

Hystrix africae australis. By Erika L. Barthelmess

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***Hystrix* Linnaeus, 1758**

Hystrix Linnaeus, 1758:56. Type species *Hystrix cristata* Linnaeus, 1758, by Linnaean tautonomy (International Commission on Zoological Nomenclature 1922).

Acanthion F. Cuvier, 1823:425. Type species *Acanthion javanicum* F. Cuvier, 1823, by original designation.

Oedocephalus Gray, 1866:308. Type species *Oedocephalus cuvieri* Gray, 1866, by original designation.

Thecurus Lyon, 1907:582. Type species *Thecurus sumatrae* Lyon, 1907, by original designation.

CONTEXT AND CONTENT. Order Rodentia, suborder Hystricognathi (Tullberg 1899), family Hystricidae (Fischer 1817). Two subfamilies, Hystricinae and Atherurinae, were proposed by Lyon (1907) and are accepted by some authors (Skinner and Smithers 1990; Smithers 1983) but rejected by others (Ellerman 1940; van Weers 1978, 1979; Woods and Kilpatrick 2005). Three subgenera (*Acanthion* Cuvier, 1823; *Hystrix* Linnaeus, 1758; and *Thecurus* Lyon, 1907) include 8 living species: *H. africae australis*, *H. brachyura*, *H. crassispinis*, *H. cristata*, *H. indica*, *H. javanica*, *H. pumila*, and *H. sumatrae* (Corbet 1978; Corbet and Hill 1992; Corbet and Jones 1965; van Weers 1978, 1979, 1983). Subgenus *Hystrix* was reviewed by Corbet and Jones (1965). The following key to the genus is modified from van Weers (1983).

1. Length of rattle quills >35 mm; many quills with >1 blackish ring (subgenus *Hystrix*) 2
 - Length of rattle quills <35 mm; quills with ≤1 blackish portion (subgenera *Acanthion*, *Thecurus*) 3
2. Crest predominantly brown *Hystrix indica*
 - Crest predominantly white 4
3. Crest present, but not conspicuous; longest hair ≥45 mm with white tip ≥5 mm *Hystrix brachyura*
 - No crest; hairs on head ca. equal in length and without white tip 5
4. Length of rattle quills <60 and usually <50 mm with diameter 2–5 mm; midline along rump black or mottled *Hystrix cristata*
 - Length of rattle quills long, >50 and usually >60 mm with diameter 5–7 mm; midline along rump white *Hystrix africae australis*
5. Length of largest rattle quill 15–20 mm with diameter 3.5–6.1 mm *Hystrix javanica*
 - Length of largest rattle quill 8–16 mm with diameter 6.3–8.3 mm (subgenus *Thecurus*) 6
6. Length of largest rattle quill 12–16 mm *Hystrix crassispinis*
 - Length of largest rattle quill 8–11 mm 7
7. Some quills with blackish terminal region and some with white tips; length of white tips 10–30 mm *Hystrix sumatrae*
 - Quills nearly completely black with only a small white base *Hystrix pumila*

***Hystrix africae australis* Peters, 1852**

Cape Porcupine

Hystrix africae australis Peters, 1852:170. Type locality “Querimba” and “Tette.” Restricted to Querimba coast (ca. 10°30' to 12°S, 40°30'E, sea level), northern Mozambique, “Of these two widely separated localities, the first, Querimba coast, i.e., that part of the coast of Mozambique extending for about 100 miles south of the mouth of the Rovuma River, may be taken as the type-locality” (Moreau et al. 1946:430).

Hystrix capensis Grill, 1860:19. Type locality “Saltriver near Knysna.”

Hystrix stegmanni Müller, 1910a:186. Type locality “Kissenji northeast of Lake Kivu.”

Hystrix africae australis prittwitzii Müller, 1910b:311. Type locality “Tabora.”

Hystrix africae australis zuluensis Roberts, 1936:240. Type locality “Mkusi River (and specimens from Umfolosi River).”

CONTEXT AND CONTENT. Content as above. Although up to 3 subspecies (*H. africae australis africae australis* Peters, 1852; *H. africae australis prittwitzii* Müller, 1910; and *H. africae australis zuluensis* Roberts, 1936) have been recognized (Ellerman 1940; Ellerman et al. 1953; Roberts 1951), and northern and southern groups have been recognized (Corbet and Jones 1965), no subspecies are currently recognized (de Graaff 1981; Meester et al. 1986; Misonne 1971; Skinner and Smithers 1990).

DIAGNOSIS. *Hystrix africae australis* (Fig. 1) is the largest rodent in Africa and is sympatric with only a single congener, *H. cristata*, in Tanzania along northeastern edge of range. *H. africae australis* can be distinguished from *H. cristata* in the field by white rather than black or mottled short spines at midline of rump and by white underside of tail (van Weers 1979, 1983). Rattle quills in *H. africae australis* are stout, 5–7 mm in diameter, and > 50 mm (usually > 60 mm) in length as compared to rattle quills 2–5 mm diameter and usually < 50 mm long in *H. cristata* (van Weers 1983). *H. africae australis* also differs from *H. cristata* in some aspects of skull morphology (Fig. 2). Ratio of length of nasal relative to frontal bones is larger in *H. africae australis* at 49–68% as compared with 23–38% in *H. cristata* (Corbet and Jones 1965; Ellerman et al. 1953). Length of nasal bone in *H. africae australis* is 51–58% length of occipitonasal, and premaxillae are narrow, usually < 23% width of nasal bones (Ellerman et al. 1953; van Weers 1979).

GENERAL CHARACTERS. Adult *H. africae australis* range from 10.0 to 24.1 kg and are not sexually dimorphic (Smith-



FIG. 1. Photograph of a 9-month-old male Cape porcupine (*Hystrix africae australis*) at Peoria's Glen Oak Zoo, Peoria, Illinois. Used with permission of the photographer, D. Petefish.

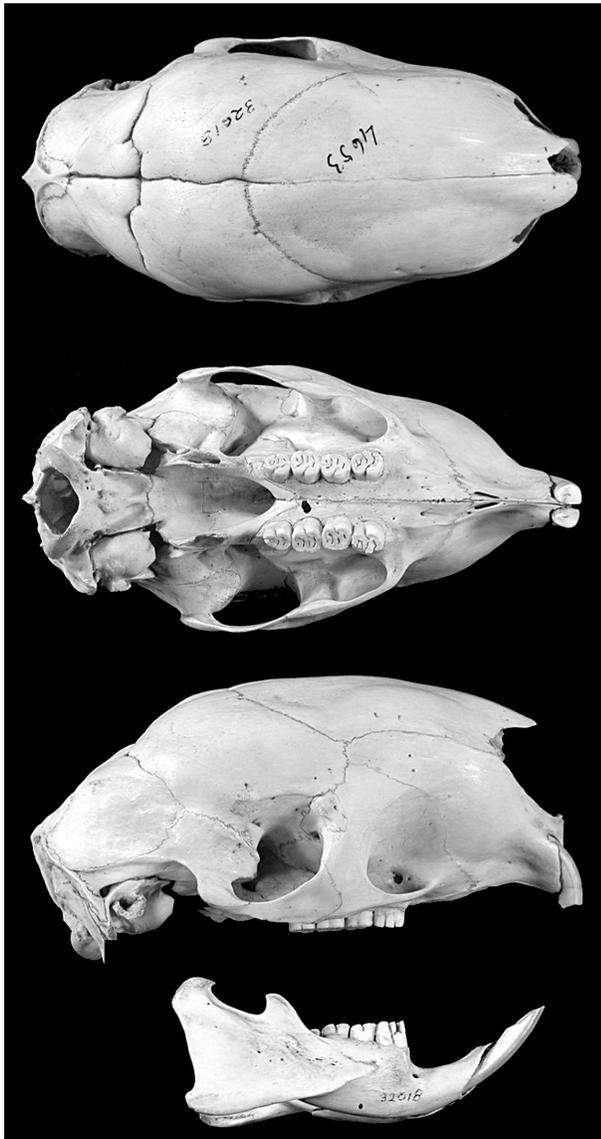


FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of an adult *Hystrix africae australis* (sex unknown; CMNMA [Canadian Museum of Nature mammal collection] 32018) from Cape Province, South Africa. Greatest length of skull is 18.18 cm.

ers 1983; van Aarde 1987a). Average body mass of 14 captive animals was 15.4 kg (Corbet 1991; Corbet and van Aarde 1996). A sample of 8 free-ranging adult males from Zimbabwe ranged in mass from 14.5 to 19.1 kg with a mean of 16.9 kg, and 9 females from the same location ranged from 13.6 to 24.1 kg with a mean of 18.4 kg (Smithers 1983). Mean body mass was somewhat lower for animals from Orange Free State in South Africa, with free-ranging males averaging 12.3 kg ($n = 69$) and females averaging 13.0 kg ($n = 56$ —Smithers 1983). Ranges (in mm) for external measurements are: total length, 630–805; length of tail, 105–130; length of hind foot, 89–114; length of ear, 39–48 (de Graaff 1981).

Cape porcupines are stout and heavily built with short, well-bristled bodies, relatively short legs, and short, well-hidden tails (de Graaff 1981; Smithers 1983). Head is rounded with a grayish brown bristled face and stout, mobile vibrissae (Smithers 1983). Eyes are small and situated far back on head; ears are inconspicuous, but humanlike in shape. Body is covered with bristly hairs, long spines (up to 50 cm), stout defense quills (up to 30 cm), and flattened bristly hairs (Skinner and Smithers 1990). Tail bears a cluster of highly modified, hollow rattle quills (Ellerman 1940).

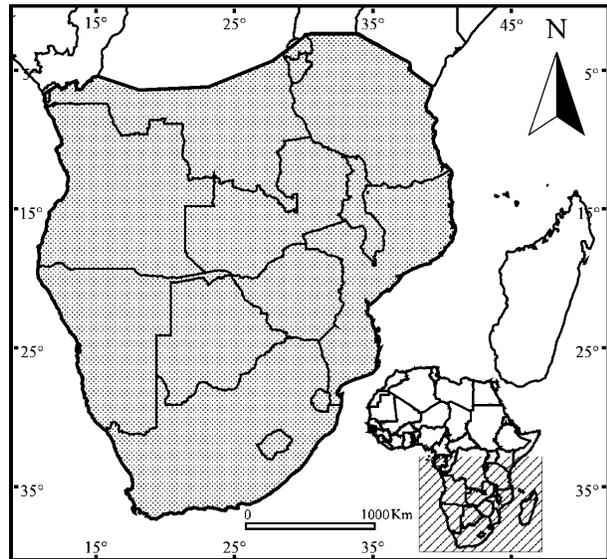


FIG. 3. Geographic distribution of *Hystrix africae australis*. No subspecies are recognized. Map redrawn with modifications from Kingdon (1984), Smithers (1983), and de Graaff (1981).

DISTRIBUTION. Cape porcupines occur in southern Africa (Fig. 3) and have been recorded from sea level to elevations of 2,000 m (de Graaff 1981; Kingdon 1984; Smithers 1983).

FOSSIL RECORD. The genus *Hystrix* is present in the fossil record of Africa from the late Miocene (Winkler 2003). In South Africa, putative fossils of *H. africae australis* occur in Pliocene and Pleistocene localities including Makapansgat (Members 3, 4, and 5), Sterkfontein (Type Site and dumps 1, 2, 8, 10, and 13), Swartkrans (Members 1 and 2), and Kromdraai A (Maguire 1978). Fossils are known from Wonderwerk Cave in the Kuruman district, South Africa (de Graaff 1981).

FORM AND FUNCTION. Several quill types exist in Cape porcupines: spines, true quills, tactile bristles, transitional quills, and rattle quills (Mohr 1964, 1965; van Weers 1983). Spines are sharp, stiff, flattened, and grooved bristle hairs that cover most of body. True quills, the primary means of defense, are thickest of modified hairs and carry very sharp points. Relatively inflexible, true quills are circular in cross section; diameter is greatest in middle of length of quill and tapers toward ends (Findlay 1977; van Weers 1983). Tactile bristles are very flexible. Like true quills, tactile bristles are circular in cross section, but diameter is greatest near base of hair and is less than typical diameter of a quill. Transitional quills are intermediate to true quills and tactile bristles in length, diameter, and flexibility. Rattle quills also are circular in cross section, but are capsule-shaped, hollow, and open at end. Rattle quills attach to tail by a thin stalk at base of quill (Mohr 1965; van Weers 1983).

In Cape porcupines, an erectile crest of coarse hairs up to 50 cm in length occurs posteriorly from top of head to top of shoulders. Hairs at front of crest are black at base, tending toward white at tips. Some Cape porcupines have a triangular patch of white bristles (flattened hair) on either side of neck. Spines and quills are distributed across the posterior two-thirds of flanks and dorsum but not on the ventrum (Smithers 1983) and are implanted in transverse grooves spaced ca. 3 cm apart. Each groove holds 5–8 spines or quills. Quills along back are banded black and white; black bands are broader with white tips (de Graaff 1981). Longer quills have multiple repeating bands of black and white, with up to 6 white sections on a quill (Findlay 1977). Rump is covered with short, flat, white bristles on dorsal and ventral sides. Tail carries a “rattle” of hollow rattle quills, with hollow portion of quills >60 mm in length. Coarse, flattened, black hairs, tending toward brown in older animals, cover entire body except for lips, nose, rounded ears, and soles of feet (Smithers 1983).

Skull of *H. africae australis* has an arched, domed shape, in part due to a high degree of pneumatization in well-developed nasals. Sagittal and occipital crests are prominent and zygomatic arch

is strong, but simple. Zygomatic plate is poorly differentiated. Compared with other hystricomorphic rodents, infraorbital foramen is small, but allows for passage of masseter medialis muscle. Infraorbital constriction is absent. Straight, wide palate ends behind molars. Palatine foramina are small and lie far forward on skull. Auditory bullae and paroccipital processes are small. On dentary bone, coronoid is low and condyle is oblong and rounded (de Graaff 1981). Mandible is loosely hinged, allowing for forward, reverse, and side-to-side mastication (Smithers 1983).

Dental formula is i 1/1, c 0/0, p 1/1, m 3/3, total 20 (Smithers 1983) and teeth are well adapted for breakdown of cell walls of plants (van Jaarsveld and Knight-Eloff 1984). Upper and lower incisors have a yellowish enamel layer on front (Smithers 1983). Teeth are hypsodont. Upper molariform teeth carry 3 outer folds on buccal side and 1 inner fold on lingual side; pattern is reversed for lower molariform teeth. Upper and lower premolars are enlarged and replaced later in life (Roberts 1951). Molariform teeth are not continuously growing (de Graaff 1981). Pattern of tooth eruption can be used to age Cape porcupines. Incisors are fully erupted at birth. Deciduous premolars begin to erupt at 14 days of age and are followed by eruption of 1st maxillary molars at 2–2.5 months. Second maxillary molars are visible above gumline at 5–6 months and 3rd maxillary molars erupt between 8 and 11 months. Deciduous tooth eruption is complete by 12 months of age, with eruption of permanent premolars complete by 23–25 months. Occlusal surface of premolars becomes slightly worn by 24–30 months (van Aarde 1985a).

Feet of *H. africae australis* have clawed digits and naked soles. Forefeet have a rudimentary pollex and hind feet have a hallux. Clavicles are present, but reduced. Females have 2 pairs of laterally placed, pendulous, slate-black mammae (Roberts 1951; van Aarde 1985b). Mammary glands have a triangular shape with 2 teats placed centrally on each gland. No variation in teat number was recorded in 130 females (van Aarde 1985b). Males lack a true scrotum and S-shaped penis is directed posteriorly (Mohr 1965; van Aarde and Skinner 1986a; Weir 1974). Surface of glans penis is covered with spicules. A sacculus urethralis is pronounced only when penis is fully erect. Vesicular, prostate, and Cowper's glands are well developed in adult males (van Aarde and Skinner 1986a). Mean mass of paired testes for 17 adult males was 6.6 g (van Aarde and Skinner 1986a). Mean mass of paired ovaries was ca. 0.71 g and did not differ among pregnant, lactating, or reproductively inactive females (van Aarde and Skinner 1986b).

Digestive tract anatomy, based on 7 animals, indicates a fully glandular, unilocular stomach that is relatively large for an herbivorous rodent (mean maximum volume, 1,019 cm³). Thickened stomach walls help mix digesta. Small intestine is long (mean length, 670 cm) and followed by an expanded caecum (length, 62 cm—van Jaarsveld 1983) that includes ca. 31 haustra, 30 semilunar folds, and 3 taeniae (van Jaarsveld and Knight-Eloff 1984). Lengths (in cm) of ascending, transverse, and descending sections of colon are 44, 54, and 64, respectively (van Jaarsveld 1983). *H. africae australis* is a hindgut fermenter. A pH of 2.0 in stomach makes gastric fermentation unlikely. Low stomach pH and lengthy small intestine may enhance protein breakdown (van Jaarsveld and Knight-Eloff 1984). Muscular and highly infolded caecum is responsible for movement of digesta and selective retention of indigestible carbohydrates. Fermentation rates (in $\mu\text{mol/g}$ of digestible matter per hour) in caecum and proximal colon are low, 91.1 and 75.2, respectively. Rates of methane production (in l/day) also are low in caecum (0.11) and proximal colon (0.01—van Jaarsveld and Knight-Eloff 1984). Last 40% of descending colon has an increased diameter that enhances water and electrolyte resorption and causes formation of characteristic droppings in the form of a series of stacked pellets (van Jaarsveld and Knight-Eloff 1984). Gut transit time in captive Cape porcupines averaged 23 h (van Jaarsveld 1983).

Cape porcupines acclimated to an ambient temperature (T_a) of 25°C and a 12L:12D photoperiod have a thermoneutral zone between 24 and 27°C with a mean resting metabolic rate (measured as oxygen consumption) of 0.209 ml g⁻¹ h⁻¹. Below lower critical temperature of thermoneutral zone, metabolic rate increases 0.017 ml g⁻¹ h⁻¹ for each 1° drop in temperature and above upper critical temperature metabolic rate increases 0.0009 ml g⁻¹ h⁻¹ for each 1° increase in ambient temperature (Haim et al. 1990a). Cape porcupines can regulate body temperature well at 30°C. At higher temperatures, *H. africae australis* becomes hyperthermic and uses

evaporative cooling; these animals are wet when removed from metabolic chambers. At $T_a = 39^\circ\text{C}$, all Cape porcupines urinated in the metabolic chamber.

Hystrix africae australis lives in habitats with broad daily and seasonal temperature changes. Metabolic rates of Cape porcupines allow them to be active during cold ($T_a = 0^\circ\text{C}$) and very hot ($T_a > 37^\circ\text{C}$) weather (Haim et al. 1990b). Cape porcupines acclimated to South African winter conditions ($13^\circ\text{C} \leq T_a \leq 28^\circ\text{C}$) have average resting metabolic rates of 0.294 ml g⁻¹ h⁻¹ and experience a thermoneutral zone between 24 and 28°C. Summer-acclimated animals ($20^\circ\text{C} \leq T_a \leq 36^\circ\text{C}$) have average resting metabolic rates of 0.190 ml g⁻¹ h⁻¹ and experience hyperthermia at $T_a \geq 36^\circ\text{C}$. Winter-acclimated Cape porcupines eat and drink more than summer-acclimated individuals (Haim et al. 1990b). However, digestion rate is significantly lower in winter-acclimated Cape porcupines compared with summer-acclimated ones, indicating that Cape porcupines use their digestive tract for heat production (Haim et al. 1990b). Body thermal conductivity also changes depending on temperature acclimation and is less in winter-acclimated than in summer-acclimated Cape porcupines. Mean thermal conductance ($\pm SD$) for 6 porcupines measured at 13°C was 0.016 ± 0.001 ml O₂ g⁻¹ h⁻¹ °C⁻¹ (Haim et al. 1990a).

Cape porcupines are well adapted to their semifossorial lifestyle. *H. africae australis* produces alkaline urine high in bicarbonates to shunt CO₂ out of the body in the hypoxic and hyperapnic conditions of their subterranean, shared burrows (Haim et al. 1992a). Winter-acclimated Cape porcupines produce a higher volume of urine than summer-acclimated Cape porcupines, which is associated with increased water intake and higher resting metabolic rates of winter-acclimated individuals (Haim et al. 1992a). Higher water intake by winter-acclimated Cape porcupines helps release calcium bicarbonate through the urine (Haim et al. 1992a).

ONTOGENY AND REPRODUCTION. Sexual maturity is reached during the 2nd year of life for females (van Aarde 1984, 1985b; van Aarde and Skinner 1986a) and between 8 and 18 months for males (van Aarde and Skinner 1986a). Nulliparous females enter their 1st estrous cycle between 273 and 552 days ($\bar{X} = 413$ days, $n = 5$) and at a body mass of 11 kg. Females typically experience 3–7 estrous cycles before conceiving. Average age at 1st conception is 612 days at an average body mass of 12.3 kg (van Aarde 1985b).

Males and females are reproductively active throughout the year (Skinner et al. 1984; van Aarde 1987b). Paired testes weight does not change seasonally and spermatogenesis occurs year-round, although weight of vesicular and prostate glands increases between May and July and then declines (van Aarde and Skinner 1986a). Females are polyestrous, with a cycle length of 17–42 days ($\bar{X} = 31.2$ days based on 43 cycles measured in 12 females) with 60.5% of cycles lasting between 28 and 36 days, regardless of whether females are nulliparous (van Aarde 1985b, 1987b). Although length and number of cycles is independent of day length (van Aarde 1985b), 78% of captive litters are born between August and March (Skinner et al. 1984; van Aarde 1987b), which corresponds to periods of summer rain in Mpumalanga Province (van Aarde 1985b).

Estrus begins with opening of a vaginal closure membrane and coincides with a surge in 17 β -estradiol (van Aarde 1985b, 1985c). Closure membrane remains open for an average of 8.3 days ($n = 34$ —van Aarde 1985b). Copulation usually is preceded by a female approaching a male (although males sometimes approach females—Morris and van Aarde 1985) and females remain receptive throughout the estrous cycle. In males, gonadotropin-releasing hormone from the hypothalamus stimulates production of testosterone and luteinizing hormone (van Wyk and van Aarde 1991). Copulation occurs between 2 and 8 days after onset of estrus (van Aarde 1985b) and 1 copulation lasted 154 s (Morris and van Aarde 1985). Secretions from seminal vesicles mix with secretions from prostate gland to form a gellike copulatory plug (van Aarde and Skinner 1986a), which is expelled from female ca. 48 h after mating (Morris and van Aarde 1985).

Mean gestation length ($n = 4$) is 94 days (Skinner et al. 1984; van Aarde 1985b). Circulating levels of plasma progesterone remain low until 25–30 days postcopulation, when they increase sharply, peaking at 42–60 days postcopulation, and then decrease gradually over the last 30 days of pregnancy (van Aarde 1985c; van Aarde and Potgieter 1986; van Wyk et al. 1994, 1995). Female *H. africae australis* produce accessory corpora lutea and other lu-

teal bodies to maintain levels of plasma progesterone (van Aarde and Skinner 1986b). Female Cape porcupines produce progesterone-binding plasma proteins that occur in a biphasic pattern during pregnancy (Louw et al. 1992; van Aarde and Potgieter 1986; van Wyk 1991; Weir 1974). These proteins include progesterone-binding globulin and corticosteroid-binding globulin (Louw et al. 1992; van Aarde et al. 1992). First peak in production of progesterone-binding proteins is 50–56 days postcopulation and 2nd is 73–77 days postcopulation (van Aarde and Potgieter 1986). Progesterone-binding plasma proteins regulate circulating levels of plasma progesterone and thus maintain conditions for gestation (Louw et al. 1992). Mammary gland development tracks circulating progesterone levels; glands begin to develop between 30 and 60 days post-conception and milk production starts 42–60 days after copulation (van Aarde 1985b).

Females average ca. 1 litter per year with a mean litter interval of 385 days. Litter size ranges from 1 to 3, with 58.8% of litters being singletons, 32.1% twins, and the remainder triplets (van Aarde 1985b). Neonate mass ranges from 300 to 440 g ($\bar{X} = 351$ g, $n = 19$) with individual mass at birth equaling ca. 2.1% of mean adult female mass (Roth 1964; van Aarde 1985b). Male and female neonates do not differ in body mass (van Aarde 1985b) and sex ratio at parturition does not differ from 1:1 (van Aarde 1987a). Back quills are soft and rattle quills are closed and pointed at birth (Mohr 1964; Roth 1964).

Mean length of lactation in 9 females was 101 days (van Aarde 1985b). Postnatal growth rates do not differ between males and females and are nearly linear for the first 20 weeks of life, reaching an asymptotic point (and presumably full adult size) at ca. 52 weeks and an average mass of 11.7 kg (van Aarde 1987c). Among some captive Cape porcupines, growth rates accelerate when individuals begin to supplement their milk diet with vegetables (Roth 1964). Lactating females are anestrous and begin cycling 2–42 days after lactation ceases (van Aarde 1987b). Females then undergo 3–11 cycles, lasting between 90 and 210 days, before conceiving, during which time they cycle normally but do not become pregnant (van Aarde 1987b, 1995). Although the hormonal basis for these “sterile” cycles is unknown (van Aarde 1987b), the reduction in energy reserves during lactation leaves females without adequate energy for conception and implantation (Skinner et al. 1984). For 14 females that lost their litters before weaning, conception intervals were shorter, averaging 148 days, and had at most 1 sterile estrous cycle (van Aarde 1995).

Captive female *H. africaeaustralis* ($n = 3$) housed in isolation from males for 111–120 days did not exhibit estrus, but began to cycle normally within 5–12 days of being housed with males (van Aarde 1985b). Population density may influence whether females reproduce in their 1st year (van Aarde 1987b). Conception in sexually mature females is suppressed until after dispersal from natal group (van Aarde and van Wyk 1991). Young females may copulate (determined by observation or presence of copulatory plugs) before dispersing, but do not become pregnant. Pseudopregnancy and failure to cycle have been ruled out as explanations for failure to conceive because breeding and nonbreeding females have estrous cycles of similar lengths and cyclic changes in progesterone levels.

ECOLOGY. *Hystrix africaeaustralis* occurs in several habitats and has wide ecological tolerance (van Aarde 1987a). Cape porcupines range from very moist tropical forests to barren deserts, although they are not found in swampy areas (de Graaff 1981; Skinner et al. 1984; van Aarde 1985a). Primarily herbivores, their diet includes bark, bulbs, fruits, leaves, roots, shoots, stems, and tubers (Bragg 2003; de Graaff 1981; de Villiers 1992; de Villiers and van Aarde 1994; de Villiers et al. 1994; Thomson 1974). Osteophagy is not uncommon, particularly in areas where phosphorous is limited (Alexander 1956; Duthie and Skinner 1986; Roth 1964; van Jaarsveld 1983) and Cape porcupines may also occasionally eat carrion (Alexander 1956).

Cape porcupines inhabit extensive burrow systems during the day. *H. africaeaustralis* either digs burrows or occupies burrows of aardvarks (*Orycteropus afer*—de Graaff 1981). Cape porcupines will excavate old termite mounds (Yeaton 1988). *H. africaeaustralis* digs circular, conical holes in the soil surface when searching for insect larvae or seeds and creates sites for seedling establishment in the harsh, semiarid environment of the Karoo (Bragg et al. 2005; Dean and Milton 1991).

Foraging by *H. africaeaustralis* can damage crops. Consid-

ered pests by many farmers, Cape porcupines may raid melon, pumpkin, and mealie (corn) crops (Roberts 1951; van Aarde 1987b). Cape porcupines can uproot young trees and damage young plantations (Greaves and Aziz Khan 1978). However, root damage is negligible to all species except *Burkea africana* (de Villiers and van Aarde 1994). When feeding on woody trees, Cape porcupines remove bark from ground level to ca. 0.5 m up the trunk and feed on live tissue beneath bark. Several trees at a site in Zimbabwe were entirely ringbarked by Cape porcupines and died when 50% or more of bark was removed (Thomson 1974). Cape porcupines did not prefer all species of tree equally; their favorite was the bush mango (*Cordyla africana*). Feeding by Cape porcupines resulted in little recruitment in *C. africana* and death of trees in all age classes. Peak tree feeding occurred at height of dry season and trees were not used as food during rainy season (Thomson 1974; Yeaton 1988). Other preferred plants are *B. africana*, *Cassia*, *Casuarina*, *Dombeya rotundifolia*, *Eucalyptus*, *Pinus roxburghii*, and *Terminalia spricea* (Greaves and Aziz Khan 1978; Yeaton 1988). In Limpopo Province of South Africa, only 17% of trees were debarked at all, and no complete ringbarking was recorded (de Villiers 1992). Also in South Africa, Cape porcupines prefer nonnative syringa trees (*Melia azedarach*) to indigenous white stinkwood trees (*Celtis africana*—van Rooyen and du Toit 1993).

Tree-feeding in natural areas may control pattern of succession in some savanna ecosystems (Lawton and Jones 1995; Yeaton 1988). Maintenance of the *B. africana* savanna in northeastern South Africa was attributed in part to Cape porcupines. By scarifying trunks, *H. africaeaustralis* made trees more susceptible to fire and thus created a level of disturbance that, in combination with fire, impeded succession of savannah (Yeaton 1988). Preferential debarking of dominant plant species in *Burkea* savanna may enhance encroachment of *Acacia* patches into broadleaf woodland (de Villiers and van Aarde 1994). Cape porcupines are agents of disturbance in the Succulent Karoo, an international hotspot of biodiversity, where they disturb soil through diggings (up to 3,463 diggings/ha) and burrows (2.6 burrows/km—Bragg et al. 2005). Holes made by Cape porcupines allow soil water to infiltrate the soil crust and provide sites for recruitment of seedlings (Bragg et al. 2005).

In a series of cafeteria experiments conducted in Nieuwoudtville, in Northern Cape Province of South Africa, Cape porcupines consumed 41 of 51 geophyte species, 12 of which were endemic and 6 of which were endangered (Bragg 2003). Cape porcupines preferred larger to smaller corms and preferred energy-rich species, as predicted by optimal foraging theory (Bragg 2003). *H. africaeaustralis* tends to eat Hyacinthaceae bulbs with high water content in summer when water is scarce in this semiarid system (C. J. Bragg, pers. comm.).

Examination of demographic data collected during a population cull and again several years later revealed that in the absence of natural predation, age structure in populations of *H. africaeaustralis* is variable, changing between seasons and years, and population regulation is density-dependent (van Aarde 1987a). Juvenile survivorship is high regardless of density; 100% of newborns lived to be 2 months old. Survivorship for Cape porcupines 2–12 months old ranged from 0.836 in high-density populations to 1.0 in low-density populations. Age-specific fecundity (m_x) was highest for females > 24 months old, followed by females 12–24 months old, regardless of density. At high density, females in the 6- to 12-month age class did not reproduce, whereas at low density age-specific fecundity reached 0.56. Average age-specific fecundity was higher in the low-density population (average $m_x = 0.69$) than in the high-density population (average $m_x = 0.49$) and was associated with a higher net reproductive rate (R_0) in the low-density population ($R_0 = 0.78$) than in the high-density population ($R_0 = 0.22$), due primarily to the increase in reproduction by females in the 6- to 12-month age class. Age distribution was similar for male and female cohorts in low- and high-density populations (van Aarde 1987a). Cape porcupines live to ca. 10 years in the wild and up to 20 years in captivity (Ellerman 1940; van Aarde 1987a). Cape porcupines reproduce slowly as a result of small litter sizes and long gestation periods, but their longevity and care of young allow populations to perpetuate themselves (van Aarde 1987a). High-density populations on riverine plains in the Karoo supported 25 individuals/km² (van Aarde 1998). In a geophyte-rich region, Nieuwoudtville, Cape porcupine density reaches 8 individuals/km², which is high for a semiarid region, and population growth is limited by available den sites and territory size (Bragg et al. 2005). In many areas, numbers

are limited only by availability of food and den sites (Roberts 1951). In other areas, population density also is regulated by extrinsic factors, including predation. Leopards (*Panthera pardus*) and lions (*Panthera leo*) are primary predators of Cape porcupines (van Aarde 1998). When threatened, a Cape porcupine defends itself by running sideways or backward into its enemy, quills erect (Ellerman 1940). This behavior develops by 3–7 days of age (Roth 1964) and is an effective defense against natural predators; humans are probably responsible for most Cape porcupine deaths (Kingdon 1984; van Aarde 1998).

HUSBANDRY. *Hystrix africaeaustralis* has been successfully reared in captivity in zoological gardens (Crandall 1964; Mohr 1965) and research institutes (van Aarde 1985d). Cape porcupines can be trapped with drop-door-style live traps baited with apples, maize, or sweet potatoes, and placed close to burrow entrances (Corbet and van Aarde 1996). Unless tamed, individuals cannot be handled without immobilization, but are relatively docile and can be herded by means of a large wooden board kept between herder and animal. Cape porcupines can be herded into a crush box and immobilized for handling (van Aarde 1985d). Immobilization has been successfully accomplished using either of 2 combinations of drugs. A dose of 0.16 mg fentanyl hydrochloride (HCl)/kg body weight with 0.66 mg xylazine HCl/kg results in a mean time to recumbency of 5 min and a mean time to recovery of 136 min. Alternatively, 5.4 mg ketamine HCl/kg with 1.51 mg xylazine HCl/kg results in a mean time to recumbency of 4.7 min and a mean time to recovery of 147 min. Neither time to recumbency nor time to recovery was influenced by repeated immobilizations over periods of up to 15 months for either drug combination (van Aarde 1985d).

Cape porcupines have been successfully kept in South Africa for years in 18.5 m² semioutdoor enclosures (ca. one-third of each enclosure was roofed and two-thirds left open) surrounded by 1-m-high brick walls. Individuals were kept under natural photoperiod, temperature, and ventilation. Enclosures were cleaned and disinfected daily (van Aarde 1985d). Although Cape porcupines were typically housed in groups of 2–5 individuals/enclosure, those new to the colony were housed separately and only allowed to intermingle after a period of habituation. Unique identification of individuals can be accomplished by clipping different holes and notches into ear pinnae or by color-coded collars. Cape porcupines were provided with water ad libitum, occasional dry wood for gnawing, but no bedding or nest boxes. They were fed a mixture of fresh fruits and vegetables (ca. 1.0 kg/individual daily) intermittently supplemented with commercial feed pellets. Breeding occurred under these housing conditions (van Aarde 1985d).

BEHAVIOR. Cape porcupines are monogamous (Morris and van Aarde 1985); an adult male–female pair forms the basic social unit (Corbet 1991; Corbet and van Aarde 1996). Individuals use up to 6 different burrows and occupy them on an irregular basis. A single burrow may be occupied for anywhere between 1 and 151 days (Corbet 1991; Corbet and van Aarde 1996). Home ranges of male and female members of a mated pair overlap on average 75%. Although 89% of free-ranging Cape porcupines forage solitarily at night (van Aarde 1987a), space use by members of a mated pair overlaps in space and time: members of a pair forage near each other, spending <25% of their active periods >400 m apart and >50% of their time within 200 m of one another (Corbet 1991; Corbet and van Aarde 1996). Within the home range, a pair probably defends an exclusive territory (Corbet 1991; Corbet and van Aarde 1996). Males scent-mark more frequently than do females and more often in feeding than in nonfeeding areas and may play a greater role in maintaining territory boundaries (de Villiers et al. 1994). Captive *H. africaeaustralis* scent-mark their enclosures and aggressively defend them against conspecifics (Corbet 1991; Corbet and van Aarde 1996).

Hystrix africaeaustralis also lives singly or in extended family groups consisting of a male–female pair and their subadult and juvenile offspring (Corbet 1991; Corbet and van Aarde 1996; Morris and van Aarde 1985; van Aarde 1987a). Cape porcupines exhibit biparental care of young; adult males accompany offspring on foraging excursions and defend them against territory intruders (van Aarde 1987a). During the day, juveniles sleep with their parents in the burrow. Thermoregulatory benefits accrue with group huddling. When 2 porcupines were held together in a metabolic cham-

ber, they huddled together, and lower critical temperature of thermoneutral zone was lower compared with that of a single individual (Haim et al. 1992b).

Size of home range varies with food availability and differs between Cape porcupines that forage primarily on natural foods and those that forage on crops (Corbet 1991; Corbet and van Aarde 1996). Foragers on natural food have larger home ranges in winter (average 95% minimum convex polygon home range = 116 ha) than in summer (67 ha). Home-range size does not vary seasonally for Cape porcupines that forage on crops, and home ranges are significantly larger than for those that forage on natural food (average 95% minimum convex polygon home range = 203 ha). Home ranges of neighboring foragers on natural food overlap more often in winter than in summer (Corbet 1991; Corbet and van Aarde 1996). *H. africaeaustralis* often follows regular routes to feeding areas within home ranges (Roberts 1951).

GENETICS. Cape porcupines hybridize with crested porcupines (*Hystrix cristata*) in captivity (Mohr 1965), but not in their natural range of overlap in East Africa (Skinner and Smithers 1990). Natural variation in museum specimens showed no tendency toward clinal variation between *H. africaeaustralis* and *H. cristata*. Differences in rump color and morphology of rattle quills (and hence presumably sound production) may aid in species recognition and prevent hybridization under natural conditions (Corbet and Jones 1965).

REMARKS. *Hystrix* is Greek for porcupine and *africaeaustralis* identifies distribution in southern Africa (Smithers 1983). Cape porcupines are killed for meat and for their quills, which are considered a fashionable commodity; in the past, rattle quills were used as containers for alluvial gold dust (C. J. Bragg, pers. comm.; Roth 1964; Smithers 1983; van Aarde 1987b). Indigenous names for Cape porcupine include *incanda* (Xhosa), *ingungumbane* (Zulu), *inungu* (Ndebele), and *nungu* (Kiswahili—Kingdon 1984; Smithers 1983). The name in Afrikaans is *Kaapse ystervark* (Smithers 1983).

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