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Gerbillurus paeba.

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Gerbillurus paeba A. Smith, 1836

Pygmy Hairy-footed Gerbil

Gerbillus paeba A. Smith, 1836:401. Type locality "Country beyond Latakoo"; Vryburg, Northwest province, South Africa nominated by Roberts (1951:401).

Gerbillus tenuis A. Smith, 1842: pl. 36, fig. 2. Type locality "North of Latakoo." Renaming of *paeba* A. Smith, 1836.

Gerbillus calidus Thomas, 1918:63. Type locality "Molopo, west of Morokwen, extreme Northern Cape."

Gerbillus paeba broomi Thomas, 1918:64. Type locality "Port Nolloth, coastal Little Namaqualand, northwestern Northern Cape."

Gerbillus swalius Thomas and Hinton, 1925:235. Type locality "Karibib, 1171 m (3,842 feet), northwest of Windhoek, Namibia."

Gerbillus swalius oralis Thomas and Hinton, 1925:236. Type locality "Rooibank, 73 m (240 feet), 32 km up the Kuiseb River from Walvis Bay, Namib Desert, Namibia."

Gerbillus swalius leucanthus Thomas, 1927:382. Type locality "Ondongwa, 1,074 m (3,525 feet), Ovamboland, Namibia."

Gerbillus calidus kalaharicus Roberts, 1932:10. Type locality "Gomodimo Pan, central Kalahari, Botswana."

Gerbillus paeba mulleri Roberts, 1946:317. Type locality "Eendekuil, north of Piquetberg, southwestern Western Cape."

Gerbillus paeba swakopensis Roberts, 1951:404. Type locality "Swakopmund, coastal Namibia."

CONTEXT AND CONTENT. Order Rodentia, Family Muridae, Subfamily Gerbillinae, Tribe Taterillini, Subtribe Gerbillurina, Genus *Gerbillurus,* Subgenus *Progerbillurus.* Four subspecies are recognized (Meester et al., 1986) as follows:

Gerbillurus p. coombsi Roberts, 1929:98. Type locality "Swarthoek, near Waterport, Soutpansberg, Northern Province, South Africa."

Gerbillurus p. exilis Shortridge and Carter, 1939:290. Type locality "Paardevlei, Sundays River mouth, Alexandria district, Eastern Cape, South Africa."

Gerbillurus p. infernus Lundholm, 1955:296. Type locality "Rocky Point, Skeleton coast, northern Namib, Namibia."

Gerbillurus p. paeba A. Smith, 1836:401, see above.

DIAGNOSIS. *Gerbillurus paeba* (Fig. 1) occurs within parts of the ranges of all other congeners. It is distinguished from other *Gerbillurus* species by its smaller size (adult body mass <30 g) and a tail tip slightly tufted, never with a conspicuous brush as in *G. vallinus* and *G. setzeri* (Griffin, 1990). Tail is <20% longer than head and body, unlike *G. vallinus* and *G. tytonis* in which the tail is >20% longer than head and body. Hind feet (with claws) are large, but <30 mm (Smithers, 1971), whereas in all other *Gerbillurus* species, the hind foot is >30 mm (Schlitter, 1973). Soles of the feet are fully haired with only a narrow central line naked (Roberts, 1951), whereas *G. vallinus* has a naked patch from the heel to the centre of the foot (de Graaff, 1981).

Skulls of *G. paeba* are distinguished from congeners by an undeveloped occipital region, which is noticeably more developed in all other *Gerbillurus* species (de Graaff, 1981). In addition, *G. paeba* is distinguished from *G. tytonis* by its posterior palatal foramina which are >1.6 mm, but <1.6 mm in *G. tytonis* (Fig. 2—Griffin, 1990).

GENERAL CHARACTERS. Although sexual dimorphism has not been recorded in *G. paeba,* geographically and within populations the color of the upper parts of the body varies considerably, from reddish-orange to grayish-red (Skinner and Smithers, 1990). Color of the upper parts varies with color of the substrate. Underparts are pure white. The tail is the same color as the upper parts; in grayer specimens it is darker along the dorsum (Skinner and Smithers, 1990). The head is slightly elongated, eyes are deep reddish-brown, and ears are a pale yellowish brown externally. Hind limbs are elongate and the tail is long and slightly tufted.

Means (and ranges) of external measurements (in mm) for 40 animals from southwestern Botswana are as follows: total length, 209.5 (187–230); length of tail, 113 (102–125); length of hind foot, 27 (26–29); length of ear, 17 (16–19—Smithers, 1971). Mean body mass (and range—in g) are 25.4 (20.0–37.0—Smithers, 1971). External measurements (in mm) of a different sample of 60 animals are the following: length of head and body, 93.5 (80–101); length of tail, 109.5 (92–127); length of hind foot, 26.5 (21–30); length of ear, 15 (10–19—de Graaff, 1981). Mean (and range) of body mass (in g) of 19 animals was 27.4 (21–35—de Graaff, 1981). Means (± *SE,* in mm) for male *G. paeba* caught in the Namib Desert are as follows: length of head and body, 86.3 ± 6.3 (n = 92); length of tail, 108.4 ± 8.9 (n = 87); length of hind foot, 28.1 ± 1.2 (n = 92); length of ear, 12.6 ± 1.0 (n = 92—D. C. Boyer, in litt.). Mean body mass (in g) was 22.2 ± 0.3 (n = 178—Boyer, 1987).

The cranium has a broad braincase and long rostrum; only the tympanic part of the bullae is well developed (Fig. 2). Zygomatic arches are not wide, but the zygomatic plate is well developed. Infraorbital foramina are narrow, palatal foramina are long, and occipital region is not strongly developed (de Graaff, 1981).

DISTRIBUTION. The range of *G. paeba* (Fig. 3) includes most of the South West Arid Zone and the periphery of the southern Savanna and South West Cape biotic zones (Davis, 1974). It is confined mainly to arid areas from southwestern Angola to the Cape (de Graaff, 1981), encompassing most of Namibia and Botswana, parts of Zimbabwe (Smithers, 1975), Mozambique, and the Northern Cape, Western Cape, Eastern Cape, and Northwest provinces of South Africa (Skinner and Smithers, 1990). *G. p. infernus* is found at Rocky Point in the northern Namib (Lundholm, 1955), *G. p. coombsi* is located in an area of relict Kalahari sand dunes in the Soutpansberg area of the Northern Province (Roberts, 1929), and *G. p. exilis* occurs in the Alexandria dunefield from the Sundays River mouth to St. George's Strand, Eastern Cape (Meester et al., 1986). No fossils of this species are known (de Graaff, 1981).

FORM AND FUNCTION. Dental formula is i 1/1, c 0/0, p

FIG. 1. *Gerbillurus paeba.* Photograph by A. Bruton.

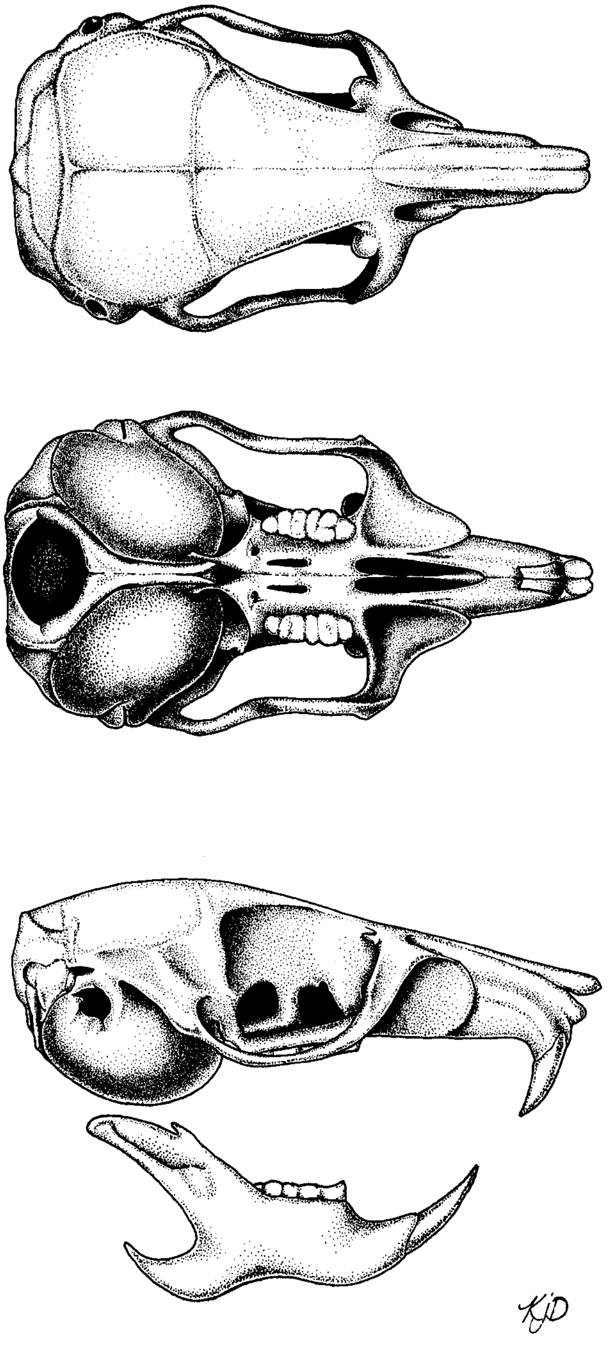

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Gerbillurus paeba*. Greatest length of cranium is 27.8 mm.

0/0, m 3/3, total 16 teeth. Upper incisors are orange and distinctly grooved, whereas lower incisors are ungrooved (Skinner and Smithers, 1990). M1 has three laminae, the anterior one with a single narrow cusp; M2 has two laminae, and M3 is small with a small posterior lamina behind the anterior one (de Graaff, 1981).

Pygmy hairy-footed gerbils possess broad hairs, each with a single chevron scale covering its width; scales are closely packed and each hair has a wide shallow groove (Keogh, 1985). Females have one pair of pectoral and two pairs of inguinal mammae (de Graaff, 1981).

Preferred ambient temperature of *G. paeba* is ca. 28°C (Downs, 1990; Downs and Perrin, 1990*a*). At 10°C animals occasionally shiver, and below 20°C individuals assume a crouched posture to reduce surface area. Above 35°C animals stretch out, salivate, and employ peripheral vasodilation to prevent hyperthermia. Exposure to environmental temperatures $\geq$40°C for periods >1 h results in death. Thermal parameters are: thermoneutral zone, 32.3–35.1°C; predicted lower critical temperature, 30.2°C; basal metabolic rate, 1.027 ml O_2 g^{-1} h^{-1}; minimal conductance, 0.1678 ml O_2 g^{-1} h^{-1} $°C^{-1}$. Pulmocutaneous water loss is low below 35°C, but evaporative water loss increases when animals become hyperthermic to aid cooling (Downs and Perrin, 1990*a*). Field water turnover rate varies markedly with environment, from ca. 85 ml kg^{-1} day^{-1} in the central Namib Desert to 232 ml kg^{-1} day^{-1} on the Namibian coast (Downs and Perrin, 1990*b*).

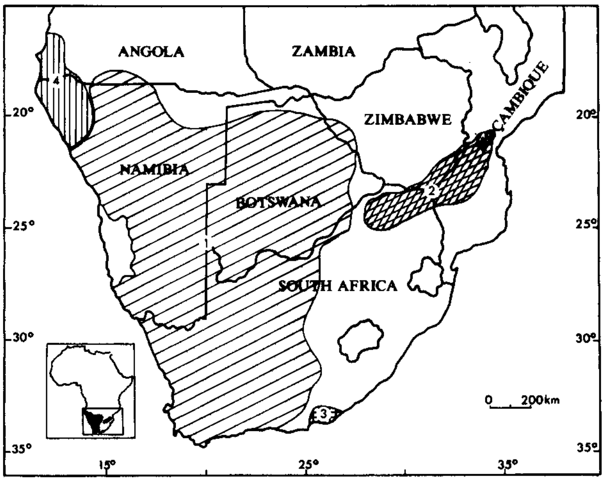

FIG. 3. Distribution of *Gerbillurus paeba* in southern Africa. Subspecies are as follows: 1, *G. p. paeba*; 2, *G. p. coombsi*; 3, *G. p. exilis*; 4, *G. p. infernus*.

Gerbillurus paeba has efficient renal function, but cannot survive on a diet of dry grass seed with succulent supplements (Louw, 1972). Urine osmolality varied from 1.73 to 4.65 osmol/kg to a maximum of 7.0 osmol/kg with diets that differed in energy and water content (Downs and Perrin, 1991*a*). Mean osmolality of urine was 2.86 osmol/l when gerbils received fresh lettuce, but without lettuce, osmolality increased to 4.035 osmol/l (Louw, 1972). When diet was shifted from seeds to insects (with a higher protein and nitrogenous concentration), urine production increased from 0.08 to 0.26 ml/day with urine osmolalities of 3.12–4.59 osmol/kg (Downs and Perrin, 1991*a*).

A well-developed papilla renis extends from the kidney into the ureter. When an animal is deprived of water, a precipitate of allantoin contributes to reducing overall water output (Buffenstein et al., 1985; Downs and Perrin, 1991*a*). *G. paeba* exhibits a high water turnover rate but good urine concentrating ability and can vary water turnover rate, depending on the protein content and potential water yield of the diet (Downs and Perrin, 1990*c*, 1991*a*). Insects or supplements of succulent plant material are important for maintenance of water balance.

Water metabolism of *G. paeba* was studied by estimating the daily metabolic water production and minimal daily water loss via urine, feces, and pulmocutaneous evaporation (Christian, 1978). Evaporative water loss correlated negatively and significantly with humidity at 23°C ambient (Christian, 1978, 1979*a*). On a high fiber diet of bran, daily energy expenditure of *G. paeba* was similar to that predicted by mass when water was freely available, but was reduced when animals were water stressed (Buffenstein, 1985). Gross energy intake of *G. paeba* was 1.74 kJ g^{-1} day^{-1} and 2.00 kJ g^{-1} day^{-1}, while on diets of mealworms and sunflower seeds, respectively; both diets were supplemented with carrots but without free drinking water (Downs and Perrin, 1990 *c*). Differential water losses were offset by differences in metabolic water production, enabling positive water balance and indefinite survival.

In xeric regions of southern Africa, *G. paeba* is exposed to low temperatures when active at night but regulates body temperature by generating supplementary heat through non-shivering thermogenesis (Downs and Perrin, 1991*b*). Neither low ambient temperature nor deprivation of food induces torpor.

ONTOGENY AND REPRODUCTION. Pregnant females occurred throughout the year in a sample of >300 *G. p. paeba* from the arid zone of Botswana (Smithers, 1971). However, in the eastern Namib Desert, reproductive activity in *G. paeba* occurs from December to April (mid to late summer) and juveniles are recruited from February to June (Boyer, 1987). Reproduction is markedly seasonal in the Namib with high densities following high summer rainfall (Christian, 1980*a*). Changes in densities of *G. paeba* populations in dune and riverbed habitats in the Kalahari Desert are closely correlated with rainfall (Nel, 1983). *G. paeba* also reproduces seasonally in the semiarid Karoo of South Africa (Kerley, 1990).

In captivity, reproduction was initiated by increased photoperiod (Keogh and Isaacson, 1978). Mean (± *SD*) length of the estrous cycle is 7.2 ± 1.5 days for *G. p. exilis* ($n = 9$) and 6.8 ± 1.7 days for *G. p. paeba* ($n = 8$—Dempster and Perrin, 1989*b*). Vaginal smears suggest that both subspecies are spontaneous ovulators. Primary and secondary follicles, but no corpora lutea, were reported in 21 wild-caught *G. p. paeba* (Stutterheim and Skinner, 1973). Vaginal casts formed from accumulation of vaginal secretions and sloughed epithelial cells have been reported in captive, unmated females (Dempster and Perrin, 1989*b*).

Mean litter size in the field is 3.7 (range, 2–5, $n = 39$—Smithers, 1990) and the gestation period is 21 days (Ascaray, 1986). Captive *G. p. paeba* has a mean litter size of 4.6 (range, 1–6; $n = 7$—Dempster and Perrin, 1989*a*) and *G. p. exilis* has a litter size of 3.7 (range, 2–6; $n = 10$—Ascaray, 1986). Nipple-clinging does not occur and was mistakenly interpreted by Ascaray (1986). Female pygmy hairy-footed gerbils brood their young with their hind feet widely spaced, and their forepaws stretched over the young. Young are regularly groomed. Mothers stimulate urination and defecation by licking the anogenital region of the young (Dempster and Perrin, 1989*a*).

Neonates are altricial and growth rate in the first 21 days of life is ca. 0.4 g/day (Dempster and Perrin, 1989*a*). Ear pinnae become free at 3–6 days of age, toes separate at 3–5 days, hair appears at 8–10 days, and eyes open at 14–18 days (Ascaray, 1986; Dempster and Perrin, 1989*a*). At 7–14 days of age, *G. p. paeba* is able to walk quadrupedally and exhibit a startle reaction. Weaning occurs from 21 days of age (Stutterheim and Skinner, 1973), self-grooming develops between days 11 and 26, socialization from 18 days, and sandbathing at 24–26 days (Dempster and Perrin, 1989*a*). Ascaray (1986) reported active crawling and a righting reflex at 3 days, incisor eruption and walking from 12 days, active exploration from 16 days, agonistic behavior from 20 days, and sexual maturity at 60–80 days of age.

ECOLOGY. *Gerbillurus paeba* is a terrestrial desert species that is active at night and seeks shelter in a burrow during daytime. Using Thornwaite's moisture index, (an empirical computation of potential evapotranspiration based on latitude, rainfall, and mean monthly temperatures), the major areas where *G. p. paeba* occurs are classified as arid (moisture index less than −40) or as semiarid (moisture index −40 to −20—Poynton, 1971). The limits of these zones define the ecological distribution of the species, although substratum is also important.

Gerbillurus paeba occurs on sandy soil or sandy alluvium that has scant cover from grass, scrub, or occasionally light woodland (Skinner and Smithers, 1990). It is common in the Kalahari Desert, where it is more abundant on dune slopes than on either calcrete riverbanks or pans with fine soil (Nel and Rautenbach, 1975).

Vegetative cover is a key environmental factor determining the distribution of *G. paeba* in the Kalahari Desert. When vegetation increases after rainfall, populations of *G. paeba* in the area decline (Nel, 1978). *G. paeba* does not occur on consolidated soils associated with mopane woodland in northeastern Botswana. Nevertheless, it occurs in the eastward extension of the Kalahari sands in northwestern Zimbabwe and is associated with the Mozambique sands of southeastern Zimbabwe and Mozambique. In northern Mozambique, it occurs on the sandy alluvium of the Bubye River (Smithers, 1983).

Sex differences in habitat preferences of *G. paeba* have been recorded at Gorrasis (25°18′S, 15°55′E) on the eastern edge of the Namib Desert (Christian, 1980*a*). Males selected microhabitats with sparse vegetation, whereas females preferred more dense cover, perhaps because energy and water demands increase significantly during lactation (Bowers and Smith, 1979).

Gerbillurus p. coombsi is restricted to sandy (preferably loose sand) areas of the Northern Province (Rautenbach, 1978), whereas *G. p. exilis* uses coastal dunes, preferring dune valleys to dune crests in the Eastern Cape. Burrows are excavated and most food is derived from plants in the valleys (Ascaray, 1986). Higher densities occur on vegetated dunes that facilitate burrow formation, but excursions also occur onto the beach to feed on littoral debris, and to unvegetated high dunes where windblown detritus, seeds, and insects accumulate (Ascaray, 1986). In the Namib Desert *G. p. paeba* occurs only on the eastern edge of the dunefield bordering the gravel plains of the Pro-Namib (Griffin, 1990). Extensive live trapping (Boyer, 1987; Griffin, 1990) indicates that *G. p. paeba* does not occur far into the immense dune system. Although *G. paeba* was recorded from the Namib dunes (Laycock, 1975), these specimens were likely *G. tytonis*. Christian (1979*a*, 1980*b*) also reported *G. paeba* from the Namib dunes; however, his study site was peripheral to the main dune system and was regarded as ecotonal dune base/gravel plains (Boyer, 1987).

The density of *G. paeba* can increase from near zero to 59 gerbils/ha following good rains (Christian, 1980*b*). After an experimental burning procedure on arid grassland, *G. paeba* recolonized immediately and established stable populations on burnt and unburnt plots (Christian, 1977). *G. paeba* responded rapidly to experimentally increased availability of water by increased rate of pregnancies, a higher proportion of lactating females, and an extension of the breeding season into the hot, dry portions of the year (Christian, 1979*b*).

In the eastern Namib Desert at Far East, where *G. paeba* and *G. tytonis* coexist, *G. paeba* avoids zones of high diversity of plant species and prefers compact soils (Boyer, 1987). Interdune valley habitat is preferred by *G. paeba*, but because of interspecific competition with *G. tytonis*, subordinate *G. paeba* are excluded from interdune habitat at certain periods or densities (Boyer, 1987; Dempster and Perrin, 1990*c*).

Simple, unbranched burrows constitute about 80% of those occupied by *G. p. paeba*. Each has a single entrance leading to a blind-ending tube which is occasionally broadened, forming a cavern-like area, or nest (Downs and Perrin, 1989). *G. p. exilis* has a high frequency of complex, branched burrows, the entrances of which are hidden in vegetation and not plugged with sand (Ascaray, 1986). A significant correlation was found between density of burrows and density of *G. p. exilis* (Ascaray, 1986). Burrow temperatures of *G. p. paeba* are 22.9–24.4°C at surface temperatures of 15.8–28.4°C, whereas humidity within the burrow is at its peak in early morning and is affected by the presence of fog or cloudy conditions (Downs and Perrin, 1989). Nests were not found at the end of tunnels but in deep, steep, side tunnels. *G. paeba* constructs a cup-shaped nest of shredded vegetation (Ascaray, 1986; Downs and Perrin, 1989). Nests of *G. p. exilis* are composed chiefly of leaves of *Sporobolus virginicus* and *Mariscus congestus* and roots, particularly those of *Juncus kraussi* (Ascaray, 1986). Seeds, grasses, and insects are cached in burrows (Ascaray, 1986; Downs and Perrin, 1989).

Mean size (± *SE*) of home ranges for male ($n = 14$) and female ($n = 11$) *G. p. exilis* based on ten location records were 1.42 (± 1.17) and 0.76 (± 0.62) ha, respectively, whereas three individuals captured >20 times had home ranges of 2.56, 3.54, and 4.13 ha (Ascaray and McLachlan, 1990). Average distance moved between successive captures for all ages, sex classes, and seasons was 102 m; adult males (*G. p. exilis*) in the breeding season exhibited the farthest mean movement (130 m), whereas adult (*G. p. paeba*) females in the breeding season moved the smallest distance (68 m—Boyer, 1987). The density of *G. p. paeba* at Far East in the eastern Namib Desert was from 1.0 to 7.7/ha (biomass, 22–140 g/ha) during 1984–1985 (Boyer, 1987), whereas average density for the Alexandria dune field population of *G. p. exilis* was 1.7/ha, with an annual range of 0.7–3.3/ha (Ascaray et al., 1991).

Early, anecdotal studies reported that *G. paeba* ate seeds of grasses, bushes, and trees (*Acacia*—Smithers, 1971), and later authors (Skinner and Smithers, 1990) included seeds of the raisin bush (*Grewia*), fallen pods of thorn trees (*Acacia*), and insects. Principal summer foods of *G. p. exilis* are seeds of *Arctotheca populifolia*, *Gazania rigens*, and *Senecio inaequideus* (Ascaray et al., 1990). Arthropods are a highly preferred food in summer. In the Karoo, foliage consumption was highest in winter, but seeds dominated the diet during summer and autumn, and insects during spring (Kerley, 1989).

Although *G. p. paeba* feeds predominantly on seeds in the Kalahari (Nel, 1978), this is not so in the Namib Desert, and granivory is limited and seasonal in the Karoo (Kerley, 1989). Mean composition (by volume) of the diet of *G. p. paeba* from the Karoo was 36.2% seeds, 46.8% foliage, and 17.1% insects (Kerley, 1989). Microscopic analyses of stomach contents of 42 *G. p. paeba* from the Namib Desert showed little seasonal variation in diet, and composition (by volume) was 52.9% arthropod, 40.6% green plant material, 3.8% seed, and 3.0% unidentified material (Perrin et al., 1992). In contrast, the diet of *G. p. paeba* in the Kalahari was 76.4% white plant material, 23.6% green plant material, and 0.0% insects in winter, and changed to 39.3%, 43,8%, and 16.8%, respectively, in summer (Nel, 1978).

Gerbillurus paeba populations remove plant material from interdune plains in the Namib Desert, and thus affect plant growth and reproduction (Perrin and Boyer, 1994); however, the impact is likely local and transient. Predation on invertebrates and seeds has little long term impact (Perrin and Boyer, 1994).

The major predators of *G. p. paeba* in the Pro Namib are the spotted eagle owl *(Bubo africanus)* and black-backed jackal (*Canis mesomelas*—Boyer, 1987). In the Alexandria dunefield *G. p. exilis* falls prey to the same predators and the large-spotted genet (*Genetta tigrina*—Ascaray, 1986). *G. paeba* has been identified in owl pellets (Grindley et al., 1973; Nel and Nolte, 1965; Skinner et al., 1980).

The parasitic mites *Haemolaelaps oliffi* and *Androlaelaps marshalli* are known from *G. paeba* (Zumpt, 1961). Four genera and 11 species of fleas occur on *G. paeba*, including *Chiastopsylla mulleri, C. numae* form *rossi, Dinopsyllus ellobius, Echidnophaga gallinacea, Xenopsylla davisi, X. h. hirsuta, X. lobengulai, X. philoxera, X. phyllomae, X. piriei*, and *X. trifaria* (De Meillon et al., 1961). Immature ticks of *Rhipicephalus capensis*, that are known to transmit the babesid protozoan *Theileria parva*, and hence East Coast fever in domestic cattle (de Graaff, 1981), occur on *G. paeba* (Theiler, 1962). *G. paeba* may also act as a reservoir for fleas (*Xenopsylla*) that transmit plague to humans (de Graaff, 1981).

BEHAVIOR. *Gerbillurus paeba* moves by quadrupedal saltation. In unrestricted locomotion, animals kick off with the hind feet, and land on the forepaws, with the hind feet placed anterior to the forepaws on landing. The distance (mean ± *SD*) between successive sets of footprints measured in the field was 22.2 ± 4.3 cm (Dempster and Perrin, 1990*a*).

The sleeping position was either a sitting position, with the head tucked under the body and the tail curled around the feet, or lying on the side (Dempster and Perrin, 1990*a*; Stutterheim and Skinner, 1973). On waking, *G. paeba* stretch, groom, and sandbathe. Grooming begins with the nose, which is wiped by both forepaws simultaneously, and proceeds in a cephalocaudal sequence. A bout of grooming terminates with shaking the whole body. Sandbathing consists of a rapid roll from flank to dorsum, repeated on the other side of the body (Dempster and Perrin, 1990*a*).

Gerbillurus paeba holds food in its forepaws and eats in a sitting position. Seed husks are stripped off using the incisors. Seeds are carried in the mouth and hoarded in different places in the cage, but insects and fresh food are not hoarded by caged animals (Dempster and Perrin, 1990*a*). Digging in the sand dominates activity during the dark phase of the light cycle. Animals dig with the forepaws and kick the sand away from the body with the hind feet. *G. paeba* cuts grass into short lengths and carries it to the nest, where it is formed into a cup shape using the nose and forepaws (Dempster and Perrin, 1990*a*).

G. p. exilis differs considerably from *G. p. paeba* in its agonistic behavior. In staged encounters, male and female *G. p. paeba* were very aggressive and highly active. Female *G. p. exilis* were less aggressive and male *G. p. exilis* were least aggressive and active, performing more contact-promoting behavior than other species (Dempster and Perrin, 1989*c*).

With respect to interspecific odor discrimination, *G. paeba* showed little preference for conspecific odors (Dempster and Perrin, 1990*b*). Female *G. paeba* preferred odors of male conspecifics, but the difference was not significant.

Gerbillurus paeba paeba footdrum with short bursts of rapid thumping of the hind feet alternately (Dempster and Perrin, 1990*a*). Ultrasonic vocalizations of *G. p. paeba* are strongly modulated sweep calls between ca. 57 kHz and 70 kHz, with a mean duration of 78 msec. *G. p. exilis* emits a similar call, but at a lower frequency range, ca. 46–57 kHz (Dempster and Perrin, 1991). *G. p. paeba* and *G. p. exilis* also emit a broadband click vocalization which has a duration of 21–22 msec. Vocalizations occur significantly more frequently than expected during and after sexual behavior, but are inhibited during agonistic and solitary behavior (Dempster et al., 1991).

With respect to behavior between males and females, *G. p. paeba* and *G. p. exilis* performed little agonistic behavior, but huddled frequently (Dempster et al., 1992). Males followed females, which retreated and reacted with aggressive and/or upright postures. Presentation by female, which occurred rarely, was followed by male mounting. Aggressive behavior led to submissive behavior or an upright posture from the partner, and this sequence was linked with sexual behavior. Huddling, groom invitation, and allogrooming occurred in sequence in both *G. p. paeba* and *G. p. exilis*. *G. p. paeba* and *G. p. exilis* differ little in behavior during conspecific male-female encounters. Male *G. p. exilis* performed significantly more sexual behavior with females of their own subspecies than with female *G. p. paeba*. Female *G. p. exilis* performed significantly more submissive behavior with male *G. p. paeba* than with males of their own subspecies. Neither male nor female *G. p. paeba* showed evidence of discrimination between their own subspecies and *G. p. exilis* (Dempster et al., 1992).

GENETICS. The diploid number of chromosomes is 36 and the number of autosomal arms is 68 (Qumsiyeh, 1986; Schlitter et al., 1984). No differences exist in the standard karyogram of *G. paeba* (all subspecies) and *G. tytonis*. All autosomes of *G. paeba* are biarmed; the X chromosome is a large submetacentric, whereas the Y chromosome was described as a small acrocentric (Qumsiyeh, 1986; Schlitter et al., 1984). Three individuals had a biarmed Y chromosome (Qumsiyeh et al., 1991). *G. p. exilis* is indistinguishable from *G. p. paeba* on the basis of G- and C-bands (Qumsiyeh et al., 1991). Intraspecific variation in G- and C-banding of *G. paeba* involves the structure of the pericentromeric region of a chromosome which probably resulted from the fusion of arms 29 and 32 of the primitive taterilline karyogram. The biarmed chromosome 33, which is entirely heterochromatic, varies in size among individuals (Qumsiyeh, 1986). Other intraspecific variations include size of the heterochromatic regions near the centromere of arm 9, and presence or absence of a distinct interstitial C-band positive segment in arm 29 (Qumsiyeh et al., 1991).

REMARKS. The specific name is variously described as being derived from the Greek *paidos* meaning child, implying small stature reminiscent of the small size of this gerbil (de Graaff, 1981), or as the Setswana name for a mouse (Skinner and Smithers, 1990). The primitive *Gerbillurus* karyotype was probably similar to that found in *G. paeba* and *Tatera robusta* (2n = 36, AA = 68—Qumsiyeh et al., 1987). *Gerbillurus paeba*, the most widespread and morphologically primitive species of the genus, was assigned to a monotypic subgenus, *Progerbillurus* (Pavlinov, 1982). A cladistic analysis based on cranial and odontological characters and the structure of the feet determined that the genus *Gerbillurus* is monophyletic, and that *G. paeba* branched first from the clade that eventually led to subgenera *Paratatera* and *Gerbillurus* (Pavlinov, 1987). The widespread distribution, generalist diet, and generalised behavior of *G. paeba* support its designation as the most primitive member of the genus (Dempster et al., 1992). Skull diagrams were drawn by K. Duxbury.

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