981). Although abundant in many water bodies, bivalves and snails are apparently rarely eaten by Cape clawless otters (Smithers 1971). Other items consumed include dragonfly larvae (*Anax imperator*), other insects (Coprinae, Cyclorhapha, Dytiscidae, Nepidae, Odonota, and Scarabaeidae), molluscs, reptiles, small birds, and very rarely mammals (*Crocidura* and *Otomys*) or seaweeds (Donnelly and Grobler 1976; Rowe-Rowe 1977a).

In freshwater habitats of southwestern Tanzania, 3 distinct groups occupied a 5-km stretch of river (Kingdon 1997). In marine habitats of coastal South Africa, minimum home ranges of 1 female and 1 male *A. capensis* were estimated at 14.4 (core area = 7.5 km) and 19.5 km (core area = 12.0 km) of coastline, respectively (Arden-Clarke 1986). Home ranges of males and females overlap (Arden-Clarke 1986; van der Zee 1982), and temporal instead of spatial avoidance may occur (van der Zee 1982). Nightly movements may reach 13 km (Tayler 1970), and males are believed to move longer distances than females (van der Zee 1982).

Density of *A. capensis* in marine habitats varies from 2 to 7 otters (adult and juveniles combined) per 10 km of coastline (Arden-Clarke 1986; van der Zee 1982; Verwoerd 1987). In ideal freshwater habitats, densities of *A. capensis* may reach 1 otter per 3–4 km of stream (Rowe-Rowe 1992). In Zimbabwe, densities of *A. capensis* were 1 otter per 8–10 km of stream: the low density of otters probably reflected the low abundance of river crabs (Butler and du Toit 1994).

Aonyx capensis may compete with the sympatric spotted-necked otter, *Lutra maculicollis*. However, *L. maculicollis* is more

dependent on permanent bodies of clear water and is better adapted for capturing fish, whereas *A. capensis* eats primarily crabs and frogs (Rowe-Rowe 1977a, 1977b, 1986; Somers and Purves 1996). Thus, segregation in diet and foraging ecology allows these 2 species to coexist (Rowe-Rowe 1977a, 1977b; Somers and Purves 1996).

Aonyx capensis is also sympatric with the water mongoose (*Atilax paludinosus*). Both species exhibit 58–66% overlap in their diet, but the water mongoose has a broader diet, is more terrestrial, and seldom ventures far from shore or into deep water (Rowe-Rowe 1977a). Cape clawless otters consume a wider range of crab sizes, a larger proportion of fish, and a smaller proportion of terrestrial prey compared with water mongooses (Purves et al. 1994; Rowe-Rowe 1977a; Rowe-Rowe and Somers 1998; Somers and Purves 1996). Thus, competition between water mongooses and Cape clawless otters is likely not a limiting factor restricting the distribution of either species (Purves et al. 1994).

Crocodiles (*Crocodilus niloticus*) and fish-eagles (*Haliaeetus vocifer*) may kill Cape clawless otters (Kingdon 1977; Kruuk and Goudswaard 1990; Lejeune and Frank 1990). However, most mortality is inflicted by humans (van der Zee 1982). Cape clawless otters can be captured with cage traps, poisoned baits attached to live crabs, or foothold traps baited with crabs (Turnbull-Kemp 1960a). Although *A. capensis* may be accidentally captured in fish nets, such incidents are rare (Smith 1993). Roadkills may cause occasional deaths of Cape clawless otters (Verwoerd 1987). Longevity in captivity is >13 years.

Endoparasites include trematodes *Baschkirovitrema incrasatum*, *Clinostomum pyriforme*, and *Prudhoella rhodesiensis* and the nematode *Cloeoascaris spinicollis* (Round 1968). No ectoparasites are known.

BEHAVIOR. In freshwater habitats, Cape clawless otters are primarily solitary but on occasion may travel as family groups of 2 adults and 2 to 3 young (Rowe-Rowe 1978a). In coastal populations of South Africa, most observations (78%, $n = 124$) were of single otters, whereas groups of 2, 3, and 4 comprised 12%, 9%, and 1% of observations, respectively (van der Zee 1982). On occasion, groups of males may forage together in a clan-type organization (Arden-Clarke 1986).

The Cape clawless otter is mainly crepuscular (Rowe-Rowe 1978a, 1978b; Verwoerd 1987). During the day, *Aonyx capensis* shelters in underground burrows, under rocks, under roots of trees, or in dense vegetation on islands (Arden-Clarke 1986; Rowe-Rowe 1978a, 1978b). In sandy soil, Cape clawless otters may dig their own burrows that may reach 3 m in depth. Some burrows have several entrances either above or below water, and tunnel length varies from 1.9 to 2.9 m (Rowe-Rowe 1978a, 1992). About 50% of dens are dug by *A. capensis*, whereas the other 50% are depressions in the ground (Rowe-Rowe 1992). The opening of excavated burrows is typically elliptical, and width and height of 8 burrows (mean \pm SD) was 361 \pm 85 mm and 246 \pm 32 mm, respectively (Rowe-Rowe 1992). Dens may have a number of saucer-shaped depressions 30–40 cm in diameter and 2–3 cm deep, usually located under thick brush and interconnected by trails and tunnels (Verwoerd 1987). All burrows contain a nest of grass or other vegetation (Rowe-Rowe 1992).

Dens of Cape clawless otter from the coast of South Africa were typically near an abundant food supply, near bushy areas, near (<15 m) fresh water, and never located >50 m from shore (van der Zee 1982; van Niekerk et al. 1998). Density was 2.1 dens/km of coastline (Arden-Clarke 1986). In addition, each den location had several rolling places, where Cape clawless otters dried their fur, as well as numerous sprinting sites. Average use of all den sites ($n = 65$) from the Tsitsikama Coastal National Park was 32%, and each site was visited on average every 3 days (van der Zee 1982). Distance between den sites averaged 1.0 km, but varied from 0.3 to 2.4 km (van der Zee 1982). Dens may be used by numerous Cape clawless otters (Arden-Clarke 1986).

Cape clawless otters have an elaborate vocal repertoire that includes 4 main vocalizations: 2 whistles (1 low-pitched and 1 high-pitched), a grunt, and a variable “Hah!” to express anxiety (Davis 1978; Rowe-Rowe 1978a). In addition, growls and snarls may be emitted as threats, and humming may be used as a begging call (Maxwell 1963). In captivity, a wailing “wow-wow-wow” or “ow-ow-ow” is an expression of appreciation or displeasure if accompanied with snarls. Other sounds may include squeals, moaning, mewling,

and snuffing noises (Maxwell 1963). The basic contact call of juveniles is a high-pitched “whee” or squeaky “whee-whee” (Maxwell 1960).

After hunting, Cape clawless otters emerge from the water, roll on grass or sand, usually defecate, then spend time, sometimes a few hours, lying in or near cover, resting or sleeping before re-entering the water or moving somewhere else. *A. capensis* dries and grooms its fur by rolling and rubbing against inanimate objects. Rolling occurs mostly in grass but may also occur on sandbars, earth ledges, and flat rocks. Scent-marking may occur during rolling (Rowe-Rowe 1978b, 1992). After rubbing and rolling, otters often bask in the sun (Turnbull-Kemp 1960a). Latrines are found near rolling places (Rowe-Rowe 1978a), and the most frequently used spraint sites occur near dens (Rowe-Rowe 1992). The mean distance (m, $\pm SD$) of spraints to water is 4.2 ± 3.2 ($n = 135$, range 1–15). Most feces (85%) were 1–7 m from water, and the 15% that were 10–15 m from water were between a river and an oxbow or on large islands (Rowe-Rowe 1992). In coastal areas, spraints occur mostly on rocks and boulders and <50 m from a freshwater source (van Niekerk et al. 1998). Spraint sites are apparently used more intensively in the spring, possibly linked to the breeding season (Rowe-Rowe 1992). When defecating, *A. capensis* often straddles its back legs and expels both urine and feces backwards (Eyre 1963; Tayler 1970). Scats are sticky enough to adhere to vertical structures (Eyre 1963).

Cape clawless otters are awkward on land and either walk slowly or employ a seal-like trot (Rowe-Rowe 1985). Order in which feet are placed on ground is right hindfoot, left front foot, left hindfoot, and right front foot (van der Zee 1982). Tail can either be carried off the ground with tip curving upward (Eyre 1963) or dragged on the ground, leaving a distinct trail (Tayler 1970). Tail is also used as a tripod when sitting up (Tayler 1970). On land, *A. capensis* carries objects or prey by holding them against the chest with 1 front paw while hobbling on 3 legs (Rowe-Rowe 1985). When transporting cubs, females may hold offspring using both front feet, and then hobble on their back legs. Travel on land is minimal, and *A. capensis* uses regular trails representing the shortest distance between water bodies (Rowe-Rowe 1978b, 1985). Occasionally, overland travel may reach up to 7 km (M. J. Somers, in litt.).

When swimming, *A. capensis* uses its hind legs for propulsion and its tail as a rudder for direction (Rowe-Rowe 1978b, 1985). Cape clawless otters also use side thrusts from their strong tail to aid swimming (Carter 1956). Locomotion in water may be a series of long underwater dives or surface swimming with the head exposed above water (Rowe-Rowe 1978a, 1978b, 1985).

When hunting, swimming animals dive straight down or at a slight angle, raising the body out of the water at first, then curving sharply and going directly to the bottom. Cape clawless otters may swim on the surface, dive underwater, and emerge still swimming in the same direction (Somers 2000). When hunting underwater, *A. capensis* emerges from 1 to 10 m from their diving point. Hunting dives last 17–21 s on average, but vary from 1 to 48 s (Rowe-Rowe 1977b; Somers 2000; Verwoerd 1987). Dives in deep water last longer than dives in shallower water (Verwoerd 1987). One adult observed diving 37 consecutive times was successful in obtaining prey during 23 dives (Rowe-Rowe 1977b). Hunting bouts last between 5 and 181 min (Rowe-Rowe 1977b; Somers 2000; Verwoerd 1987). Cape clawless otters eat small prey while swimming and hold the prey with the forefeet. Large prey are taken to shore for consumption (Rowe-Rowe 1977b).

In coastal waters, Cape clawless otters moved along the shoreline while hunting. Average foraging speed was 21.4 m/min ($n = 5$, range 8.3–34.1 m/min), and *A. capensis* were never observed >40 m from shoreline (Somers 2000). In coastal waters of the Cape province, *A. capensis* preferred hunting in water <1.5 m deep (Somers 2000).

When hunting in shallow water, Cape clawless otters immerse their heads underwater and scan for prey while constantly feeling under rocks with their forefeet (Rowe-Rowe 1977b, 1977c; Somers 2000; Verwoerd 1987). Once prey is sensed, Cape clawless otters move rapidly and prey is captured following a direct chase. Most prey are captured by the forefeet then bitten (Rowe-Rowe 1977b).

Crabs may be eaten while the Cape clawless otter maintains an upright position in the water. When consuming large crabs, Cape clawless otters usually consume the chelae and limbs first and tilt

their heads back while chewing. Pieces that fall out of the mouth are caught against the chest with the forefeet (Rowe-Rowe 1977b).

Freshwater mussels (*Aspatharia wahlbergi*) with shells that are too hard for otters to crush with their jaws may be opened by smashing on nearby rocks (Donnelly and Grobler 1976). However, Cape clawless otters were not observed to perform this behavior, and evidence for this behavior was based on tracks (Donnelly and Grobler 1976). Most likely, tracks of *A. capensis* were confused with those of *Atilax paludinosus*, a species that frequently uses anvils for opening mussels (Baker 1989; Rowe-Rowe 1978b).

Fish are captured in proportion to their swimming abilities, and smaller fish are captured more easily than larger ones (Rowe-Rowe 1977c). Fish are more easily captured during winter, when the cold temperature reduces their activity, and in clear instead of murky water (Rowe-Rowe 1977c). When a fish is spotted, *A. capensis* immediately gives chase, surfacing only briefly to breathe. Dives for fish last 18 s and range from 6 to 49 s ($n = 389$ —Rowe-Rowe 1977b). Fish are grabbed with the forefeet or bitten while swimming. Once successful, the Cape clawless otter immediately bites the head. Fish are consumed in water, but only small (<80 mm) fish are consumed while *A. capensis* maintains an upright position. Larger fish are taken to shallow water or to shore (Somers 2000). Most species of fish, as well as amphibians, are eaten head first (Rowe-Rowe 1977b).

Prey are consumed as soon as they are captured. Captive Cape clawless otters may store food in their sleeping box and later take their prey to water for consumption. When transporting prey in water, Cape clawless otters hold prey by the forefeet or occasionally in the mouth (Rowe-Rowe 1977b). In captivity, 1 Cape clawless otter grabbed most dead fish with the right forefoot (50/80 trials) or both forefeet (30/80 trials—Rowe-Rowe 1977b). This same individual placed food into its mouth equally often with the right forefoot or both forefeet (Rowe-Rowe 1977b).

In captivity, *A. capensis* captured birds using its forefeet and subsequently killed the prey by biting the head. Birds offered in captivity were almost entirely eaten, including feathers. In captivity, eggs were left untouched by captive *A. capensis*, and the sight of terrestrial prey such as rats did not elicit predatory behavior (Rowe-Rowe 1977b).

Hunting efficiency of Cape clawless otters foraging for crabs and frogs is not affected by water temperature, stony substrate, water clarity, or darkness (Rowe-Rowe 1977c). However, fish-catching efficiency is affected by water temperature and clarity, with colder and clearer water facilitating prey capture (Rowe-Rowe 1977c). Cape clawless otters do not hunt in deep water and are therefore restricted by steep coastlines (Verwoerd 1987).

After eating, the Cape clawless otter cleans its face and feet. On dry land, food may be dunked in water before being eaten. After feeding, a captive female in Botswana washed her hands, dunked her head in water, then swam for a few minutes before returning to the food dish (Smithers 1971).

Play is common in young animals and involves play-fighting, romping, sliding, and manipulation of inanimate objects or dead prey (Maxwell 1960; Rowe-Rowe 1978a). Play may also involve dropping a pebble or small rock in the water and retrieving it before it reaches the bottom (Harris 1968) or diving with a floating object, releasing it underwater, and watching it float to the surface (Smithers 1971).

The Cape clawless otter may use its tail to scoop objects within reach of its forefeet (Maxwell 1960) or for defense (Tayler 1970). Fighting occurs rarely (Tayler 1970), but Cape clawless otters are fierce when cornered. When attacked on land, Cape clawless otters head for water (Tayler 1970). When brought to bay, Cape clawless otters can drag large dogs underwater and drown them (Harris 1968). When pursued by marine predators, *A. capensis* will head for land (M. J. Somers, in litt.).

When captured at an early age, Cape clawless otters can be tamed easily (Eyre 1963; Shortridge 1934). However, some Cape clawless otters remain unpredictable as pets and may bite without any apparent reason (Maxwell 1963). Captive *A. capensis* show no inclination for digging (Smithers 1971).

CONSERVATION STATUS. *Aonyx capensis* is not endangered in South Africa (Rowe-Rowe 1978a), but it is rare throughout most of its range because of its specialized niche. Throughout its distribution, protected areas have been established and are be-

lieved to sustain viable populations of *A. capensis* (Rowe-Rowe 1990b).

Cape clawless otters are threatened by direct killing for their pelts or because they are seen as pests or as competitors for fish, especially introduced rainbow trout (Butler 1994; Rowe-Rowe 1986). However, rainbow trout constitute only 1% of the diet of Cape clawless otters (Butler 1994). In addition, crabs eaten by *A. capensis* are much larger (median carapace size 20–25 mm versus 10–15 mm for trout) than those consumed by trout in similar habitats (Butler and Marshall 1996). Thus, predation upon, or competition with, rainbow trout for crabs is not a significant factor affecting trout populations (Butler and Marshall 1996).

The most important factor threatening Cape clawless otters is increasing human populations and associated habitat changes (Butler 1994; Rowe-Rowe 1986, 1990b, 1995; Rowe-Rowe et al. 1995). Changes to the water system due to agricultural practices may affect Cape clawless otters indirectly by affecting the abundance of their prey (Rowe-Rowe 1986). The major limiting factor for *A. capensis* populations is the availability of clean, unpolluted water (Rowe-Rowe 1985). In polluted waters, prey such as crabs, fish, and frogs become so rare that Cape clawless otters cannot persist (Rowe-Rowe 1985). In coastal areas, the availability of freshwater is critical to the subsistence of *A. capensis* populations (van Niekerk et al. 1998).

GENETICS. *Aonyx capensis* has $2n = 38$ chromosomes (van Zyll de Jong 1987).

REMARKS. Other vernacular names include African clawless otter, loutre à joues blanches (French), Weisswangen-Otter (German), groototter (Afrikaans), le Nyibi (Tswana), and umThini (Zulu).

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