

*Taphozous mauritanus*. By Carol A. Dengis

Published 17 May 1996 by the American Society of Mammalogists

*Taphozous mauritanus* Geoffroy, 1818

Mauritian Tomb Bat

*Taphozous mauritanus* E. Geoffroy, 1818:127. Type locality "Island of Mauritius."

*Taphozous leucopterus* Temminck, 1838:12. Type locality "Interior of South Africa."

*Taphozous dobsoni* Jentinck, 1879:123. Type locality "Mohambo, Madagascar."

*Taphozous mauritanus* (sic) var. *cinerascens* Seabra, 1900:77. Type locality "Benguela, south-western Angola."

**CONTEXT AND CONTENT.** Order Chiroptera, Suborder Microchiroptera, Family Emballonuridae, Genus *Taphozous*, Subgenus *Taphozous*. There are no subspecies.

**DIAGNOSIS.** *Taphozous mauritanus* (Figs. 1, 2) can be distinguished from all other bats by its entirely white ventral surface, grizzled-gray dorsal surface (salt and pepper effect), parchment-colored translucent wings, forearm length of 58-64 mm (Happold and Happold, 1989; Rosevear, 1965), an ill-defined patch of brown inside the first phalanx of the longest finger, and wings attached at the ankles (Dobson, 1878). The distinctive head has erect triangular-shaped ears with rounded edges and no papillae on the inner margins, a large gular sac under the chin in males, and no black throat patch in the gular area (Koopman, 1975; Rosevear, 1965). Both sexes have a radio-metacarpal pouch and a 1-mm pad or tubercle on the underside of the foot. The anterior emargination of the palate is a broad U, about 2-2.5 mm wide (Fig. 2).

**GENERAL CHARACTERS.** *Taphozous mauritanus* has a sleek appearance because the short hair is pressed closely to the body. The grizzled appearance of the dorsal surface is due to the three-banded hairs, which are pale brown at the base, dark grayish-brown in the middle, and whitish at the tips. This gives a grayish effect of varying tints as light hits the pelage at different angles. The interfemoral membrane is also covered with short, grayish hairs (Rosevear, 1965), and the fur of the back extends down onto the interfemoral membrane just beyond the point of perforation by the tail (Dobson, 1878). There is no difference in color and size between the sexes and both have the radio-metacarpal pouch. All males have a gular sac (Dobson, 1878; Hayman and Hill, 1971), but there appears to be geographic variation in the occurrence of a gular sac in females. In Nigeria and Mozambique, only the males have a gular sac (Happold, 1987; Smithers and Tello, 1976). In West Africa, this pouch is reduced to a small fold in the skin in females (Rosevear, 1965). In the Sudan, however, a gular sac is present in both sexes, but is more highly developed in males (Koopman, 1975).

The face is covered with short hairs in front of the eyes (Dobson, 1878) and there is a deep longitudinal furrow below the eyes (Rosevear, 1965). Eyes are large (2-3 mm in diameter—Rosevear, 1965; Verschuren, 1957), resulting in good visual acuity. The naked tragus is oval-shaped, never parallel-sided, and is at least as broad (4.5 mm) as it is high (Dobson, 1878; Rosevear, 1965). The cone-shaped snout is devoid of a nose-leaf (Happold, 1987), the nostrils do not hang over the lower jaw, and the muzzle does not appear obliquely truncated as, for example, in *Coleura* (Rosevear, 1965).

The long, thin, and well-developed postorbital processes of the skull (Fig. 3) taper to a point and curve down about the eye-sockets. The rounded braincase rises above the plane of the face, resulting in a curved profile with little or no sagittal crest. There is a deep saucer-like depression in the frontal area, which is reflected in the face of the living animal. Since only the nasal branches of the premaxillaries are developed, an anterior notch (U-shaped) at the margins of the palate is caused by the absence of anterior palatal

branches of the premaxillae. The posterior edge of the palate ends abruptly at the last molar, and there are gaps on the inner edge of the palate due to incomplete auditory bullae (Rosevear, 1965).

The wing is long and narrow, with the metacarpals declining in length progressively from the third to fifth digits (Rosevear, 1965). The second digit consists of the metacarpal only and there are two phalanges on the third, fourth, and fifth digits. When the bat is at rest, the long narrow tip of the wing is shortened in a way unique to this family, facilitating crawling. The first phalanx of the third digit folds forward and up on the top side of the metacarpal and the second phalanx folds down on the bottom part of the first. Simultaneously, the second phalanx of the fourth digit folds forward and down on the underside of the first phalanx.

Sexual dimorphism in size of Mauritian tomb bats is not evident, but there appears to be a degree of geographic variation within Africa. General measurements (in mm) for West Africa are: length of head and body, 75-93; length of forearm, 58.5-64.5; length of tail, 22-28; and height of ear, 17-21 (Rosevear, 1965). Measurements of 13 males and 8 females (in mm), respectively, for Zimbabwe are: length of head and body, 101-109, 100-112; length of tail, 21-27, 22-27; and height of ear, 14-20, 17-20 (Smithers and Wilson, 1979). Measurements of males and females (in mm), respectively, for South Africa are: length of head and body, 100-131, 105-116; length of forearm, 61-63, 61-66; length of tail, 17-25, 20-23; height of ear, 13-21, 18.5-21; and length of hind foot, 9-14, 12.5-14 (Rautenbach, 1982). Range of measurements (in mm) of 82 adult females from Cameroon are: total length of tail, 24-27; length of free tail, 13.5-15; length of tibia, 25; length of foot, 13-13.5; length of first digit, 11-11.5; length of second digit, 5.6-5.8; length of third digit (metacarpal), 59.6-63.5; length of third digit (phalanx I), 21.5-23; length of third digit (phalanx II), 25-26; length of fourth digit (metacarpal), 47-50; length of fourth digit (phalanx I), 13-13.5; length of fourth digit (phalanx II), 7.5-8.5; length of fifth digit (metacarpal), 32.5-37; length of fifth digit (phalanx I), 11.5-13; and length of fifth digit (phalanx II), 10.5 (Aellen, 1952). Average measurements (in mm) for Cameroon of 787 "immature" males, as identified by Aellen (1952), are: length of head and body, 72; length of forearm, 60.5; length of tibia, 22;



FIG. 1. *Taphozous mauritanus*, in Kruger National Park, South Africa. In profile, the white ventral surface is visible. Photograph by M. Brock Fenton.



FIG. 2. *Taphozous mauritanus*, roosting on a tree trunk in Kruger National Park, South Africa. The white ventral surface is camouflaged while the bat roosts. Photograph by M. Brock Fenton.

length of foot, 12; total length of tail, 19; length of free tail, 9; length of first digit, 11; length of second digit, 51; length of third digit (metacarpal), 54; length of third digit (phalanx I), 19; length of third digit (phalanx II), 23; length of fourth digit (metacarpal), 42; length of fourth digit (phalanx I), 11.5; length of fourth digit (phalanx II), 7.5; length of fifth digit (metacarpal), 33; length of fifth digit (phalanx I), 12; and length of fifth digit (phalanx II), 9. Other measurements are: wingspan: 181–204; length of head, 24.5–26.5; length of tragus, 5–7 (Happold et al., 1987). Body mass ranges (in g) for East Africa are: 20–25 (Kingdon, 1974); for Transvaal, 26–32 (males), 31–32 (females—Rautenbach, 1982); for Zimbabwe, 20–36 (11 males), 27.5–31.6 (7 females—Smithers and Wilson, 1979); and for Malawi, 20–29 (Happold et al., 1987).

Cranial measurements (in mm) for West Africa are: total length of skull, 19.5–22.5; zygomatic breadth, 12.5–13.2, length of maxillary tooththrow, 8.7–9.4; and width of maxillary tooththrow, 9.7–9.3 (Rosevear, 1965). Measurements of 787 immature males and 25 adult females, respectively, for Cameroon are: total length of skull, 20.3, 22; condylobasal length, 19.3, 20; zygomatic breadth, 11.6, 13.3; interorbital breadth, 5.4, 6.1; postorbital breadth, 5.2, 4.8; braincase breadth, 10, 10; length of maxillary tooththrow, 9.6, 9.7; width of maxillary tooththrow, 8.2, 9.2; and mandible length, 15.3, 16.3 (Aellen, 1952).

**DISTRIBUTION.** *Taphozous mauritanus* is widely distributed from the south coast of Cape Province northward to southern Sudan and Somalia, west to Senegal (Hayman and Hill, 1971; Fig. 4), and primarily north of the Zambezi River (Shortridge, 1934). There are records from the island of Fernando Po; Gabon; Cameroon (Aellen, 1952); Zaire (Allen et al., 1917); Malawi (Happold and Happold, 1989); Mozambique (Smithers and Tello, 1976); Zambia (Ansell, 1960); Zimbabwe (Smithers and Wilson, 1979; Wilson, 1975); Botswana, in the Tati Concession and the marshy Okavango Delta (on the Chobe river—Meester et al., 1986); and Angola (Shortridge, 1934). There are no records from northwest Transvaal and

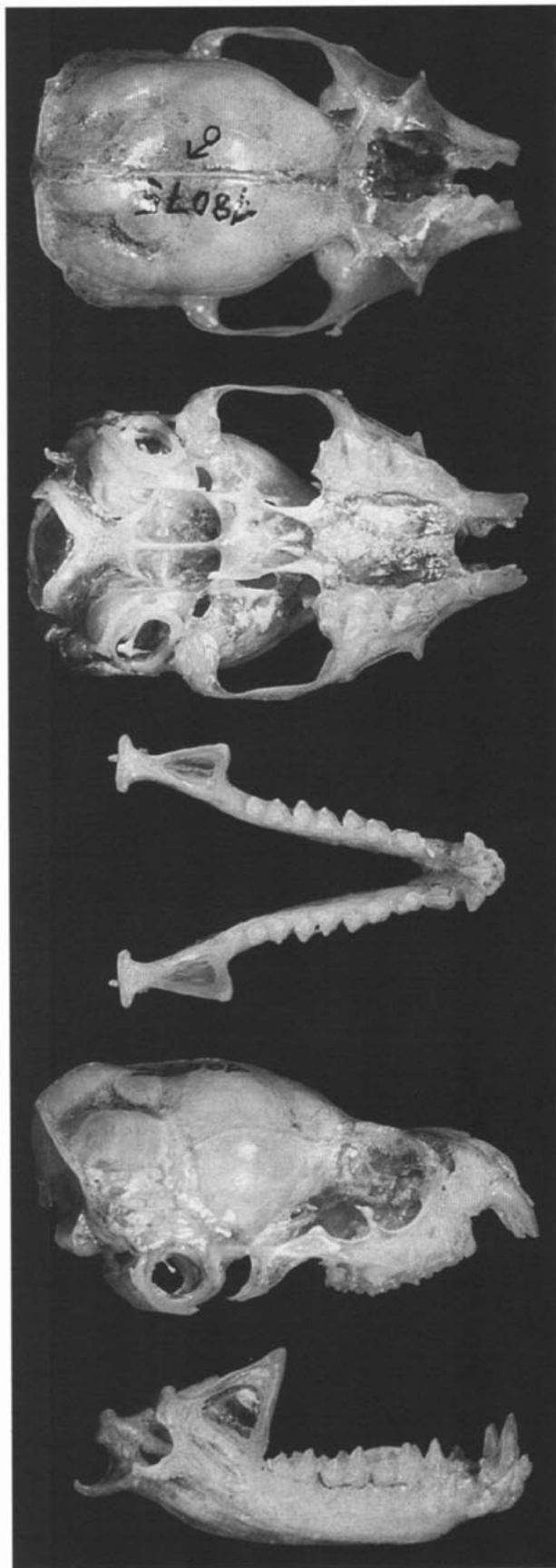


FIG. 3. Dorsal, ventral, and lateral views of cranium, and dorsal and lateral views of mandible of *Taphozous mauritanus* (Royal Ontario Museum 78075), from Kenya. Greatest length of skull is 20.8 mm.

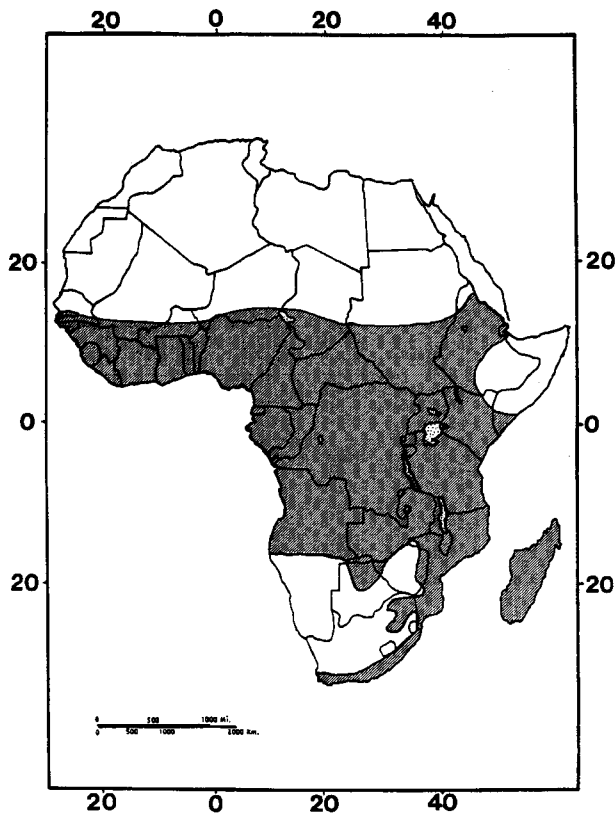


FIG. 4. Distribution of *Taphozous mauritanus* in Africa and Madagascar.

the adjoining area of Botswana (Rautenbach, 1982). Largen et al. (1974) report one specimen from Gambela, Ethiopia and note that this may be the first record of the species from Ethiopia. However, there are earlier records from Ethiopia, as well as from the islands of Madagascar and Bourbon (Dobson, 1878). This species also occurs on the Indian Ocean islands of Reunion, Assumption, Mauritius and Aldabra (Meester et al., 1986). The range of Mauritian tomb bats correlates with areas that receive at least 500 mm of rain per year; those areas with less rain have recordings only near swamps and rivers, as in Steilloopbrug district (Transvaal) and Francistown in Botswana (Rautenbach, 1982; Smithers, 1971). There is no fossil record for *Taphozous mauritanus*.

**FORM AND FUNCTION.** The gular sac in male *T. mauritanus* lies between the angle of the lower jaw and may function in sexual attraction or stimulation (Rosevear, 1965). The width of the sac's opening is almost equal to half the distance between the rami of the jaw (Dobson, 1878), or about 7–8 mm (Verschuren, 1957). The sac opens anteriorly and contains glands that pass secretions to the outside through small pores (Dobson, 1878). These secretions are presumed to be useful in attracting females during the breeding season and, as in some other Emballonuridae, in marking each male's territory (Bradbury and Vehrencamp, 1977).

There is a radio-metacarpal pouch at the forward angle of the wing. This triangular pocket is formed by a small fold of skin stretched between the forearm (radius) and the basal joint (metacarpal) of the fifth digit. It is not known whether this pouch is used to store insects while the bat is in flight (Rosevear, 1965). The arrangement of the interfemoral membrane and the tail is unique to Emballonuridae. Hence, the name from the Greek, *emballo* (to throw in) and *oura* (tail), as though resembling a spear thrown at an angle into a sheet of water. The hind-margin of the interfemoral membrane is supported on each side by two strong ankle-spurs (calcanea), but is without a central prop because the short tail passes through the middle of the membrane (Rosevear, 1965) and projects from its upper surface. Thus the membrane is free to slide up and down the tail and be extended during flight (Yalden and Morris, 1975).

The upper incisors are minute or absent, but there are four

lower incisors that are chisel-edged, trilobed, and may slightly overlap. The dental formula is  $i \frac{1}{2}$ ,  $c \frac{1}{1}$ ,  $p \frac{2}{2}$ ,  $m \frac{3}{3}$ , total 30. The anterior upper premolar is small, but the posterior one is much bigger and often caniniform or subcaniniform in shape. The posterior upper molar is always reduced from back to front, retaining only two legs of the W-pattern (Rosevear, 1965).

In Malawi, the renal function of three captive individuals maintained at 21–24°C was examined (Happold and Happold, 1988). Each was kept in captivity for a different length of time (3 days, 6 days, or 30 days) and none became torpid. None would drink although water was offered twice daily, but when offered termites, they ate 27–37% of their body mass each day for one to five days. The mean renal index, as the ratio of the inner medulla to the cortex of the kidney, was calculated to be 5.55, and the predicted mean maximum urine concentration was calculated to be 3,921 mosmol/kg. The authors tentatively concluded that *T. mauritanus*, in arid zone habitats, deserts and dry savannas, have kidneys that aid in water conservation.

The mean aspect ratio of *T. mauritanus* ( $n = 3$ ) is 8.16, one of the highest recorded in Malawian bats (Happold and Happold, 1988). This study revealed *T. mauritanus* to be one of the few species unable to effect a turn in the one meter wide corridor during flight. This species flew less than 5 min/night, likely due to problems maneuvering in the confined space.

**ONTOGENY AND REPRODUCTION.** Mauritian tomb bats may be polyestrous in some regions of Africa and monestrous in others (Happold and Happold, 1990). In Zimbabwe, females carrying single young were observed in October (Smithers, 1971), one juvenile was taken in February (Ansell, 1960), and three pregnant females, each with a single fetus, were taken in February (Smithers and Wilson, 1979). In Zambia and southeast Zaire, births were reported in February. In northern Zaire, Tanzania, and Kenya, births occurred in April–May, while in the southern Sudan, northeast Zaire, Tanzania, and Zanzibar, births were reported in October–November (Anciaux de Faveaux, 1983). In Zaire, males with well-developed sex organs were captured in December, while in March, males showed less developed sex organs, suggesting that the mating season is in December and the birth-season is in April–May (Verschuren, 1957). In Malawi, births of single young were recorded in both November–December and in March–April (Happold and Happold, 1990). Reproduction may occur all year in Zaire because young of various sizes have been found in April, May, November, and December (Allen et al., 1917). After birth, the single young clings to the mother's abdomen while she is in flight and she carries it until it can fly on its own (Smithers, 1971).

The degree of development of the gular sac in males coincides with the development of the sex organs. There are two stages of genital development in the adult male (Verschuren, 1957). In the mating season, the testes increase in size and the penis extends 1–2 mm beyond the black-pigmented scrotum. Outside the mating season, the testes are retracted into the abdominal cavity, the penis appears slightly longer, and the pigmented skin of the scrotum is less obvious. In a male embryo, the sexual organs resemble those of a non-breeding adult, the forearms are about 26 mm long, and the back claws and tail are almost adult-sized (Verschuren, 1957). In the female, the vulva is enlarged prior to and just after parturition, deeply pigmented, and extends out from the ventral surface of the abdomen. At other times, the vulva is less conspicuous and has two pigmented patches.

**ECOLOGY.** Generally, *T. mauritanus* is found in moist open habitats, vegetation zones (Kingdon, 1974), and savanna regions south of the Sahara (Hayman and Hill, 1971). The species occurs in open woodland and generally avoids the interior of dense forests (Malbrant and Maclatchy, 1949). Because it is found either in areas receiving >500 mm rain per year or near swamps and rivers, it is apparently dependent on open water or riparian forests (Rautenbach, 1982). During daylight, roosts are chosen in the open but away from direct sunlight. These roost sites include outer walls of buildings beneath over-hanging eaves, cliff walls with overhanging rock shelves, and trunks of large trees (*Mangifera indica*, Palmaeaceae, *Cocos nucifera*, *Eucalyptus globulus*) where shade is always available (Rautenbach, 1982; Rosevear, 1965; Verschuren, 1957). Upper and middle branches of trees are selected and this species hangs 4–6 m from the ground in all roosts (Verschuren, 1957). Generally, it tends to roost near human settlements (Kock,

1981) and to prefer buildings inhabited by man rather than buildings under construction (Verschuren, 1957). Buildings are chosen where roof-beams jut through the top of the wall as opposed to plain walls, as these let the bats escape easily around a corner if disturbed (Smithers, 1971). Once the site has been selected, it becomes a permanent roost with each individual returning to its station after every disturbance (Kingdon, 1974).

Mauritian tomb bats feed primarily on moths found in proximity to day roosts (Allen et al., 1917; Kingdon, 1974), termites (e.g., *Macrotermes falciger*—Happold and Happold, 1988), butterflies (Wilson, 1975), and insects (Smithers, 1971). *T. mauritianus* rests against the roost surface either singly, in pairs, or in small groups of up to 12 individuals (Allen et al., 1917; Ansell and Dowsett, 1988; Rosevear, 1965). Only mothers and their young cling together, while all other individuals maintain a spacing of 10–15 cm (Happold et al., 1987). When another member of the group arrives, several of the roosting bats emit a penetrating three-syllable call at 2–3 second intervals. The African sheath-tailed bat, *Coleura afra*, intermingles with this species in some coastal caves (Kingdon, 1974). *T. mauritianus* is preyed on by snakes and carnivorous birds (for example, owls). Parasites of the genus *Anchitrema* are found on all of the sheath-tailed bats of Africa (Allen, 1939).

**BEHAVIOR.** While roosting during the day, this species appears alert and seems never to sleep as it keeps watch for danger (Rosevear, 1965). When disturbed, it sometimes flies to a nearby tree and then scurries out of sight with audible chirping and squabbling (Kingdon, 1974; Verschuren, 1957). It scurries sideways, crab-like, while still hanging upside down, using the folded wing and thumb claw to assist in movement (Smithers and Tello, 1976). In Lagos, a pair of *T. mauritianus* never attempted to escape by flight, but instead tried to hide around a corner by shuffling sideways while keeping their bellies pressed against the wall's surface (Rosevear, 1965). If an entire band is killed, the same roosts are recolonized the following year (Kingdon, 1974). These sites become characteristically stained over a 15 by 10 cm area with urine (Smithers, 1971) or gular sac secretion (Kingdon, 1974).

The daylight roost is always chosen so that unhindered take-off is possible and *T. mauritianus* swoops down and away from the roost in a curve, shifting immediately into powerful and rapid flight (Rosevear, 1965). A definite flight pattern is observed both before sundown and at night, and these bats seem to chase each other while in flight (Kingdon, 1974). Furthermore, they produce a whirring sound when turning sharply while in flight, probably from vibrations of the radio-metacarpal pouch (Allen et al., 1917). They are capable of sustained fast flight necessary for foraging, but have poor maneuverability (Happold and Happold, 1988).

At night, this species usually waits until total darkness before foraging, and does not return to the day roost to eat, as evidenced by the lack of insect debris or droppings beneath the roost (Rosevear, 1965). In Sehitwa, Botswana, it swooped over water to take insects (Smithers, 1971). This species has been observed darting out approximately 17 m from a building to capture a butterfly in daylight (Wilson, 1975). It is a silent and solitary flier and does not hunt higher than the tops of trees (Rautenbach, 1982).

Mauritian tomb bats turn the head and use vision, not echolocation, to observe intruders during the day. The large eyes, choice of outdoor day roosts, and avoidance of dark interiors suggests that vision plays a large part until the light fades below a certain intensity and echolocation takes over. Echolocation sounds are emitted through the mouth, not from the nostrils (Rosevear, 1965). *T. mauritianus* can emit calls of high intensity (40 kHz, range 30–50). In Zimbabwe, when the species was observed flying around a room, it emitted ultrasonic calls, and did not collide with objects in the room, but after 1–5 min it flew directly into windows. Apparently it had switched the processing of orientation cues from echolocation to vision, yet had not stopped emitting the ultrasonic vocalizations or altered the rate of the calls. There was no increase in the rate of repetition as it flew toward the windows and before collision (Fenton, 1975).

*Taphozous mauritianus*, studied in riparian forest 300 m from the Sengwa River in Zimbabwe, detects its prey at long range and frequently hunts in the open (Fenton et al., 1980). The species was observed flying 5–40 m above the river, and diving periodically with drops in altitude of up to 10 m. While doing so, it increased the rates of pulse repetition (echolocation calls). Over a 45-minute period, there were 19 attempts to catch actual prey and seven dives

toward sand tossed into the air by observers. The species appeared to detect the sand at a range of 3 m. Search calls were long narrow band calls that, in duration and frequency (Fenton et al., 1980), were quite suited for detecting targets (Simmons and Stein, 1980). Echolocation calls had rapid onset times with full amplitude within 0.7 ms (15 sound waves), appreciable energy in the fundamental frequency (11–13 kHz), and most energy contained in the second harmonic. The narrow band search calls were multiharmonic with no broad band sweeps. In the approach phase, the calls became shorter with a pronounced broad band component added as the bat neared the target. When the target disappeared, the calls of the terminal phase became less abrupt and increased in duration. Since this species consumes moths, its diving behavior may be associated with defensive tactics of the moths as the calls are within frequencies heard by sympatric moths (Fenton et al., 1980). The calls of the above phases are distinctive of *T. mauritianus* in that the search phase contains no broad band component, while in the approach and terminal phases, the multiharmonic structure and the rate of the two broad band sweep calls (shallow and sweep) are unique.

When at rest, this species chirrups, but in aggressive situations, it screeches (Allen et al., 1917; Kingdon, 1974). An individual *T. mauritianus* in captivity, emitted a single "ping" sound when a bat from another species came within 15–20 cm of the individual's roost, and it deserted the roost if the intruder persisted in approaching (Happold et al., 1987). Other vocalizations were emitted as well, but their meaning was not deduced.

**REMARKS.** The genus name, *Taphozous*, originated from the Greek *taphos*, a grave, and *zoos*, living (Rosevear, 1965). The habitat of the Mauritian tomb bat is not in tombs or in tomb-like structures, but rather out in the open on the walls of buildings, tree trunks, or cliff walls and, if roosting in caves, it hangs near the entrance rather than in the dark recesses.

#### LITERATURE CITED

- AELLEN, V. 1952. Contribution à l'étude des chiroptères du Cameroun. Mémoires de la Société neuchâteloise des sciences naturelles, 8:1–121.
- ALLEN, G. M. 1939. A checklist of African mammals. Bulletin of the Museum of Comparative Zoology, 83:1–763.
- ALLEN, J. A., H. LANG, AND J. P. CHAPIN. 1917. The American Museum Congo expedition collection of bats. Bulletin of the American Museum of Natural History, 87:405–563.
- ANCIAX DE FAVEAUX, M. 1983. Les cycles annuels de reproduction chez les chiroptères phytophiles au Shaba (S. E. Zaire). Zoologische Wetenschappen, 237:27–34.
- ANSELL, W. F. H. 1960. Mammals of Northern Rhodesia. The Government Printer, Lusaka, 155 pp.
- ANSELL, W. F. H., AND R. J. DOWSETT. 1988. Mammals of Malawi. The Trendline Press, Cornwall, Great Britain, 170 pp.
- BRADBURY, J. W., AND S. L. VEHRENCAMP. 1977. Social organization and foraging in emballonurid bats (mating systems). Behavioral Ecology and Sociobiology, 2:1–17.
- DOBSON, G. E. 1878. Catalogue of the Chiroptera in the collection of the British Museum. British Museum, London, 567 pp.
- FENTON, M. B. 1975. Observations on the biology of some Rhodesian bats, including a key to the chiroptera of Rhodesia. Life Science Contribution, Royal Ontario Museum, 104:1–72.
- FENTON, M. B., G. P. BELL, AND D. W. THOMAS. 1980. Echolocation and feeding behaviour of *Taphozous mauritianus* (Chiroptera: Emballonuridae). Canadian Journal of Zoology, 58: 1774–1777.
- GEOFFROY, E. 1818. Description de L'Égypte. Histoire naturelle. Description des mammifères qui se trouvent en Égypte, 2:99–135 (not seen, cited in Koopman, 1975).
- HAPPOLD, D. C. D. 1987. The mammals of Nigeria. Clarendon Press, Oxford, 402 pp.
- HAPPOLD, D. C. D., AND M. HAPPOLD. 1988. Renal form and function in relation to the ecology of bats (Chiroptera) from Malawi, central Africa. Journal of Zoology (London), 215:629–655.
- . 1989. The bats (Chiroptera) of Malawi, central Africa. Nyala, 14:89–112.
- . 1990. Reproductive strategies of bats in Africa. Journal of Zoology (London), 222:557–583.

- HAPPOLD, D. C. D., M. HAPPOLD, AND J. E. HILL. 1987. The bats of Malawi. *Mammalia*, 51:337-414.
- HAYMAN, R. W., AND J. E. HILL. 1971. The mammals of Africa. An identification manual (J. Meester and H. W. Setzer, eds.) Part 2. Order Chiroptera. Smithsonian Institution Press, Washington, D.C., 173 pp.
- JENTINCK, F. A. 1879. Mohambo, Madagascar. Notes from the Leyden Museum, 1:123 (not seen, cited in Meester et al., 1986).
- KINGDON, J. 1974. East African mammals: an atlas of evolution in Africa. IIA (Insectivores and bats). Academic Press, London, 341 pp.
- KOOPMAN, K. F. 1975. Bats of the Sudan. *Bulletin of the American Museum of Natural History*, 154:355-443.
- KOCK, D. 1981. Zur chiropteren-fauna von Burundi. *Senckenbergiana biologica*, 61:329-336.
- LARGEN, M. J., D. KOCK, AND D. W. YALDEN. 1974. Catalogue of the mammals of Ethiopia. 1. Chiroptera. *Monitore Zoologico Italiano*, (supplement) 5:221-298.
- MALBRANT, R., AND A. MACLATCHY. 1949. Faune de l'équateur africain français. II. Mammifères (P. Lechevalier, ed). *Encyclopedie biologique*, 36:3-323.
- MEESTER, J. A., I. L. RAUTENBACH, N. J. DIPPENAAR, AND C. M. BAKER. 1986. Classification of southern African mammals. Transvaal Museum, Pretoria, 359 pp.
- RAUTENBACH, I. L. 1982. Mammals of the Transvaal. Transvaal Museum, Pretoria, 211 pp.
- ROSEVEAR, D. R. 1965. The bats of west Africa. *British Museum (Natural History)*, London, 418 pp.
- SEABRA, A. F. 1900. Diagnoses de quelques nouvelles espèces et variétés de Chiroptères d'Afrique. *Jornal de Sciencias, Mathematicas, Physicas e Naturaes*, Lisboa, 2nd Ser., Tomo VI, No. XXII:77.
- SHORTRIDGE, G. C. 1934. The Mammals of South West Africa (Vol. 1). William Heinemann Ltd, London, 72 pp.
- SIMMONS, J. A., AND R. A. STEIN. 1980. Acoustic imaging in bat sonar: echolocation signals and the evolution of echolocation. *Journal of Comparative Physiology*, 135:61-84.
- SMITHERS, R. H. 1971. The mammals of Botswana. The Trustees of the National Museums and Monuments of Rhodesia, Salisbury, 340 pp.
- SMITHERS, R. H. N., AND J. L. P. L. TELLO. 1976. Checklist and atlas of the mammals of Moçambique. The Trustees of the National Museums and Monuments of Rhodesia, Salisbury, 184 pp.
- SMITHERS, R. H. N., AND V. J. WILSON. 1979. Checklist and atlas of the mammals of Zimbabwe, Rhodesia. The Trustees of the National Museums and Monuments of Rhodesia, Salisbury, 193 pp.
- TEMMINCK, C. J. 1838. *Tijdschrift voor natuurlijke geschiedenis en physiologie*, Amsterdam 5:12 (not seen, cited in Meester et al., 1986).
- VERSCHUREN, J. 1957. Ecologie, biologie et systematique des chiroptères. Exploratie van het Nationaal Garamba Park. Institut des parcs nationaux du Congo Belge. Brussels, 7:1-473.
- WILSON, V. J. 1975. Mammals of the Wankie National Park, Rhodesia. The Trustees of the National Museums and Monuments of Rhodesia, Salisbury, 147 pp.
- YALDEN, D. W., AND P. A. MORRIS. 1975. The lives of bats. *Quadrangle/The New York Times Book Company*, New York, 232 pp.
- Editors of this account were ALICIA V. LINZEY, KARL F. KOOPMAN, and ELAINE ANDERSON. Managing Editor was ALICIA V. LINZEY.
- C. A. DENGIS, DEPARTMENT OF PSYCHOLOGY, B. S. B., YORK UNIVERSITY, 4700 KEELE ST., NORTH YORK, ONTARIO, CANADA M3J 1P3.