

*Procavia capensis*. By Nancy Olds and Jeheskel Shoshani

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***Procavia* Storr, 1780**

*Procavia* Storr, 1780:40. Type species *Cavia capensis* Pallas, by original designation.

*Hyrax* Hermann, 1783:115. Type species *Cavia capensis* Pallas, by original designation.

*Euhyrax* Gray, 1868:46. Type species *Hyrax habessinicus* Hemprich and Ehrenberg, by original designation.

**CONTEXT AND CONTENT.** Superorder Paenungulata, Order Hyracoidea, Family Procaviidae (= Hyracidae Gray, 1821:306, invalid). The genus *Procavia* contains two extinct and one living species, *P. capensis* of Africa and southwest Asia (Corbet, 1979; Ellerman and Morrison-Scott, 1951; Meyer, 1978).

***Procavia capensis* (Pallas, 1766)**

**Rock Hyrax**

*Cavia capensis* Pallas, 1766:30. Type locality "Promontorii Africae," Cape of Good Hope, Cape Province, Republic of South Africa.

*Hyrax syriacus* Schreber, 1792(4):923 and plate CCXLB. Type locality Mount Lebanon, Syria. See Remarks.

*Hyrax habessinicus* Hemprich and Ehrenberg, 1828:dec. 1, folio g, pl. II, lower fig. Type locality, "Arkiko et Eilet in Habessiniae montibus Gedam" (= Ethiopia, coastal mountains of Abyssinia, near Arkiko and Eilet).

*Hyrax ruficeps* Hemprich and Ehrenberg, 1828:dec. 1, folio h, pl. II, upper fig. Type locality "ad aquas deserti inter Dongalam et Sennaar" (= Sudan, Dongola).

*Hyrax Burtonii* Gray, 1868:43. Type locality "North Africa, Egypt."

*Hyrax Welwitschii* Gray, 1868:43. Type locality "Rocky places on the shores of the River Maiomba, in the district of Mossamedes" (= Angola).

*Hyrax Alpini* Gray, 1868:45. Type locality "North Africa, 'Abyssinia (Leadbeater)'" (= Ethiopia).

*Hyrax sinaiticus* Gray, 1868:45. Type locality "Asia, Palestine . . . Arabia, Mount Sinai."

*Euhyrax abyssinicus* Gray, 1868:47. Type locality "Abyssinia, Ankober" (= Ethiopia).

*Hyrax dongolanus* Blanford, 1869:642. Type locality Dongola, Anglo-Egyptian (NW of Dartoom) Sudan.

*H(yrax) ferrugineus* Gray, 1869a:242. Type locality "Abyssinia" (= Ethiopia).

*Dendrohyrax semicircularis* Gray, 1869b:285. Type locality "S. Africa?" (see Gray, 1873).

*Hyrax scioanus* Giglioli, 1888:21. Type locality Ankober, Shoa (= Ethiopia).

*Procavia pallida* Thomas, 1891:908. Type locality Hebeke Plateau, Northern Somaliland (= Somalia).

*Procavia latastei* Thomas, 1892:69. Type locality "Senegal."

*Procavia johnstoni* Thomas, 1894:142. Type locality Fort Lister, Nyasaland.

*Procavia Kerstingi* Matschie, 1899:59. Type locality "Tshyati, 50 km. süd-östlich von ungefähr auf in der Nähe der Grenze 7 do' zwischen Togo und Dahome" (= Togo-Dahomey border, 50 km SE Pessi, about 7°50'N).

*Procavia meneliki* Neumann, 1900:555. Type locality "Muansa" (= Tanzania).

*Procavia jacksoni* Thomas, 1900:176. Type locality "Ravine Station, British East Africa" (= Kenya).

*Procavia mackinderi* Thomas, 1900:176. Type locality "Teleki Valley, 13,000 ft." (= Kenya).

*Procavia erlangeri* Neumann, 1901:238. Type locality "Quellgebiet des Webbi Shebeli, und greift nach Norden nur einige stunden Über die wasser-scheide hinüber" (= Somalia, headwaters of Webbe Schibeli).

*Hyrax habessinicus* Anderson and de Winton, 1902:326. Type locality not given.

*Procavia meneliki* Neumann, 1902:143. Type locality "Abuje and Badattino, Province of Ginderberat, south of Blue Nile" (= Ethiopia).

*Procavia Goslingi* Thomas, 1905:82. Type locality "Nertang, Yergum Country, Northern Nigeria. Alt. 360 m." (presumably = Niger).

*Procavia slatini* Sassi, 1906:270. Type locality "bewohnt die niedrigen Hügel südlich von Gondokoro am Weißen Nil, zirka am 5. Grad Nordlicher Beite" (= Sudan, hills on the White Nile, S of Gondokoro, 5°N).

*Procavia Lopesi* Thomas and Wroughton, 1907:520. Type locality "Kodja Hill, Gaima Range; River Kibali, Monbuttu" (= Zaire).

*Procavia sharica* Thomas and Wroughton, 1907:521. Type locality "Kajibu, Shari River" (= French Equatorial Africa).

*Procavia daemon* Thomas, 1910:199. Type locality "Mount Elgon. Elonyi. Alt. 7000'" (= Kenya).

*Procavia oweni* Thomas, 1911:123. Type locality "Nr. Daley, Fouta Dualon, 3000'" (= Guinea).

*Procavia butleri* Wroughton, 1911:461. Type locality "Jebel Fazogli, Blue Nile. Alt. 3500 feet" (presumably = Sudan).

*Procavia bamendae* Brauer, 1913a:127. Type locality "Bamenda, Südwestkamerun" (= Cameroon).

*Procavia kamerunensis* Brauer, 1913a:127. Type locality "Lagdobergen etwas südöstlich von Garua in NordKamerun" (= Cameroon, Lagdo hills, SE of Garua).

*Pr(ocavia) volkmanni* Brauer, 1914:35. Type locality "bei Franzfontein im Norden von Deutsch-Südwestafrika" (= South Africa, Namibia, Franzfontein).

*Procavia (Procavia) ebneri* Wettstein, 1916:162. Type locality "Talodi, Sud-Kordofan" (presumably = Sudan).

*Procavia elberti* Brauer, 1917:300. Type locality, "Höhle bei Jade in 1250 m Höhe" (= Cameroon, cave at Jade, about 7°N, 15°E).

*Procavia flavimaculata* Brauer, 1917:303. Type locality "Kakofeld im Nordwesten von Deutsch-Südwestafrika" (= South Africa, Namibia, Kaokoveld).

*Procavia ituriensis* Brauer, 1917:303. Type locality "Ituri" (= Zaire).

*Procavia naumanni* Brauer, 1917:300. Type locality "Am Bole, einem Nebenfluß des Uham in Neu-Kamerun" (= Cameroon).

*Procavia buchanani* Thomas and Hinton, 1921:13. Type locality "Aouderas," Asben, 2,700 ft (= Niger).

*Procavia (Heterohyrax) antineae* Heim de Balsac and Begouen, 1932:479. Type locality "Ahaggar, Sahara central" (= Algeria).

**CONTEXT AND CONTENT.** Content noted in generic summary above. Forty living subspecies were recognized (see Allen, 1939, and Bothma, 1971). We follow Roche (1972) and Corbet (1979) and list 17 subspecies recognized by them:

*P. c. bamendae* Brauer, 1913a:125, see above.

*P. c. capensis* (Pallas, 1766:30), see above (*semicircularis*, Gray, *marlothi* Brauer, *reuningi* Brauer, *schultzei* Brauer, *waterbergensis* Brauer, *windhuki* Brauer, *chiversi* Roberts, *orangeae* Roberts, *letabae* Roberts, *natalensis* Roberts, and *coombi* Roberts are synonyms).

*P. c. capillosa* Brauer, 1917:302. Type locality Adaba (= Agada), 7°00'N, 39°24'E, Western Bale Province, Ethiopia.

*P. c. erlangeri* Neumann, 1901:238, see above (*comata* Brauer a synonym).

*P. c. habessinicus* (Hemprich and Ehrenberg, 1828), see above (*abyssinicus* Gray, *alpini* Gray, *ferrugineus* Gray, *luteogaster* Gray, and *meneliki* Neumann are synonyms).

*P. c. jacksoni* Thomas, 1900:176, see above (*varians* Granvik, and presumably *daemon* Thomas are synonyms).

*P. c. jayakari* Thomas, 1892:63. Type locality, "Dofar, S. Arabia."

*P. c. johnstoni* Thomas, 1894:142, see above.



FIGURE 1. An adult *Procavia c. capensis* basking in the morning sun. Taken in the Pretoria Zoological Gardens, Pretoria, Republic of South Africa. Photo by J. Shoshani.

- P. c. kerstingi* Matschie, 1899:59, see above (*goslingi* Thomas, *lopesi* Thomas and Wroughton, *oweni* Thomas, *elberti* Brauer, *naumanni* Brauer, *ituriensis* Brauer, and presumably *kamerunensis* Brauer are synonyms).
- P. c. mackinderi* Thomas, 1900:176, see above (*zelotes* Osgood a synonym).
- P. c. matschiei* Neumann, 1900:555, see above.
- P. c. pallida* Thomas, 1891:908, see above (*minor* Thomas a synonym).
- P. c. ruficeps* Hemprich and Ehrenberg, 1828, see above (*burtonii* Gray, *dongolanus* Blanford, *latastei* Thomas, *bounhioli* Kollman, *ebneri* Wettstein, *buchanani* Thomas and Hinton, *marnensis* Thomas and Hinton, *antinea* Heim de Balsac and Begouen, and presumably *slatini* Sassi are synonyms).
- P. c. scioanus* Giglioli, 1888:21, see above (*butleri* Wroughton a synonym).
- P. c. sharica* Thomas and Wroughton, 1907:521, see above (*melifica* Mertens a synonym).
- P. c. syriaca* (Schreber, 1792), see above (*sinaiticus* Gray, *ehrenbergi* Brauer, and *schmitzi* Brauer are synonyms).
- P. c. welwitschii* (Gray, 1868), see above (*volkmanni* Brauer and *flavimaculata* Brauer are synonyms).

**DIAGNOSIS.** Because the genus includes only one living species (Fig. 1), the following diagnosis applies to genus and species, and is intended to distinguish *Procavia* from the other genera in the family.

In *Procavia*, the upper incisors are strong and close together; the lower incisors are chisel-shaped with tricuspid cutting edges; molars are broad, lophodont, and hypsodont. The length of the premolar series is much less than that of molar series. Upper molars resemble rhinoceros molars; the second molar is the largest. Postorbital processes are well developed; postorbital bar is never complete (Fig. 2). In almost all other respects, *Procavia* and the other two genera in the family, *Dendrohyrax* and *Heterohyrax*, are much alike. The above diagnosis is compiled from Bothma (1971), Flower and Lydekker (1891), Hoffmeister (1967), and Sale (1960).

**GENERAL CHARACTERS.** *Procavia capensis* is heavily built, weighing up to 4.3 kg. The average weights are 3.6 kg for females and 4 kg for males. The general appearance is rabbit-like, crouched, but with short ears and tail. Total length of adults ranges from 305 to 550 mm; crouching height is 140 mm on average, and range of height at the shoulder is 202 to 305 mm. Body measurements (in mm) of 16 adults (Hatt, 1936) were as follows: total length, 475 to 585; length of tail, 11 to 24; length of hindfoot, 65 to 76; and length of ear, 27 to 38. Cranial measurements (in mm) of 10 adults (Hatt, 1936) were as follows: greatest length, 92.0 to 103.0; height of skull, 30.8 to 34.6; zygomatic breadth, 51.8 to 62.3; postorbital breadth, 23.1 to 26.8; breadth of palate, 15.0 to 16.7; length of mandible, 80.5 to 90.0; and length of maxillary tooththrow, 39.0 to 42.7. See Hahn (1934) for additional measurements. Sexual dimorphism is present but slight. Males av-

erage slightly heavier (see above), have thicker necks, thinner bodies, and heavier and better-developed upper incisors.

The pelage is dense, with short, thick underfur and long scattered guard hairs. General coloration of the upper parts is brownish gray, the flanks are lighter, and the underparts are creamy in color. The patch on the dorsum is variable in color, either black, yellow, or orange, and covers a cutaneous gland that secretes odoriferous material.

The gait is plantigrade (forefeet) and semiplantigrade (hindfeet). The feet are mesaxonic, with the axis of symmetry through the third digit. Soles of feet have soft, enlarged, black elastic pads that allow cohesion to the substrate. The pads are kept moist by secretions from numerous sudorific glands.

The above description is compiled from Bothma (1971), Flower and Lydekker (1891), Hatt (1936), Hoffmeister (1967), Mendelssohn (1965), Sale (1960), Thomas (1892), and Walker et al. (1964). For longer descriptions see Grassé (1955) and Hahn (1934).

**DISTRIBUTION.** *Procavia capensis* occurs throughout most of Africa from the southernmost tip north, except in the dense jungle of the Congo basin and in Madagascar, to a line from Senegal through southern Algeria and Libya into Egypt, and in Arabia, Israel, Jordan, Lebanon, and Syria (Fig. 3).

**FOSSIL RECORD.** The oldest known hyraxes are from the lower fossil wood zone, Jebel el Qatrani Formation, Fayum, Egypt, from the Oligocene (Meyer, 1978). Dubrovo (1978) placed the earliest fossil record as "Upper Eocene-Lower Oligocene. . . ." Africa is believed to be the center of origin of this order (Simpson, 1945). The 16 recognized genera are placed in two families, Procaviidae (5 genera) and Pliohyracidae (11 genera). All pliohyracids and two genera in the Procaviidae are extinct. Hyraxes possess a number of characters (anatomical, behavioral) that are primitive or generalized. Past distribution of this order extends from Africa to Europe, Asia Minor, USSR, and China (Dubrovo, 1978).

**FORM.** The pelage coloration is highly variable between the different subspecies. Bothma (1966) looked at specimens from the cape region in Africa, and found that color depended on environment; animals are darker in wetter areas. Long vibrissae are present in the pelage of the back, are distributed bilaterally (Sale, 1970a), and function as tactile sensors. Vibrissae also occur around the mouth, where they are black and measure up to 180 mm in length.

An unusual gland, known only in hyraxes, is the dorsal gland in the center of the back at the junction of the thoracic and lumbar regions. The gland is indicated by a bare patch, variable in color (see above), oval in shape, and approximately 15 mm long in adults. The gland is surrounded by long hairs, which are variously yellow, orange, brown, or black. The gland produces the characteristic odor of the species, and appears to have the social functions of marking rocks and helping the young get acquainted with their mothers. The gland is most active during mating activity (Sale, 1970a).



FIGURE 2. Views of the skull and mandible of *Procavia capensis* (AMNH 169131). From top to bottom, dorsal, ventral, lateral views of skull, and lateral view of the mandible. Condylobasal length is 92.0 mm. Courtesy of American Museum of Natural History.

The skull (see Fig. 2) has a short rostrum, anteriorly situated orbits, weak temporal crests, a well-developed interparietal, small tympanic bullae, and a large jugal which contributes to the mandibular fossa. A distinct antorbital (lacrimal) process and the alisphenoid canal are present. The paraoccipital processes are long, sharp, and curve anteriorly and medially. The premaxillae form a tubercle between the incisive foramina. The premaxillae and the frontals are not in contact. The dentary is large, and has the angular region expanded into a thin plate. The coronoid process is small and recurved. The coronoid canal is present. The hyoid bone is present and has an unusual scoop-like construction (Flower and Lydekker, 1891; Fox, 1933). For a description of the ear region see Grassé (1955), and for drawings of the skull see Hatt (1936).

The permanent dental formula is  $i \ 1/2, c \ 0/0, p \ 4/4, m \ 3/3$ , total 34. Deciduous dental formula is  $i \ 3/3, c \ 0/0, p \ 4/4$ , total 32. The long and curved upper incisors grow from persistent pulps, are separated by a gap, are triangular in cross-section, and have pointed tips with enamel-free posterior surfaces. There is a wide

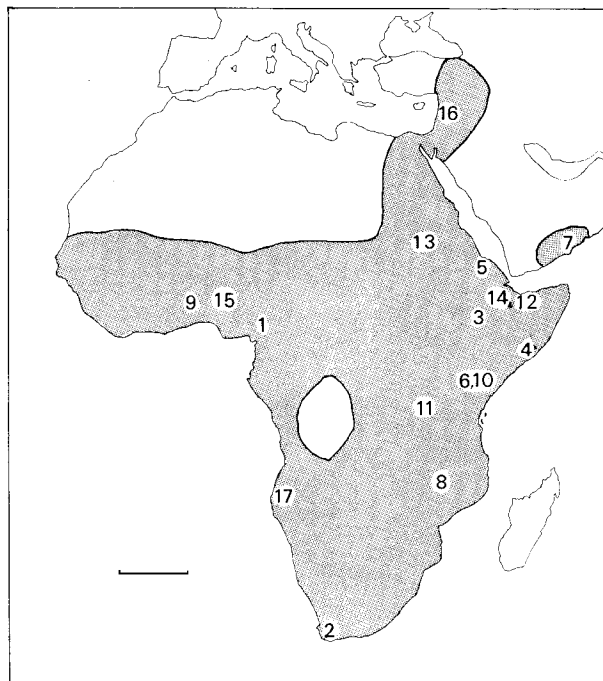


FIGURE 3. Map showing the distribution of *Procavia capensis* and type localities of the recognized subspecies: 1, *P. c. bamendae*; 2, *P. c. capensis*; 3, *P. c. capillosa*; 4, *P. c. erlangeri*; 5, *P. c. habessinicus*; 6, *P. c. jacksoni*; 7, *P. c. jayakari*; 8, *P. c. johnstoni*; 9, *P. c. kerstingi*; 10, *P. c. mackinderi*; 11, *P. c. matschiei*; 12, *P. c. pallida*; 13, *P. c. ruficeps*; 14, *P. c. scioanus*; 15, *P. c. sharica*; 16, *P. c. syriaca*; 17, *P. c. welwitschii*. Scale represents 1,000 km.

diastema between the incisors and premolars. The premolars become progressively molariform from front to rear. (Modified from Flower and Lydekker, 1891; and Hoffmeister, 1967.) For drawings of the mandible and teeth see Brauer (1913b).

The vertebral formula is C 7, T 20–21, L 7–9, S 5–7, Cd 4–8. Two sacrals are fused to the ilium. Of the 27 to 30 thoracic and lumbar vertebrae, 19 or 20 bear ribs, and 7 or 8 pairs of ribs are in direct contact with the sternum. Clavicles are absent, and the humerus lacks an entepicondylar foramen. The radius and ulna are complete, subequal, and pronated; the third femoral trochanter is at most a slight ridge; the fibula is complete and has the proximal end fused to the tibia. The astragalus is truncate distally, and does not articulate with the cuboid. Carpal bones are in serial arrangement and are cube-like when viewed in pronation. There is a freely articulating centrale in the carpus. The manus is five-toed, with only three functional. The toes are united as far as the bases of the terminal phalanges except for the fifth digit, which is united for its entire length. The pollex is rudimentary and concealed beneath the skin. The pes is three-toed. The fifth digit is rudimentary and the hallux is absent. The inner toe (second digit) has a deeply cleft terminal phalanx. Most digits on the feet have short hoof-like nails; the second digit of the pes bears a long curved claw, presumably for use in grooming. For pictures and a description of the carpus and tarsus see Fischer (1903) and Gregory (1910, 1951).

The brain is of the macrosomatic type (Hoffmeister, 1967) and has been described as resembling that of typical ungulates (Flower and Lydekker, 1891). The eye is unique in having an umbraculum which presumably allows the animals to "stare" into the sun.

Observations on the alimentary canal have been made by Flower and Lydekker (1891), Mitchell (1905, 1916), and Sale (1965a, 1966a). The stomach has two cavities. There is no gall bladder. At the junction of the small and large intestines, there is a large, sacculate caecum. In addition, and unique to hyraxes, there is a pair of large, pointed, cone-shaped supplemental caecae on the ascending colon, which are similar to structures seen in birds. Mitchell (1916) noted that similar paired caecae are found in Edentata and Sirenia. The function of the supplemental caecae may be water resorption.

The female reproductive system was described by Wislocki (1928). There are three pairs of mammae: one pectoral pair and two inguinal pairs. The uterus is round, about 40 mm in diameter, two-horned, and similar to the type found in insectivores, rodents, and *Tarsius*. The placenta is of a primitive, burrowing type, at first diffuse and then zonary, and resembles that of sirenians and proboscians (Steven, 1975; Wislocki and van der Westhuysen, 1940). For more complete descriptions and diagrams, see Wislocki (1930) and Wislocki and van der Westhuysen (1940).

In males the testes are permanently abdominal, as in elephants, sirenians, insectivores and others. There is no inguinal canal or scrotal sac (Flower and Lydekker, 1891). The penis is short, simply built, slightly elliptical in cross-section, and is slightly larger in diameter towards the tip (Hoeck, 1978). There is no baculum. For complete description and diagrams see Glover and Sale (1968).

**FUNCTION.** Temperature regulation was described as poor by Taylor and Sale (1969) and by Sale (1970b). At low ambient temperatures, oxygen consumption increases to maintain warmth, and at high temperatures, panting and grooming with saliva help to prevent overheating. No sweating was observed at temperatures as high as 40°C and higher, although salivating and grooming occurred. At 10°C, oxygen consumption was double that at 30°C. At ambient temperatures above 30°C, rectal temperature and respiratory rates increased. Meltzer (1973) found that respiratory rates alternated between high and low; the high rate was 52.4 breaths/min at 10°C, 31.9 at 28°C, 106.8 at 35°C, and 162 to 164 at 36°C. The low rate was 31 breaths/min at 10°C, 21.5 at 28°C, and 51.9 at 35°C.

At an ambient temperature of 40°C, Taylor and Sale (1969) found that body temperatures of hyraxes were 40°C, despite respiratory rates greater than 200/min.

Body temperatures of rock hyraxes bear an approximate relationship to ambient temperature and show a diurnal pattern. Body temperatures are always higher than ambient temperature and are different for males and females. Animals kept under constant conditions showed diurnal patterns similar to animals under non-constant conditions, indicating an internal mechanism for this diurnal cycle. The body temperature is highest at about 0900 h, after 1 to 2 h of basking in the sun. It declines around midday, rises throughout the afternoon, and falls during the night. The minimum temperature in the cycle is reached at about 0400 h. The effect of the diurnal cycle is to reduce the gradient between body temperature and ambient temperature, and thus minimize water loss from the body by evaporative cooling. Basking in the morning (Fig. 1) seems to replace heat lost overnight. However, at an experimental temperature of 29°C, diurnal fluctuations disappear and animals are able to maintain a constant body temperature. Huddling and heaping behaviors by hyraxes probably serve as heat retention mechanisms (Sale, 1970b).

Sale (1966a) studied daily food consumption in relationship to body weight. He found that water content greatly influences the amount of food consumed. Hyraxes exhibit a voluntary lowering of water intake with a reduction of protein intake, as is usual during the dry season when the quality of the vegetation decreases. A large adult male weighing 3.3 kg ate approximately 111 g (dry weight) per day, or 33.6 g/kg body weight/day. This ratio is similar to that found in sheep, implying that the rock hyrax has a modest food intake for its size. Meltzer (1973) measured and calculated daily food consumption for the Syrian hyrax (*P. c. syriaca*). He found protein to be a limiting factor. Adults required 11.6 g protein/day (15% of the energy requirement for maintenance per day), which they obtain by eating approximately 650 g food/day (3 to 4 h of continuous eating).

Meltzer (1973) determined that 180 ml of water was normally obtained from the food ingested. Meltzer (1973) estimated water loss at 0.562 mg g<sup>-1</sup> h<sup>-1</sup> at 10°C and 0.660 mg g<sup>-1</sup> h<sup>-1</sup> at 28°C. An adult Syrian hyrax produced at least 10 to 15 ml of urine per day; maximal urine osmolality was 2,340 mOsm/kg; maximal urea concentration was 1230 mM/l and maximal electrolytes concentration was 760 meq/l (Meltzer, 1973).

**ONTOGENY AND REPRODUCTION.** The relatively long gestation period has been estimated at 6 or 7 months (van der Horst, 1941); 7.5 months (Murray, 1942; Sale, 1965a); and 7.5 to 8 months (Mendelssohn, 1965). Coe (1962) estimated the breeding season in Kenya to be August to November, which Sale (1965a, 1965b) extended on the basis of January births. Mendelssohn (1965) estimated the mating season in the Syrian hyrax to be August to September with young born in mid-March through early May. Hanks (1977) noted that "It is possible that the long

gestation period of the hyrax is an evolutionary vestige from the times when the ancestral forms were much larger."

Parturition takes place in the dark, and is accompanied by a hoarse squeaking noise, the frequency of which coincides with contractions. The female makes no attempt to rupture the fetal membranes, lick the newborn, or eat the placenta. The membranes are ruptured by the activity of the newborn (Sale, 1965a).

Litter size has been estimated at 2 or 3 (Coe, 1962; Roche, 1962; Sale, 1965a, 1965b; Shortridge, 1934), 3 (Mollaret, 1962), and 3 or 4 with a mean of 3.2 (Mendelssohn, 1965). The litter weight has been estimated at 10.8% of the mother's weight (Sale, 1965b).

The young are well developed at birth, have eyes opened and a fully-developed pelage, weigh between 170 and 240 g (average is 202 g), and are fully active. At day 2, the young can jump to a height of 40 or 50 cm; at days 3 to 4, they can nibble food; and at week 2, they can ingest solid food (Mendelssohn, 1965). Suckling occurs at about 1.5 h intervals during the first few days, and does not occur at significant intervals after 10 weeks (Sale, 1965a). Reproductive maturity is reached at month 16. Adult size and weight are attained at 3 years or 28% of life expectancy (Mendelssohn, 1965). See Meltzer (1973) for growth curve.

Roche (1978) described the pattern of tooth replacement for the upper teeth. At month 5, P4 develops; at months 5 to 8, M1 begins to erupt; at months 8 to 14, M1 is fully developed and the milk incisors are replaced; at months 14 to 24, the milk premolars are replaced and M2 develops; at month 24, M3 erupts; and by month 68 (minimum) to 81 (maximum), M3 is fully developed. In all, it takes approximately 6 years for adult dentition to be fully developed.

Infants make only five of the 21 sounds used by adults. Three of these are vocal and two are non-vocal. Infants show no use of combinations of sounds. Between months 2 and 15, all except five vocal sounds appear, four of which are characteristic of adult females, and the one remaining is characteristic of mature males (Fourie, 1977).

**ECOLOGY.** The diet of *Procavia capensis* usually consists of a variety of herbaceous plants from areas around their burrows and up to 50 m beyond (Sale, 1965c); however, during drought conditions, greater distances may be travelled. On the west slope of Mt. Kenya, Coe and Foster (1972) found the major foods to be giant lobelia (*Lobelia gibberoa*) and *Senecio* sp. If the colony is close to a valley bottom, the animals will graze on swampy vegetation. The species shows a wide tolerance to different plant species (Hoeck, 1975; Sale, 1965c, 1965d). *P. capensis* is a non-discriminating grazer, and may change from one plant species to another during feeding, although some species are avoided, such as the camphor bush, *Tarchonanthus camphoratus*. In lowland sites (up to 3,500 m), the majority of food is from woody plants. New shoots are preferred, as are fruits, berries, and figs. Few species of trees are eaten because they are hard to climb. Food preference is seasonal (Hoeck, 1975). In the wet season, and after a rainfall, tender new shoots, buds, and leaves are preferred. Grasses make up 78% of the diet in the wet season, and only 57% of the diet in the dry season. In drought, *Procavia* will eat coarse material, bark, lichens, and liverworts. In alpine sites (3,200 to 4,700 m), there is less choice of vegetation and plant species with the highest moisture content are eaten (Sale, 1965c; Hoeck, 1975). There is one reported incidence of hyraxes feeding on a poisonous plant, *Phytolacca dodecandra*, to which they are thought to be immune (Sale, 1965d). The most likely competitors for food are giraffes and elephants (Hoeck, 1975). Rock hyraxes are diurnal, but they may browse on moonlit nights (Coe and Foster, 1972; Turner and Watson, 1965).

Hyraxes are gregarious and live in colonies or herds numbering up to 80 individuals. A flock may consist of a few families, each of which is headed by an adult male (Coe, 1962; Meltzer, 1973). They live in rocky outcrops where they do not burrow, but instead live in crevices and cavities in the rocks (Coe, 1962). Shortridge (1934) reported a considerable amount of digging by hyraxes, and they are also known to inhabit holes of other animals (Roberts, 1951), especially those of the aardvark, *Orycteropus afer*, and meercat, *Suricata suricatta*. In areas where overpopulation of rocky habitats occurs, animals are forced onto the plains. If they occur in regions of human habitation, they may become pests, living in road culverts and holes in stone walls (Roberts, 1951).

Floor space seems to be the critical factor in hole size, as many holes are no deeper than an adult in the crouching position (14 cm) (Sale, 1966b). Holes with high ceilings are generally not used as living quarters. If several holes are each large enough to

house a family group of approximately five adults (about 1 m<sup>2</sup> of floor space), then a small colony may become established (Hoeck, 1975). It is rare to find a single group in an isolated crevice. If holes are not connected internally, then there will be well-worn paths covering the area. Although there is no fixed pattern in the use of crevices and holes, holes are never directly exposed to the wind.

Sale (1966b) noted a relationship between hole size and predator size. Regularly used entrances are smaller than the diameters of the local predators. Leopards are the main predators, except in high mountains. On Mt. Kenya, leopards are absent and the burrow openings are quite large.

The advantages of crevice-living for hyraxes include water retention, protection, proximity to surrounding vegetation, and climatic constancy (Meltzer, 1973; Turner and Watson, 1965). In Israel, the temperature of the crevices never fell below 16°C in the winter or rose above 19°C in the summer. The minimal relative humidity was 87%. Animals left their crevices only after the morning temperature rose to 10 to 12°C, and they returned to their crevices when the ambient temperature dropped to 10°C. Animals also generally returned to crevices when the ambient temperature was greater than 30°C (Meltzer, 1973).

Hyraxes are preyed upon by many species; most common predators are leopards, Egyptian cobras, puff adders, caracals, wild dogs, and eagles (Coe, 1962; Turner and Watson, 1965). They are also eaten by humans in Africa.

Twenty-five species of lice have been reported to infest *Procavia capensis* (Cloudsley-Thompson, 1969).

Rock hyraxes urinate and defecate in a single communal spot on the rocks. As the material accumulates, it eventually congeals into a large, sticky mass. This material has been used by humans for a variety of purposes, one of which was as medicine (hyraxeum) for treatment of epilepsy, convulsions, and "women's diseases" (Dorst and Dandelot, 1970).

**BEHAVIOR.** Feeding behavior was observed by Sale (1965c, 1966a) and by Hoeck (1975). Feeding activity was similar to that of ungulates in speed and intensity. The total time that a colony has been observed to feed was extremely short, lasting less than 1 h/day. This time was divided into two feeding periods, averaging about 20 min each: one in the early morning, about 3 hours after sunrise (0730 to 0930 h or somewhat later on overcast days); and a second one in the evening, about 2 hours before sunset (1530 to 1830 h). The evening feeding period was of higher intensity. In the dry season, the morning peak was at about 0830 h; in the wet season, there were two small peaks at 0830 and 1330 h. There was one marked evening peak, which occurred 1 hour earlier in the wet season than in the dry season. Feeding was usually a communal activity. However, a second type of feeding, casual feeding, occurred less frequently, was of shorter duration, and involved only one individual.

The mode of ingestion permits an unusually rapid rate of food intake. The feet are not used in feeding except to reach or hold down a twig. Rock hyraxes have not been observed carrying food into burrows. While browsing, the head is turned sideways at a 90° angle, and the molars are used to bite off the vegetation. There is a long cutting edge on the molars which permits a large amount of food to be taken at once. Once food is ingested, it is rapidly chewed in a side-to-side motion and then swallowed. There is no rumination (Sale, 1966a).

While drinking, the lips are placed just below the water surface and the water is sucked up into the mouth in little gulps (Sale, 1966a).

Most of the time hyraxes are either basking or huddling in holes. During bad weather, hyraxes remain below ground for up to 3 days (Coe, 1962). Coe suggested that they may eat their feces during these periods.

Sale (1970b) described resting behavior, which constitutes 95% of adult time. Some of this time is also spent in grooming. There are three main resting patterns: heaping, which usually takes place inside the hole; huddling, which is similar to heaping, but animals do not lie on top of one another, and it may take place outside or inside the hole; and solitary resting, in which there is no physical contact.

Behavioral patterns are closely associated with body temperature and are thought to be mechanisms of temperature regulation. As the ambient temperature increases, the behavioral cycle progresses from heaping to huddling to solitary resting.

There is a low threshold of intraspecific aggression in adults. The threat posture consists of raising the dorsal gland hairs, accompanied by a slight retraction of the upper lip. Most of the behaviors of the species are accompanied by vocalizations. Hoeck

(1978) described the territorial call of *P. c. johnstoni* as loud and repetitious. The call becomes louder and longer toward the end of the sequence and ends with guttural noises. For a sonogram of the call see Hoeck (1978). During the breeding season when there is more activity, males become more aggressive and give more calls. At this time, several females will form a herd with a single male; at other times of the year the sexes freely intermix (Mendelssohn, 1965).

Mating behavior was described by Hoeck (1978). The male gave an initial mating call and then executed weaving head movements; the penis was then erected and the dorsal hairs raised. The female pressed her rump against the male's flank or breast, and the male mounted. After mounting, the male grasped the sides of the female vigorously with his forelegs, made several thrusting motions, the last of which was a short jerk. He then jumped down. Copulation lasted only a few seconds.

As parturition approaches, the aggressiveness of the pregnant females increases. The females isolate themselves and form temporary nursing groups.

Newborn show a tendency to climb onto their mother's back, presumably because they are attracted by the scent gland located there (Sale, 1965a). While suckling, neonates use all three pairs of mammae; suckling may take place either inside holes or outside on the rocks.

Young animals "play"; they are therefore slightly more active than adults (Sale, 1970b).

**GENETICS.** The diploid chromosome number of *P. capensis* is 54 (Hungerford and Snyder, 1969). Autosomes consist of 21 pairs of acrocentrics, 2 pairs of relatively large, submetacentrics, and 3 pairs of small metacentrics. The X chromosome is the largest chromosome; it has a submedian centromere. The Y chromosome is a very small acrocentric.

**REMARKS.** "Hyrax" is a word of Greek origin meaning "shrewmouse" (Fox, 1933). In Hebrew, *P. capensis* is called "Shaphan" which translates loosely into "the hidden one." The hyrax was known in Biblical times as the "cony" ("The high mountains are for the wild goats; the rocks are a refuge for the conies"—Psalms, 104:18). Other names include dassie and rock dassie.

The phylogenetic affinity of the Hyracoidea to Proboscidea and Sirenia was first noted by Gill (1870). This relationship was later supported by Buettner-Janusch and Buettner-Janusch (1964), Gregory (1910), Heap et al. (1975), Hungerford and Snyder (1969), Meyer (1978), Simpson (1945), Thenius (1969), Weitz (1953), and Wislocki and van der Westhuysen (1940). Le Gros Clark and Sonntag (1926) pointed out the affinity of Hyracoidea to Tubulidentata. Shoshani et al. (1981) provided immunological evidence to support this view. No evidence was found to indicate a Hyracoidea-Perissodactyla relationship as proposed by McKenna (1975), Owen (1868), and Whitworth (1954). The phylogenetic relationships among the hyracoid taxa were given by Hahn (1934), Matsumoto (1926), and Whitworth (1954).

Bothma (1971) remarked that *Hyrax syriacus* was described by Schreber in 1784 and not in 1792, as stated by Allen (1939). We found no description of *H. syriacus* in Schreber (1784), but found both text and plate in part 4 of his work, published in 1792. However, Roche (1972) noted that Schreber's work of 1784 had a plate, and that of 1792 had a text. Nevertheless, Roche considered *H. syriacus* as a nomen dubium. Corbet (1979) listed Hemprich and Ehrenberg, 1828, as the authors of *P. c. syriaca*.

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Editors of this account were DANIEL F. WILLIAMS and SYDNEY ANDERSON. Managing editor was TIMOTHY E. LAWLOR.

N. OLDS, DEPARTMENT OF BIOLOGY, QUEENS COLLEGE, FLUSHING, NEW YORK 11367 AND J. SHOSHANI, DEPARTMENT OF BIOLOGICAL SCIENCES, WAYNE STATE UNIVERSITY, DETROIT, MICHIGAN 48202.