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Gerbillurus tytonis Bauer and Niethammer, 1959
Dune Hairy-footed Gerbil

Gerbillurus (Gerbillurus) ravidus tytonis Bauer and Niethammer, 1959:255. Type locality, “Sossusville, Namib Desert, Namibia.”

CONTEXT AND CONTENT. Order Rodentia, Family Muridae, Subfamily Gerbillinae, Tribe Taterellini, Subtribe Gerbillurina, Genus Gerbillurus, Subgenus Paratatera. G. tytonis was given species rank by Schlitter (1973) and generic status by Davis (1975). No subspecies have been described.

DIAGNOSIS. Gerbillurus tytonis (Fig. 1) is similar in color and size to G. paeba where they coexist, but G. tytonis is distinguished by its longer tail (ca. 30% longer than head and body in G. tytonis, ca. 20% longer in G. paeba), and the different hind feet, with those of G. tytonis considerably longer and broader than those of G. paeba (length of hind foot = 33.4 mm in G. tytonis, 26.5 mm in G. paeba). G. tytonis has a fringe of hairs on each toe of the hind foot, which is absent in all other Gerbillurus species (Griffin, 1990).

Skulls of G. tytonis (Fig. 2) are distinguished from those of G. paeba by larger tympanic bullae (oblique length ca. 9.8 mm versus <9.0 mm) and shorter posterior palatal foramina (ca. 1.1 mm versus >1.6 mm—Griffin, 1990; Schlitter, 1973). Tympanic bullae of Gerbillurus tytonis are smaller than those of G. ravidus (oblique length ca. 9.8 versus ca. 10 mm—Schlitter, 1973).

GENERAL CHARACTERS. Gerbillurus tytonis is a small, gracile gerbil with long, broad hind feet. Soles of the feet are well-furred. Upper body is rich reddish or russet brown and underparts are white. The two colors are sharply demarcated; white of the underparts extends to fore and hind feet and well up the flanks. Tail is brown on the dorsum and white on the ventrum, and has a small tassel of gray hairs on the end. Ears are cinnamon buff (Kinner and Smithers, 1990). Fur is loose and long (de Graaff, 1981).

Gerbillurus tytonis is not sexually dimorphic (Schlitter, 1973). Body mass (mean ± SE) for G. tytonis collected in the dunes of the Namib Desert is 24.0 ± 0.9 g (n = 711—Boyer, 1987). Mean (and range) of external measurements (in mm) for G. tytonis are as follows: total length, 225.7 (205-240, n = 55); length of tail, 126.5 (113-141, n = 55); length of hind foot, 33.4 (28-36, n = 57); length of ear from notch, 13.0 (12-14, n = 57—Schlitter, 1973). Cranial measurements (mean and range) in mm for G. tytonis are the following: occipito-nasal length, 29.3 (28.1-30.4, n = 43); breadth across zygomatic arches, 15.6 (14.2-16.6, n = 39); greatest breadth of braincase, 13.9 (13.4-14.6, n = 43); least interorbital breadth, 5.5 (5.2-6.0, n = 57); breadth of rostrum, 4.1 (3.7-4.5, n = 50); greatest length of nasals, 11.6 (10.5-13.0, n = 55); oblique length of auditory portion of auditory bulla, 9.8 (9.3-10.4, n = 47); length of maxillary toothrow, 4.2 (4.0-4.5, n = 50); breadth of palate at M3, 4.9 (4.5-5.3, n = 38); length of anterior palatal foramina, 3.4 (3.1-3.6, n = 56); length of posterior palatal foramina, 1.6 (1.6-1.8, n = 57); greatest height of skull, 12.4 (12.0-12.8, n = 29); breadth of auditory bulla, 8.3 (7.9-8.9, n = 49—Schlitter, 1973).

DISTRIBUTION. Gerbillurus tytonis is the only gerbil species permanently resident in the main sand sea of the Namib Desert south of the Kuiseb river from Swakopmund to Luderitz and immediately adjacent areas (Fig. 3; Griffin, 1990). This includes Sossusvlei (Bauer and Niethammer, 1959), Sandwich Harbour, Gobabeb, the Farm Canaan adjoining the diamond area of Namibia (Meester et al., 1986) and at Far East, Bushman’s Circle, and Nara Valley (Boyer, 1987, 1989). It occupies coastal and inland dune systems. No fossorial species of this kind are known.

FORM AND FUNCTION. Dental formula is i 1/1, c 0/0, p 0/0, m 3/3, total 16 teeth. At Uisimab in the dunes of the Namib Desert, field water turnover rates of G. tytonis decreased from 178.0 ml kg⁻¹ day⁻¹ in November to 98.4 ml kg⁻¹ day⁻¹ in March (Downs and Perrin, 1990a). Water turnover rate, daily energy expenditure, and assimilation efficiency in the laboratory were 554.1 ml kg⁻¹ day⁻¹, 2.1 kJ g⁻¹ day⁻¹, and 91.09%, respectively, when animals were fed a diet of mealworms and carrots without free water, compared to 365.4 ml kg⁻¹ day⁻¹, 2.56 kJ g⁻¹ day⁻¹, and 91.95%, respectively, when fed sunflower seeds. When diet was changed from seeds to insects, urine production increased from 0.119 to 0.988 ml/day (Downs and Perrin, 1990b). Maximum urine osmolality varied with diet in the laboratory, from 5.213 osmol/kg on millet seed to 6.129 osmol/kg on mealworms, whereas urine osmolality in the field was considerably less at 3.152 osmol/kg (Downs and Perrin, 1991b). Water turnover rates decrease with decrease in potential water yield of diet in the laboratory (Downs and Perrin, 1990b). Without any succulent material as a supplement, G. tytonis maintains body mass on an invertebrate diet but loses mass on a dry seed diet.

Urea concentration varied from 1.813 mM/ml on a diet of mealworms to 4.769 mM/ml on a diet of sunflower seeds; both diets were supplemented with carrots and water. Low resolution mass spectrometric analysis of urine crystalline fractions confirmed the presence of allantoin (Downs and Perrin, 1991a). G. tytonis has a simple kidney, with characteristic outer and inner medullary zones and an elongated papilla renis extending into the ureter (Downs and Perrin, 1991a).

Basal metabolic rate of G. tytonis is 1.06 mol O₂ g⁻¹ h⁻¹ (72.1% of that expected for its body mass) at thermoneutrality (32.4–34.9°C), and thermal conductance is 0.168 ml O₂ g⁻¹ h⁻¹ °C⁻¹ (92.3% of that expected by mass—Downs and Perrin, 1990c). Body temperature is regulated from ambient temperatures of 5°C to 30°C. G. tytonis overcomes high daytime temperatures by nocturnal activity and use of burrows (Downs and Perrin, 1991b).

ONTOGENY AND REPRODUCTION. Reproduction and recruitment into the G. tytonis population occurs in summer. On the northern fringe of the central Namib Desert dune system at

FIG. 1. Gerbillurus tytonis. Photograph by A. Bruton.
Nara Valley and Bushman’s Circle, 48 km and 85 km east of the coast, respectively, G. tytonis bred during summer of 1984 and 1985, which is the period of potential rainfall (Boyer, 1987). Adult males had scrotal testes throughout the year. About 25% of females captured between February and May of 1984 were reproductively active, whereas a year later, ca. 50% of females were reproductively active between December and May.

Cyclical changes in vaginal smears (n = 2 females, 5 cycles) had a mean duration (± SD) of 6.2 ± 1.2 days. A vaginal cast was visible in three unmated females (Dempster and Perrin, 1989). Copulation was observed in two pairs of G. tytonis (Dempster, 1990). G. tytonis has an unusual pattern of copulatory behavior, with a single ejaculation, lock, and deposition of a copulatory plug. For two observations, the lock lasted 20 and 26 s. Precopulatory behavior was brief and included several postures which may enhance olfactory communication (Dempster, 1990). Females indicated readiness to mate by stopping adjacent to males, with the forepaws extended anteriorly, but lordosis was not clearly discernible. The male clasped the female while making pelvic thrusts; several deep thrusts indicated that intromission had occurred. Pelvic thrusting ceased once a lock had occurred. After separating, both animals groomed their genitals, both sunbathed, and males marked by perineal dragging. Copulatory plugs were visible in the vaginæ of both females after copulation. No further intromissions occurred after ejaculation.

Seven litters of G. tytonis have been born and raised in captivity (Dempster and Perrin, 1989a). One female G. tytonis was observed giving birth to the last neonate of a litter of four pups. Strong abdominal contractions preceded the birth, and the female groomed her agonal region and rested between contractions. The neonate was expelled while the female was in a quadrupedal posture and the female then consumed the placenta and groomed the neonate. Several bouts of grooming of the young, and of the agonal region of the female, were interspersed with periods of rest in 2 h following parturition.

At birth, G. tytonis has an individual mean body mass of 1.9 g (n = 22) and litter size averages 4.4 (range 2–6, n = 7—Dempster and Perrin, 1989a). Mean length of head and body of newborn individuals is 34.2 mm and mean length of hind foot is 6.5 mm (n = 17). At birth, G. tytonis weighs 7.6% of adult size and gains 1.6% of adult mass per day during the linear phase of growth (10–50% of adult body size). Neonates are hairless but with vibrissae present on the nose. Ear pinnae are folded flat and fused to the skin of the head in neonates, becoming free at 6–7 days of age. Toes are fused at birth but separate at 6–8 days, whereas hair appears at 10–13 days and eyes open at 22–24 days of age. Walking, jumping, quadrupedal salutations, and sand-digging are evident at 21 days of age. Social interactions, involving mounting between cage mates, aggressive interactions, and all grooming, occur after 35 days of age.

ECOLOGY. Gerbillurus tytonis is a terrestrial species that is active at night and seeks shelter in a burrow during daytime. Populations occur in hot, dry areas on shifting red sand dunes of the Namib Desert where the mean annual temperature is >18°C, and rainfall is <125 mm/year (Downs and Perrin, 1989). Most G. tytonis burrows occur in sand stabilized by vegetation, either Triandema hereroensis or Siphogrostis sabulicola. Burrows have one or two entrances, with an average diameter of 55 mm, an average depth of about 225 mm, and an approximate length of 1 m; they may be simple (unbranched) or complex (branched—Downs and Perrin, 1989).

Densities of 17 animals/ha (biomass, 363 g/ha) have been re-
corded (Boyer, 1987), but abundance is highly variable, both spatially and temporally. In May 1983, five of nine G. tytonis snap- trapped at night were males from a live trap 1 km to the north, and four had been live-trapped within the previous 48 h (Boyer, 1987). This suggests extremely large home ranges and foraging distances.

At Far East on the eastern edge of the dune sea (138 km from the coast) that borders on the Pro Namib, G. paeoa coexists with G. tytonis. Habitat preferences facilitate niche segregation because G. tytonis prefers zones with high plant species diversity, but avoids compact soils such as interdune valleys, a habitat preferred by G. paeoa (Boyer, 1987). G. tytonis is competitively superior to G. paeoa in interspecific encounters staged in the laboratory (Dempster and Perrin, 1990b), and may exclude G. paeoa from valley beds at certain times (Boyer, 1987). Trapping surveys (Griffin, 1990) in vegetated dunes and the adjacent Kuiseb River bed in 1976 and in the Swakop River bed and adjacent vegetated dunes at Swakopmund in 1978 showed equal abundance of G. tytonis and G. paeoa in dunes, but G. paeoa was four times more abundant than G. tytonis in river bed areas. These years were characterized by high rainfall and high rodent densities.

Predation risk and intra- and interspecific competition influences habitat selection and activity of G. tytonis (Hughes et al., 1994). At the Namib Desert Research Unit of Namibia at Gobabeb (25°24'S, 15°03'E), G. tytonis co-occurs with the striped mouse (Rhabdomys pumilio) in a vegetated island in the dune sea. Both species prefer the same microhabitat (nara; Acanthoscyos horrida), although G. tytonis also inhabited a second microhabitat (grietebos; Sabulculus) where predation risk was greater. Two different study techniques (tracking and seed trays) suggest that G. tytonis decreased foraging activity in vegetated areas during periods of increased illumination (full-moon periods). Removal of striped mice or conspecifics resulted in a significant increase in the foraging activity of G. tytonis. High seed viability of G. tytonis to predation may result in shared occupancy of the safest habitat and competition for limited resources (Hughes, 1990).

Stomach contents of G. tytonis from several localities within the Namib Desert suggest an omnivorous diet (Boyer, 1987; Perrin et al., 1992). By volume, seeds, green plant material, and arthropods comprised 7.9%, 36.4%, and 52.6% of the diet respectively at Far East; 17.1%, 45.9%, 33.5% respectively at Bushman’s Circle; and 10.4%, 28.9%, and 58.4% respectively at Nara Valley. The amount of green plant tissues in the diet peaked during the hot dry summer (October–January), whereas the maximum intake of seeds occurred during winter (May–October), when 33.5% of the diet was comprised of seeds. In addition to seasonal variations in diet, marked differences occurred among individuals. Major predators of G. tytonis are the spotted eagle owl (Bubo africanus) and the black-backed jackal (Canis mesomelas—Boyer, 1987).

BEHAVIOR. G. tytonis moves by quadrupedal salation. Tracks in the desert sand indicate that hind feet are placed anterior to front feet during locomotion across open sand. Distance between successive sets of footprints was ca. 31 cm (SD = 10.1—Dempster and Perrin, 1990c). G. tytonis digs in sand using the forepaws simultaneously to dig sand under the body and then kicks the sand back with the hind feet. Nests are constructed from grass, which is cut into short sections and carried in the mouth. Nests are shaped using the nose and forepaws. Seeds are scoured-haard.

The normal sleeping posture is a curled position with the head tucked under the body and the tail curled around the feet. On waking, animals emerge from the nest, stretch, and urinate in a selected spot. Grooming begins with the nose and proceeds in a cephalocaudal sequence. Sandbathing is important in maintaining coat condition in G. tytonis (Dempster and Perrin, 1990c).

Agnostic behavior of G. tytonis has been studied in staged encounters in the laboratory (Dempster and Perrin, 1989a, 1989d). Groups of four behaviors were identified by motivational analysis: tolerance, aggression, and solitary, aggressive, submissive, and sexual. In intraspecific same-sex pairings, G. tytonis was the most aggressive and active of all Gerbillus species. Dominance was clearly established in >80% of G. tytonis encounters by chasing, attacking, fleeing, and crouching, rather than by fighting. In intraspecific male-female pairings, females G. tytonis dominate males, and behaved aggressively toward unfamiliar males (Dempster and Perrin, 1989d). Behavior of G. tytonis in staged male-female encounters was characterized by high levels of upright aggressive postures and low levels of huddling (Dempster et al., 1992).

G. tytonis may identify conspecifics by deposited chemosignals. Male G. tytonis significantly preferred conspecific odors of females in artificially induced estrus, whereas female G. tytonis preferred odors of male G. tytonis to those of G. paeoa (Dempster and Perrin, 1990c).

Ultra-social calling occurs during male-female encounters of G. tytonis in the form of a unique stutter vocalization which consists of a series of clicks and a strongly modulated sweep call (Dempster and Perrin, 1991). The sweep calls range from 63 to 48 kHz and have a mean duration of 58 ms (n = 61). Stutter calls cover the frequency range 34–11 kHz and have a mean duration of 1.418 ms (n = 19—Dempster and Perrin, 1991). Vocalizations are positively associated with sexual and contact-promoting behavior, and rarely accompany non-contact and agonistic behavior (Dempster et al., 1991). Ultra-social vocalizations accompanied copulation in two observed copulations (Dempster, 1990).

GENETICS. G. tytonis has a diploid chromosome number of 36 with 68 autosomal arms. The standard karyotype of G. tytonis is indistinguishable from that of G. paeoa (Schlittler et al., 1984). Comparison of G- and C-bands of G. tytonis and G. paeoa identified a pericentric inversion in arms 11/12 and the absence of a heterochromatic addition on 33 in G. tytonis (Quensiyeh et al., 1991).

REMARKS. G. tytonis was first described from skulls found in pellets of the barn owl, Tyto alba (Bauer and Niehsmann, 1959). Its type locality is roughly described by Schlitter (1973). The specific name “tytonis” is derived from the generic name of barn owls, and means “of tyto”.

Morphometric data place G. tytonis closer to G. setzeri and G. vallinii than to G. paeoa (Schlittler et al., 1984). Pavlinov (1987) performed a cladistic analysis of the genera and subgenera of the Taterrillinae based on morphological features including structure of the foot, odontological characters, and craniodental characters. Cladograms based on morphological characters present a different branching sequence from karyological data (Quensiyeh, 1986; Quensiyeh et al., 1991). Based on morphometrics, Pavlinov (1987) proposed that the subgenus Progerbillus (G. paeoa) be split first from the subgenus Gerbillus (G. vallinii and G. setzeri) and Paratatera (G. tytonis). According to Pavlinov (1987), subgenus Gerbillus and Paratatera should be regarded as “species groups” within one subgenus Gerbillus. Progerbillus should be retained as a subgenus. The cladogram derived from G- and C-banding of chromosomes proposes an unresolved trichotomy, with G. paeoa, G. tytonis and a separate clade leading to G. vallinii and G. setzeri diverging at the same time (Quensiyeh et al., 1991). Skulls were drawn by K. Duxbury.

LITERATURE CITED


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