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Elephantulus rufescens.

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Elephantulus Thomas and Schwann, 1906

Elephantulus Thomas and Schwann, 1906:577. Type species *Macroscelides rupestris* Smith, 1831, by original designation.
Nasilio Thomas and Schwann, 1906:578. Type species *Macroscelides brachyrhynchus* Smith, 1836, by original designation.
Elephantomys Broom, 1937:758. Type species *Elephantomys langi* Broom, 1937, by original designation.

CONTEXT AND CONTENT. Order Macroscelidea, Family Macroscelididae, Subfamily Macroscelidinae. *Elephantulus* includes 10 extant species confined to the African continent; the following key, modified from Corbet (1971), should aid in their identification.

1 Sternal (pectoral) gland present, a naked or short-haired patch in center of thorax 2
Sternal gland absent 4
2 (1) Prominent brown mark behind eye; two lower molars, i.e., 10 lower teeth 3
No brown mark behind eye; three lower molars, i.e., 11 lower teeth ..... *Elephantulus fuscipes*
3 (2) Hair of tail becoming long towards the tip, forming a brush; tail about 120% of head and body; I2 equal in size to I1 and I3 ..... *Elephantulus revoili*
Hair of tail not forming a brush; tail about equal to head and body; I2 much smaller than I1 ..... *Elephantulus rufescens*
4 (1) Tail shorter than head and body; three lower molars, i.e., 11 lower teeth 5
Tail not shorter than head and body; two lower molars, i.e., 10 lower teeth 6
5 (4) Supratragus swollen and twisted backwards on a constricted stalk; upper toothrow less than 18 mm ..... *Elephantulus fuscus*
Supratragus untwisted ..... *Elephantulus brachyrhynchus*
6 (4) P1 with a lingual cusp; P2 molariform, with two well-developed lingual cusps 7
P1 lacking a lingual cusp; P2 sectorial with or without small lingual cusps 8
7 (6) Size larger; upper toothrow over 18.7 mm; tail about 115% of head and body, distinctly tufted at tip; P2 and P3 with three cusps arranged in a triangle ..... *Elephantulus rupestris*
Size smaller; upper toothrow under 18.7 mm; tail about 106% of head and body, not distinctly tufted; P2 and P3 with only two cusps arranged transversely ..... *Elephantulus intufi*
8 (6) Ectotympanic parts of bullae inflated to same level as entotympanic parts; I2 equal to I1 and I3; South African distribution 9
Ectotympanic parts of bullae much less inflated than entotympanic parts; I2 larger than I1 and I3; North African distribution ..... *Elephantulus rozeti*
9 (8) P2 with one or two lingual cusps; P1 with two roots; supratragus small and thick; premaxillary suture slightly sinuous; tail bicolored throughout its length, yellow-brown above ..... *Elephantulus myurus*
P2 without a lingual cusp; P1 with a single root; supratragus large and thin; premaxillary suture straight; tail black above, distal half black all around and slightly tufted ..... *Elephantulus edwardi*

Elephantulus rufescens (Peters, 1878)

Rufous Elephant-Shrew

Macroscelides rufescens Peters, 1878:198. Type locality (cited by Corbet and Hanks, 1968:82) Ndi, Taita, Kenya.
Macroscelides pulcher Thomas, 1894:69. Type locality "Usambiro, south of Victoria Nyanza" (Lake Victoria, Tanzania).
Macroscelides boranus Thomas, 1901*a*:802. Type locality "Mega, Western Boran Galla, south east of Lake Rudolf." Moreau et al. (1946) stated that this locality was "doubtless Mega, at 4° N, in Abyssinia (Ethiopia), not Kenya Colony, and east of the middle of Lake Rudolf."
Macroscelides peasei Thomas, 1901*b*:154. Type locality "Hoolul, Abyssinia" (30 miles northwest of Harar, Ethiopia; Moreau et al., 1946).
Macroscelides somalicus Thomas, 1901*c*:255. Type locality "Arabsiyo, Somaliland" (25 miles northwest of Hargeisa, Somalia; Moreau et al., 1946).
Elephantulus dundasi Dollman, 1910:95. Type locality "Harich, near Lake Baringo, British East Africa" (Kenya).
Elephantulus phaeus Heller, 1910:8. Type locality "Njoro O Solali, Sotik District, British East Africa" (Kenya).
Elephantulus delicatus Dollman, 1911:652. Type locality "Orr Valley, Mt. Nyiro" (Kenya).
Elephantulus ocularis Kershaw, 1921:563. Type locality "Dodoma, Tanganyika Colony, 36°10′E., 6°5′S."
Elephantulus renatus Kershaw, 1923:588. Type locality "Gwao's, near Itiga, Singida, 30°40′E., 4°25′S., about 85 miles N.W. by N of Kilimatinde" (Tanzania). Swynnerton (1945) reported the correct location of Gwao (=Ikungi village) as 34°47′E, 5°7′S.

CONTEXT AND CONTENT. Context in generic account above. Corbet and Hanks (1968) concluded that no objective subspecific boundaries could be recognized. Corbet (1971), however, considered the following six subspecies provisionally valid:

E. r. boranus (Thomas, 1901*a*:802), see above.
E. r. dundasi Dollman, 1910:95, see above (*delicatus* Dollman, *phaeus* Heller, *rendilis* Lonnberg, and *hoogstraali* Setzer are probable synonyms).
E. r. peasei (Thomas, 1901*b*:154), see above.
E. r. pulcher (Thomas, 1894:69), see above (*renatus* Kershaw and *ocularis* Kershaw are probable synonyms).
E. r. rufescens (Peters, 1878:198), see above (*mariakanae* Heller a synonym).
E. r. somalicus (Thomas, 1901*c*:255), see above.

DIAGNOSIS. A hairy ventral surface on the rhinarium of *E. rufescens* distinguishes it from all other species of elephant-shrews, except *E. revoili*. *Elephantulus rufescens* can be differentiated from *E. revoili* by the following characteristics: *E. rufescens* is smaller (mean total length about 255 mm compared with about 291 mm in *E. revoili*), I2 of *E. rufescens* is much smaller than I1 whereas in *E. revoili* I2 equals I1, and the tail of *E. rufescens* is equal to its head–body length but the tail of *E. revoili* is about 120% of its head–body length with hair that becomes long toward the tip, forming a brush.

GENERAL CHARACTERS. *Elephantulus rufescens* exhibits no secondary sexual dimorphism. Rathbun (1979) reported mean measurements (mm ± 1 SD) based on 18 adult specimens (11 males, 7 females) collected near Kibwezi, Kenya, as: total length, 255.3 ± 9.9; tail length, 133.3 ± 7.3; mass, 58.0 ± 7.3 g. Animals collected by Neal (1982) near Rainkombe, Kenya, were smaller; female body mass was 45–65 g and male body mass was 35–55 g. Adult captive animals (10 males, 10 females) maintained at the National Zoological Park (Washington, D.C.) had a hindfoot (sin unguis) length of 31.4 ± 0.8 and an ear (inside) length of 18.0 ± 2.0. The large eyes are surrounded by a white ring interrupted by a dark patch that extends caudally about 12 mm from the periphery of the eye (Fig. 1). The proboscis is long (hence the vernacular name "elephant-shrew"), flexible, and almost always in motion. The dark-brown tail is sparsely haired and about equal to the head–body length. The pinnae are relatively large and naked. The dense, fine dorsal fur is brown, reddish brown, or buff and the ventral fur is white. Adults have white feet but those of juveniles are brown; otherwise the young are colored the same as adults. The

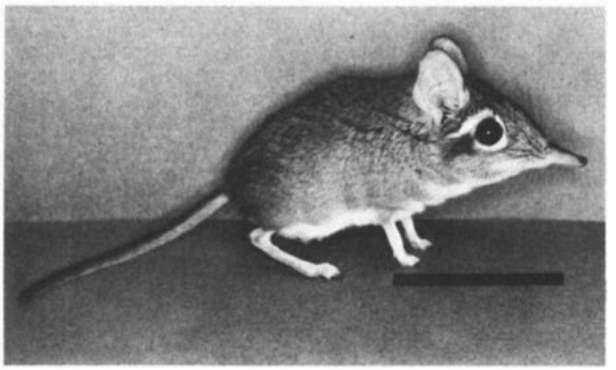

FIGURE 1. Adult male *Elephantulus rufescens* (bar = 60 mm).

prepuce is far forward on the abdomen and the testes are internal. Females have three pairs of teats. Both sexes have a prominent sternal gland fringed by short, wholly white hairs distinctive from the surrounding pelage. Elephant-shrews are semi-digitigrade, with hindlimbs much longer than forelimbs (Corbet and Hanks, 1968; Rathbun, 1979).

DISTRIBUTION. This elephant-shrew occupies dry woodland and grassland zones of East Africa from central Tanzania, at least as far south as the River Ruaha, northeast to northern Somalia and eastern Ethiopia and northwest to eastern Uganda and extreme southern Sudan (Fig. 2). An isolated population also may exist in extreme western Tanzania (Corbet and Hanks, 1968). Except for low-lying regions in Somalia and along the Tana River in Kenya, *E. rufescens* generally occurs above 300 m on well-drained soils (Kingdon, 1974).

FOSSIL RECORD. According to Patterson (1965) the Macroscelididae date from the early Oligocene of the Fayum (Egypt) as represented by a mandibular ramus of *Metoldobotes stromeri*. McKenna (1975), however, believed that members of the extinct Asiatic Paleocene-Oligocene family Anagalidae were early macroscelideans. Thus, Macroscelididae possibly descended from early Tertiary stock close to the Anagalidae if not from the anagalids themselves, before the early Oligocene. *Elephantulus* species are unknown in the fossil record until the Pleistocene. Butler and Greenwood (1976) reported that *E. fuscus leakeyi* commonly occurred in the Lower Pleistocene beds of Olduvai and that many *E. antiquus* dating from the Pliocene-Pleistocene were found at Makapansgat (Transvaal, South Africa). The major radiation of the Macroscelidinae must have occurred earlier because *Macroscelides* and *Elephantulus* were well-differentiated at Makapansgat (Butler, 1978). *Elephantulus antiquus* bears some resemblance to contemporary *E. rufescens* although Butler and Greenwood (1976) believed it had no living descendants.

FORM AND FUNCTION. Pelage coloration varies with the soil color (Kingdon, 1974). Adults have a well-developed sebaceous sternal gland, a rudimentary perineal gland (Kingdon, 1974), and neonates have active pedal glands (Rathbun and Redford, 1981). Mammae are pectoral (one pair) and abdominal (two pairs).

Evans (1942) analyzed the osteology of *Elephantulus*. When viewed from above, the skull of *E. rufescens* (Fig. 3) is roughly triangular with a long, tapering snout, a broad interorbital region and a swollen brain case. The skeleton of the proboscis is cartilaginous (Corbet and Hanks, 1968). Large maxillae form most of the side of the muzzle (Evans, 1942). Auditory bullae are inflated, although not as much as in *Macroscelides* (Corbet and Hanks, 1968; Evans, 1942).

The vertebral formula is C 7, T 13, L 7, S 3, Cd 25–26; the ilium is fused with the first and second sacral vertebrae (Corbet and Hanks, 1968). In Macroscelididae, a secondary shortening of the various segments of the forelegs coupled with a lengthening of the segments of the hindlegs resulted in proportions intermediate between quadrupedal and ricochetal mammals (Evans, 1942). The well-developed clavicles (Kingdon, 1974) and vertebral spinous processes are modifications for a "pseudo-hopping habitus" (Evans, 1942).

The dental formula is i 3/3, c 1/1, p 4/4, m 2/2, total 40. Incisors are short and peg-like with a single cusp; canines are small with two roots; and cheekteeth are quadritubercular, subhypsodont, and without cingula (Evans, 1942). Neonates have partially-erupted deciduous teeth.

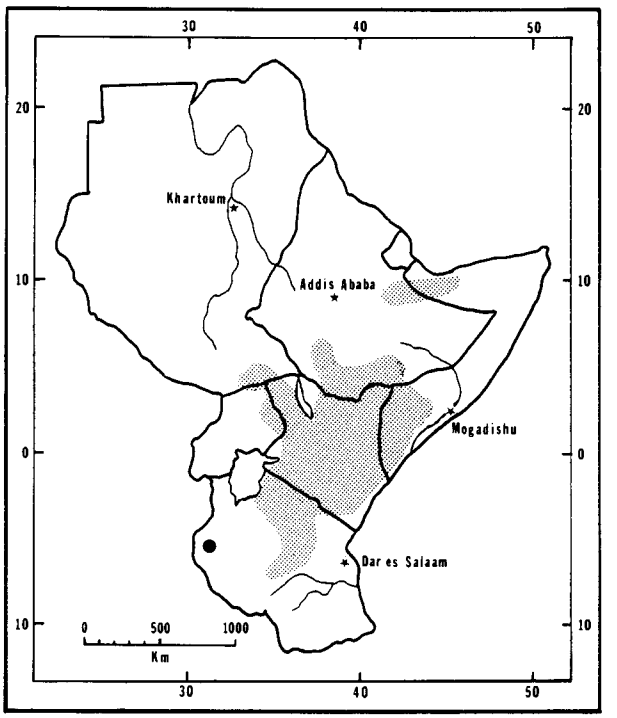

FIGURE 2. Distribution of *Elephantulus rufescens* (adapted from Corbet and Hanks, 1968, and Rathbun, 1976) in East Africa. The dot represents a small isolated population in western Tanzania.

A large, well-developed caecum is present (Anderson and Jones, 1967). The uterine horns join to form a median, slightly glandular uterus, lined by columnar epithelium. A cervix and true vagina (based on histological evidence) are absent; the vagina is replaced by a median extension of the uterus that opens into a shallow urinogenital sinus (Tripp, 1971).

ONTOGENY AND REPRODUCTION. Most literature on reproduction in *Elephantulus* is based upon histological examination of reproductive organs from preserved specimens of *E. myurus* (Tripp, 1970). The paucity of studies with live animals is a result of earlier difficulties of breeding captive elephant-shrews (Rathbun et al., 1981; Tripp, 1972). Since 1976, however, the National Zoological Park (NZP) has maintained a breeding colony of *E. rufescens* on which the following information on reproduction is based. There have been over 300 elephant-shrews born in this colony, including several sixth-generation individuals. Results of studies based on animals from the NZP colony are available on husbandry and breeding (Rathbun et al., 1981) and hand-rearing techniques (Koontz, 1981).

Gestation was estimated at 57 days (Rathbun et al., 1981) and 61 to 65 days (Koontz, pers. observ.). Only singleton and twin births were recorded and twinning is uncommon in primiparous females (Rathbun et al., 1981). There was no seasonality of births in captivity (Rathbun et al., 1981), at Rathbun's (1979) study site (Kibwezi, Kenya), or Neal's (1982) study site (Rainkombe, Kenya). Neal (1982) also found no seasonality in the number of young entering the population or in the testes mass of adults. Interbirth intervals for captive *E. rufescens* ranged from 58 to 145 days (n = 50) with peaks at 61 to 65 days and 76 to 80 days (Rathbun et al., 1981). Seven interbirth intervals for three free-ranging females ranged from 56 to 65 days with a mean of 61 ± 3.3 days (Rathbun, 1979). Neal (1982) estimated a potential mean annual production of 8.3 young per adult female.

Serial laparotomies performed on adult females housed alone indicated that *E. rufescens* is a spontaneous ovulator (Lumpkin et al., 1982). Tripp (1971) reported that some elephant-shrews (especially *E. myurus*) released many ova at ovulation but *E. rufescens* released only one or two. Physiological estrus or ovulation cannot be detected by the vaginal smear technique (Tripp, 1971; Lumpkin et al., 1982). A modal estrous cycle of 13 days (range 12 to 49 days) was estimated from observations of sexual behavior of vasectomized males during daily introductions to females (Lumpkin et al., 1982). In addition, copious vaginal secretions usually were present on days when females were sexually receptive.

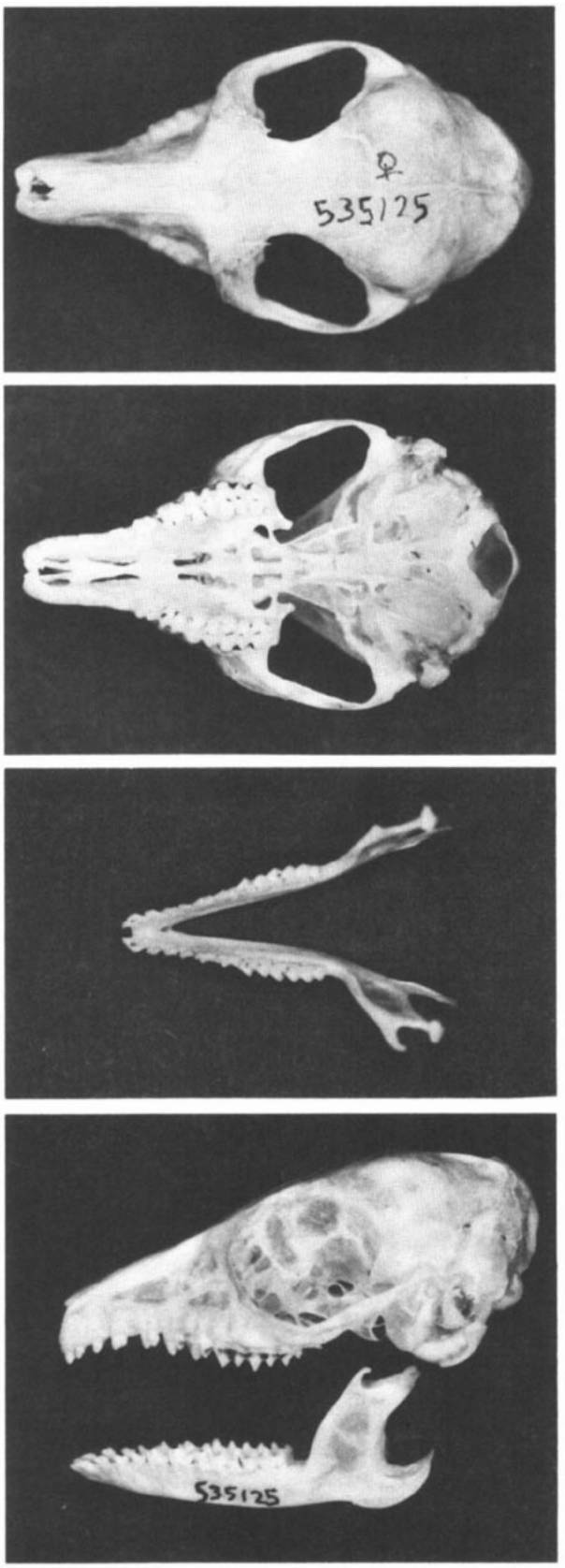

FIGURE 3. Dorsal and ventral views of cranium, occlusal view of mandible, and lateral view of cranium and mandible of *Elephantulus rufescens* (USNM No. 535125, female from Kibwezi, Kenya). Greatest length of skull is 35.2 mm.

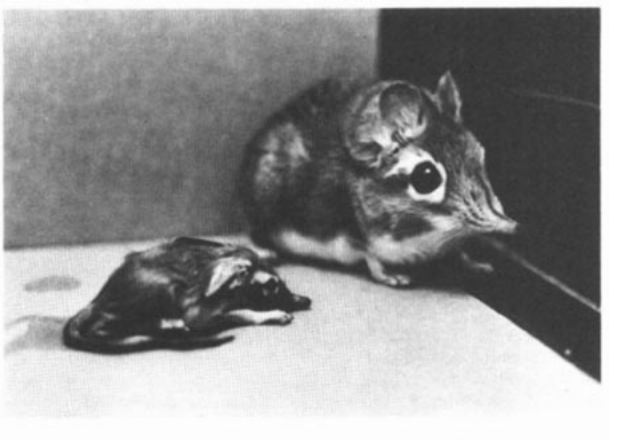

FIGURE 4. One-hour-old male and adult female *Elephantulus rufescens*.

Young are precocial at birth (Fig. 4). Rathbun et al. (1981) reported that 1-day-old young had an average mass of 10.6 g, (range 9.3 to 13.0 g, N = 11) and an average gain in mass between birth and day 50 of 0.77 g/day. Juveniles are weaned by day 25 (Rathbun, 1979). At about 40 days, the brown feet begin to turn white. Young reach adult size, are driven from their parental territory, and are able to conceive when approximately 50 days old (Rathbun, 1979; Rathbun et al., 1981).

Elephantulus rufescens has a relatively long life expectancy; three marked animals that Rathbun (1979) studied in Kenya lived at least 19 months and one of 26 wild-caught animals at NZP is still alive after 6 years in captivity.

ECOLOGY AND BEHAVIOR. Rathbun (1976, 1979) conducted a field study of the rufous elephant-shrew at Kibwezi, Kenya, where wooded bushland and environmental characteristics are typical of *E. rufescens* habitat. Rainfall patterns at Kibwezi are bimodal. The two wet seasons are March through April and November, whereas the dry seasons occur from December through February and May through October. The temperature ranges from 15°C to 30°C and averages about 23°C.

Elephantulus rufescens is active throughout the day, although peaks occur at dawn and dusk, with a midday rest period (Rathbun, 1979). Much activity, particularly in males, is devoted to "trail cleaning." Trails are constructed and maintained by removing leaves and loose debris with laterally directed forefoot sweeps. Grass and twigs are bitten in two and also swept off the trails. Except for foraging, activities are confined to these trails. Swift cursorial locomotion along unobstructed trails may be vital to escape predation by snakes (Rathbun, 1979). Elephant-shrews were never observed to sleep with eyes shut, although sometimes they rested with partially closed eyes for 2 to 3 min. Usually they rest, seemingly alert, with their feet under the body, probably to facilitate rapid escape. Rest spots, established at various points along trails, are used for short periods and then abandoned; they do not use burrows, tree holes, nests, or other secure retreats (Rathbun, 1979).

The tail is held horizontally off the ground both when walking and running (Brown, 1964). Elephant-shrews move rapidly and take flight at any sudden movement or noise. Usually cursorial, they are capable of making long leaps (Kingdon, 1974) both horizontally and, when suddenly frightened, vertically at least 38 cm. In captivity they are highly excitable; Koontz (1982) recommends the use of one-way screens to minimize observer disturbance.

Rathbun (1979) found that *E. rufescens* is facultatively monogamous (Kleiman, 1977) with each pair sharing a territory of about 0.34 ha. Members of a monogamous pair spend little time together and social interactions are brief. Intraspecific aggression occurs during food defense, parent-offspring interactions, and boundary disputes between individuals from contiguous territories (Rathbun, 1979). The female of a pair usually dominates the male. Territories are defended from conspecifics sex-specifically; males chase males and females chase females (Rathbun, 1979). A boundary encounter usually begins with foot drumming, the rapid beating of one or both rear feet on the substrate. This is followed by "mechanical walking" (Rathbun, 1979) during which the legs are straightened so the body becomes elevated, the upper part of the tail is held close to the rump with the lower part in contact with the ground, and the animal takes small steps in a rigid, but not

jerky manner. High-speed chases often follow, after which both elephant-shrews return to their respective territories.

Stomach analyses made during dry seasons (at Kibwezi, Kenya) indicate that insects form almost the entire diet; major prey insects are ants and termites, the latter contributing nearly 75% by volume (Rathbun, 1979). Minor prey items include spiders, coleopterans, and orthopterans. Green plant tissue and fruits contribute less than 2% of the diet. During wet seasons, however, termites seem to be depended upon slightly less and vegetation somewhat more. When foraging in leaf litter, the nose is used as a probe and the forefeet clear away obstructions. The tongue flicks in and out rapidly when feeding on ants and termites (Rathbun, 1979).

Elephant-shrews face-wash by licking and rubbing their forefeet, then wiping the face, nose and vibrissae (but not the ears) with both forepaws simultaneously. Other grooming includes scratching with a hindfoot and rolling on the side in open sandy areas, especially at rest sites.

Both male and female *E. rufescens* scent-mark by periodically rubbing their sternal gland on the substrate. Defecation and urination patterns also suggest possible scent-marking functions: dung is located in piles at territory boundaries and urine is deposited throughout the territories (Rathbun, 1979). Both sexes have rudimentary perineal glands at the base of the tail that are pressed to the ground during perineal marking (Kingdon, 1974). Juveniles were observed to climb onto the back of either parent and vigorously and rapidly rub all four feet back and forth; this might be a form of pedal gland scent-marking (Rathbun and Redford, 1981).

Estrus is apparently brief, usually lasting less than 12 h; a post-partum estrus is common (Rathbun, 1979). The perineal marking rate of estrous females is greater than that of non-estrous females. Lumpkin et al. (1982) suggested that perineal marking distributes the increased volume of vaginal fluids produced during estrus and probably functions in chemical communication.

The speckled sand snake, *Psamnophis punctulatus* (Rathbun, 1979), and the barn owl, *Tyto alba* (Laurie, 1970), are the only known predators of *E. rufescens*, although Rathbun (1976) listed other potential predators. Elephant-shrews rely on both cryptic coloration and immobility to avoid detection by predators. They flee only when approached closely. Elephant-shrews often return to the source of disturbance and drum one or both feet on the ground (Rathbun, 1979). Other members of the family may be attracted to the site, drum, and mob the predator, although Roeper (1981) could find no evidence of attraction to drumming during experiments with captive animals. Drumming may serve to warn other elephant-shrews, to assemble elephant-shrews for a mobbing effort, or to invite pursuit (Rathbun, 1979). Alternatively, Roeper (1981) concluded that the primary function of drumming may be to deter pursuit by communicating to a predator that it has been seen, that the elephant-shrew is about to run, and that the predator should seek less alert prey.

Besides foot-drumming, the only audible signal produced by adult elephant-shrews is a loud shriek elicited by rough handling. Juveniles make squeaking noises when nursing and occasionally emit a chirping vocalization. Hand-raised young also produce this chirping noise, apparently when hungry (Roeper, 1981).

Elephantulus rufescens is sympatric with several other elephant-shrews of the subfamily Macroscelidinae: *Petrodromus tetradactyla* in parts of Tanzania and Kenya, *E. revoili* in northern Somalia, *E. fuscipes* in Uganda, and *E. brachyrhynchus* in parts of Tanzania and much of Kenya (Corbet and Hanks, 1968). Rathbun (pers. comm.) believes that *E. rufescens* occurs in different microhabitats than these species. No data have been published on interactions between *E. rufescens* and other elephant-shrews.

Aggressive encounters with grey wren warblers, *Calamonastes simplex*, and d'Arnaud's barbet, *Trachyphonus d'arnaudi*, were observed when these birds tried to enter a termite outbreak defended by an elephant-shrew (Rathbun, 1979). Neal (1982) suggested that *Acomys percivali* may competitively exclude *E. rufescens* from areas of apparently suitable habitat.

Free-ranging elephant-shrews harbor ticks, fleas, mites, mosquitos, roundworms (Brown, 1964), and a malarial parasite (Hoogstraal, 1950). Hoogstraal et al. (1950) were not able to determine the natural vector for elephant-shrew malaria nor were they successful in transferring the infection from an elephant-shrew to a domestic rat or even to a conspecific. They also were unable to find malarial stages other than those within the elephant-shrew's red blood cells.

Tail lesions affect captive elephant-shrews. Inflammation and necrosis of the tail often is accompanied by necrosis of the ear tips. No infectious agents were isolated and in spite of medical treatment and changes in environmental factors the condition was not controlled (Hoopes and Montali, 1980).

REMARKS. Peters (1864) and Haeckle (1866) originally placed the Macroscelididae in the order Insectivora, a traditional arrangement (Anderson and Jones, 1967; Corbet, 1971; Vaughan, 1978; Walker et al., 1964). However, Butler (1956) and Patterson (1965) referred elephant-shrews to a separate order, Macroscelidea. This interpretation is supported by Corbet and Hanks (1968), Eisenberg (1981), McKenna (1975), and Rathbun (1979). McKenna (1975) suggested, based on osteological and dental comparisons, that the Macroscelididae, Anagalidae (extinct), and Lagomorpha possibly had a relatively close, ancient common ancestry. Szalay (1977) referred elephant-shrews to a subordinal level of Lagomorpha. Thus, phylogenetic affinities are somewhat uncertain but it seems clear from Patterson's (1965) revision of the fossil Macroscelididae, Goodman's (1975) blood protein studies, and Rathbun's (1979) ecological and behavioral data that elephant-shrews are a unique, monophyletic taxon with only plesiomorphic similarities to the Insectivora.

Elephantulus (probably *E. rozeti*) is the animal model used for the characteristic head of the Egyptian god Set (van der Horst, 1946). Egyptologists often dispute the assignment of a particular animal to the head of Set; the donkey, pig, okapi (*Okapia johnstoni*), and even extinct quadrupeds were proposed. *Elephantulus* looks more similar to the recovered drawings of Set than other suggested animals, but because elephant-shrews are relatively unknown the resemblance was overlooked (van der Horst, 1946).

Other vernacular names for *E. rufescens* are East African elephant-shrew and spectacled elephant-shrew.

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