MAMMALIAN SPECIES No. 534, pp. 1–8, 5 figs.

Eumops perotis.

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Published 27 December 1996 by the American Society of Mammalogists

Eumops perotis (Schinz, 1821)

Greater Mastiff Bat

Molossus perotis Schinz, 1821:870. Type locality "Brazil, Rio de Janiero, Campos do Goita Cazes, Villa São Salvador" (Koopman, 1993:234).

Dysopes (Molossus) gigas Peters, 1865:383. Type locality "in dem Gebirge Taburete, District Callajabas auf Cuba," which subsequently was restricted to "Loma Taburete, en el partido de Cayajabos, jurisdicción del Mariel, Pinar del Río, Cuba" (Varona, 1974:41). However, Carter and Dolan (1978:91) reported that the holotype was from "Rio Negro [in state of Amazonas], Brazil."

Molossus californicus Merriam, 1890:31. Type locality "Alhambra, Los Angeles County, California."

Promops trumbulli Thomas, 1901:190. Type locality "Cordova" (Para, Brazil—Sanborn, 1932:350).

CONTEXT AND CONTENT. Order Chiroptera, Suborder Microchiroptera, Family Molossidae. The genus *Eumops* contains eight species; *E. auripendulus, E. bonariensis, E. dabbenei, E. glaucinus, E. hansae, E. maurus, E. perotis,* and *E. underwoodi* (Eisenberg, 1989; Freeman, 1981*a*; Koopman, 1993). A key to the species of *Eumops* is presented in Eger (1977) and Kiser (1995). Three subspecies of *E. perotis* are recognized (Hall, 1981; Koopman, 1971, 1978):

E. p. californicus (Merriam, 1890:31), see above.

E. p. perotis (Schinz, 1821:870), see above (*renatae* Pirlot is a synonym).

E. p. trumbulli (Thomas, 1901:190), see above (because the type locality of *gigas* Peters is within the range of *E. p. trumbulli,* we consider *gigas* Peters to be a synonym).

DIAGNOSIS. Members of the genus *Eumops* have large, rounded pinnae that arise from a single point or are joined medially on the forehead. Smooth upper lips distinguish *Eumops* from *Tadarida* (Eger, 1977). Absence of a gap between the two upper incisors, which project forward in contact with each other except at the tips, is a distinguishing feature of *Eumops* (Anderson, 1972; Miller, 1907). The antitragus of *Eumops* is well developed, and the tragus is either small and pointed or broad and square. Species vary in size from *E. bonariensis* with a minimum length of forearm of 37 mm, to *E. perotis,* with a maximum length of forearm of 83 mm. The skull is cylindrical in shape and the basisphenoid pits are well developed. The upper incisors are slender, with a curved shaft. The palate is slightly arched, as compared with the domed palate of *Promops* (Eger, 1977).

Eumops perotis (Fig. 1) is the largest bat in the United States. The greater mastiff bat resembles other North American free-tailed bats, but is distinguished from other molossids by its large size and lack of long guard hairs on the rump (Barbour and Davis, 1969). *E. perotis* has the thinnest dentary of any *Eumops* (Freeman, 1981*a*). In the United States, *E. perotis* can be separated from *E. underwoodi* by its larger size (forearm is 73–83 mm in *E. perotis* and 65–77 mm in *E. underwoodi*), darker color, and lack of long guard hairs on the rump. The ears are longer (36–47 mm in *E. perotis* and 28–32 mm in *E. underwoodi*), they extend beyond the nose when laid forward, and they are joined at the midline. In *E. perotis,* the tragus is large, broad, and square, the greatest length of the skull usually is >30 mm rather than less, the basisphenoid pits are large, deep, and not oval shaped, and the third transverse commissure of the M3 hardly is discernible (Barbour and Davis, 1969; Hoffmeister, 1986). Compared with *E. perotis,* the skull of *E. underwoodi* (Fig. 2) is shorter, wider, and less robust, and the interorbital region is distinctly hourglass-shaped rather than nearly cylindrical as in *E. perotis* (Benson, 1947). Compared with *E. perotis, E. dabbenei* has shorter ears, smaller pointed tragus, more massive skull, and the basisphenoid pits are shallower and less developed (Eger, 1977).

GENERAL CHARACTERS. The tail extends far beyond the interfemoral membrane (Elliot, 1901; Hoffmeister, 1986). The dorsum, wings, tail, and ears of *E. perotis* are dark; the venter barely contrasts. The dorsum usually is dark gray, brownish gray, or pale chocolate-brown; the white at the bases of the hairs frequently shows through, both ventrally and dorsally. The venter often is ashy brown (Barbour and Davis, 1969; Eisenberg, 1989; Redford and Eisenberg, 1992).

Eumops perotis is a large bat (total length, 157–184 mm) with long (515–535 mm) slender wings (Grinnell, 1918) and large ears (36–47 mm—Hoffmeister, 1986). Males are significantly larger than females in cranial measurements (Eger, 1977). Average measurements (in mm) of males (n = 12–40) and females (n = 16–102), respectively, of *E. p. californicus, E. p. perotis,* and *E. p. trumbulli,* respectively, are (Eger, 1977): length of forearm, 76.1, 75.1, 80.2, 78.6, 71.6, 70.2; length of cranium, 32.3, 31.4, 33.7, 32.5, 29.2, 28.3; condyloincisive length, 31.3, 30.4, 32.1, 31.0, 27.9, 26.9; zygomatic width, 18.0, 17.6, 19.0, 18.4, 16.7, 16.2; mastoid width, 15.4, 15.1, 15.8, 15.4, 14.3, 13.9; height of braincase, 9.0, 9.0, 10.2, 9.8, 8.7, 8.5; length of maxillary toothrow, 12.4, 12.2, 13.1, 12.8, 11.4, 11.1; postorbital constriction, 5.0, 5.0, 5.5, 5.4, 4.9, 4.9. Mass is 45–73 g (Leitner, 1966; Redford and Eisenberg, 1992; Vaughan, 1966).

DISTRIBUTION. The greater mastiff bat has an unusual distribution consisting of two widely separated populations (Fig. 3; Barbour and Davis, 1969). One population occurs from the south-

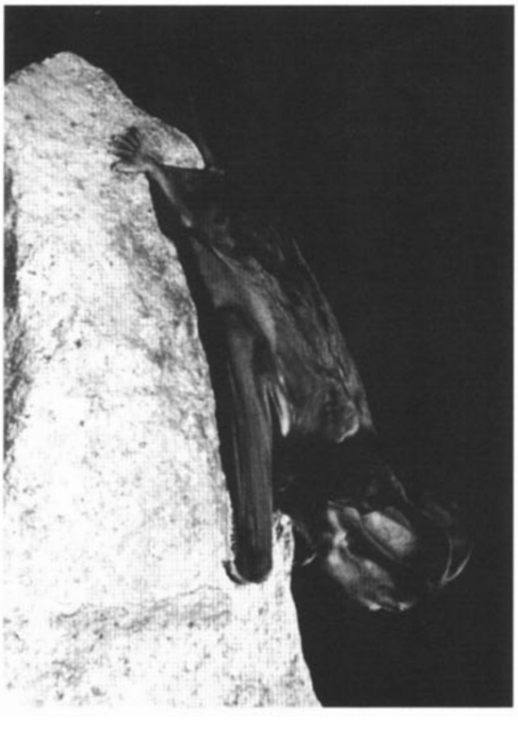

FIG. 1. Photograph of *Eumops perotis californicus* from San Diego Co., California. Courtesy of J. S. Altenbach.

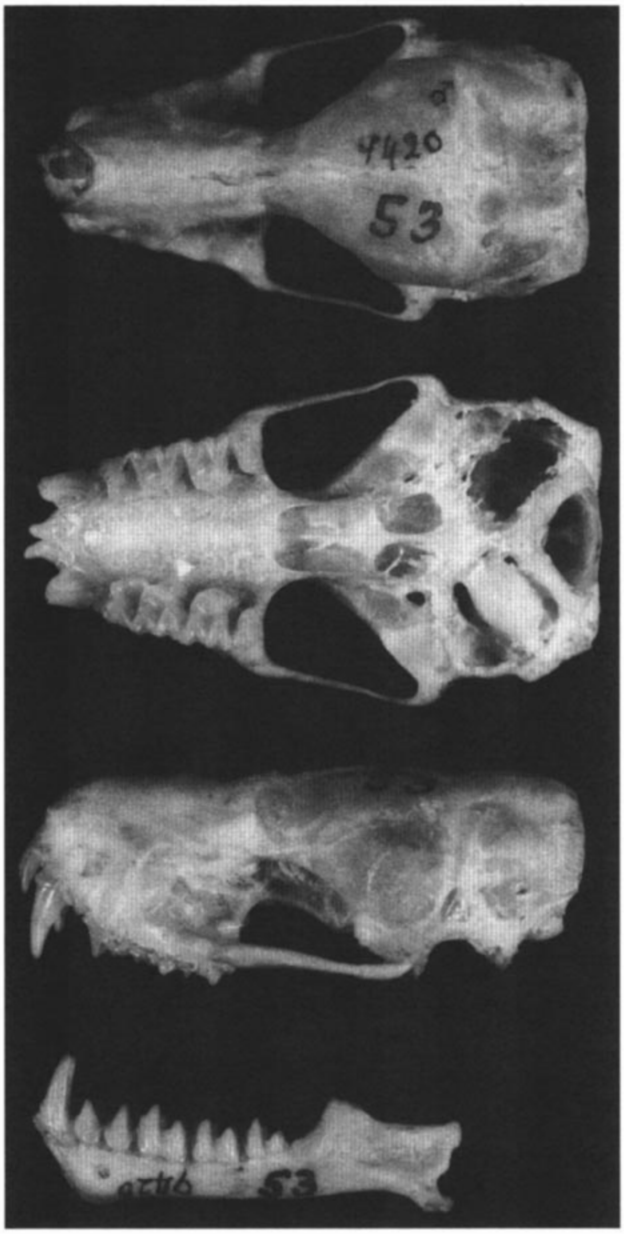

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Eumops perotis californicus* from San Bernardino Co., California (male, University of Kansas Museum of Natural History 9420). Greatest length of cranium is 32.1 mm. Photographs by T. L. Best.

western United States to southern Mexico, and the second is present from northern South America to northcentral Argentina. No specimens are known from Central America (Barbour and Davis, 1969; Eger, 1977; Davis, 1974; Hall, 1981; Polaco et al., 1992; Redford and Eisenberg, 1992; Villa-R., 1967), but it may occur there (Eisenberg, 1989; Koopman, 1982). Although a specimen was reported from Cuba (Peters, 1865; Varona, 1974), it was later determined to be from Brazil (Carter and Dolan, 1978; Silva Taboada, 1979). *E. perotis* is a resident of lower and upper Sonoran lifezones in the southwestern United States (Krutzsch, 1943). Elevational range is from −60 to 375 m in California (Grinnell, 1933) and it is present at ca. 1,100 m elevation in Texas (Ohlendorf, 1972). In the Amazonian drainage, the greater mastiff bat is known to occur in lowlands at <500 m and up to ca. 3,000 m elevation in Peru, but its maximal elevational limits are not known (Koopman, 1978).

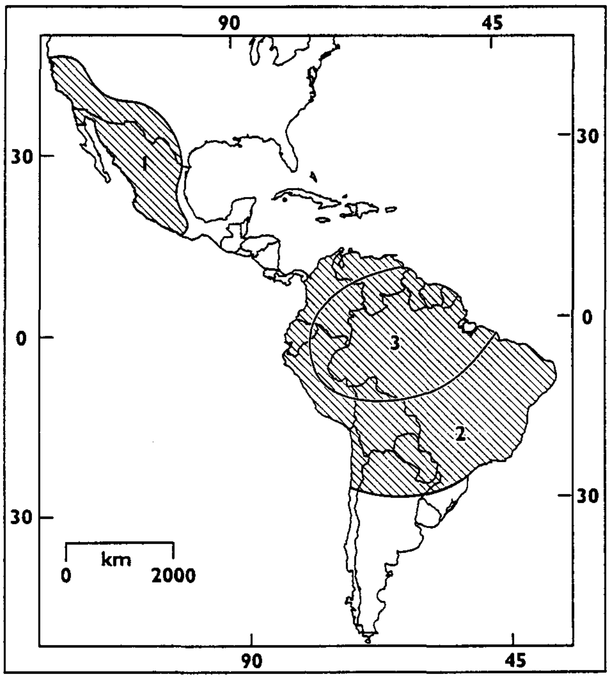

FIG. 3. Distribution of *Eumops perotis* in North and South America (Barquez et al., 1993; Eger, 1977; Koopman, 1982; Polaco et al., 1992; Redford and Eisenberg, 1992; Sanchez H. et al., 1993): 1, *E. p. californicus*; 2, *E. p. perotis*; 3, *E. p. trumbulli.*

FOSSIL RECORD. Remains of *E. perotis* have been recovered from Tertiary (late Blancan—Czaplewski, 1993) deposits in Arizona and late-Pleistocene deposits in Tamaulipas, Mexico (Arroyo-Cabrales, 1992; Dalquest and Roth, 1970). Recent remains have been found in cave deposits near Cuatro Cienegas, Coahuila, Mexico (Gilmore, 1947) and in Val Verde Co., Texas (Epstein et al., 1963).

FORM AND FUNCTION. The pelage is soft, varies in length from 5 to 10 mm, and is denser and shorter on the abdomen than elsewhere (Grinnell, 1918). Structure of hairs on the mid-dorsum and glandular areas is the same (Hickey and Fenton, 1987). On the venter, hair has a distribution similar to that on the dorsum, but hairs do not reach so far along the thigh, and more is found along the forearm. A thin line of dark unicolored hair is present on the upper border of the proximal one-third of the forearm in front of the elbow. A larger line of similar hair extends from the proximal one-third of the forearm to the wrist, and a white-defined patch overlies the carpal portion of the interspace of the fourth digit (Allen, 1893).

The head is elongate (ca. 40 mm in length and 20 mm in width). The muzzle pad is prominent, deeply emarginated above, and its upper edge and median ridge have minute horny processes and small spoon-hairs. The upper lip has a thick fringe of downward-directed hairs. The nostrils are large and directed downward and outward. The upper lip appears smooth rather than deeply wrinkled (Elliot, 1901; Hoffmeister, 1986), but the surface actually is covered with fine, numerous wrinkles that give the lip a flaring appearance and an expandable function (Freeman, 1981*a*). The eyes are placed far back on the sides of the head and are almost concealed by the drooping anterior border of the auricle. In front of each eye is a prominent glandular swelling (Grinnell, 1918).

The skull (Fig. 2) is massive, but slender (Hoffmeister, 1986). Ratio of mass of the head to total mass is 0.23 (Vaughan, 1966). The braincase is scarcely elevated above the vertex of the face. The metencephalon is slightly higher than the mesencephalon, and the mesencephalonis is a little higher than the face. There is a slight depression only between the mesencephalon and metencephalon. The tympanic bone does not conceal the cochlea. The otic capsule comes to the periphery at both squamosal bone and occiput. The semicircular canals are filled with bone, except the superior canal, which retains a minute foramen. The anterior temporal ridge is faintly marked, the sagitta are barely defined, and the posterior temporal ridge is trenchant. The vertex of the face is straight. The inner wall of the orbit is nearly flat. The anterior nasal spine has a flat, thin, lateral process. The infraorbital foramen is in front of the second premolar (PM4). The squama at the base of the zygoma is indented. The distance from the infraorbital canal to the anterior nasal aperture equals twice the diameter of the base of the canine. The hard palate extends a short distance posterior to the last molar. The lower jaw has a semilunar notch that exceeds the distance from the angle to the condyle. The angle exceeds the mesolateral diameter of the condyle in length and lies below the lower border of the horizontal ramus. The symphyseal spine, seen from in front of the symphysis menti, is crested at the lower one-half (Allen, 1893). The basisphenoid pits are elongate and deep, and the interorbital-postorbital region of the skull is narrow and elongate (Hoffmeister, 1986).

The dental formula is i 1/2, c 1/1, p 2/2, m 3/3, total 30 (Eisenberg, 1989; Hoffmeister, 1986). Upper incisors are slender, curved (Hoffmeister, 1986), in contact at their bases, and diverge toward the tips (Grinnell, 1918). The incisor almost touches the canine, yet reaches the middle line and is contiguous with the other incisor at the base. Canines are about triangular in cross-section and are deflected laterally at the tips causing a slight divergence from one another. The tooth has a prominent incisor-directed edge, which is considered sharp (Freeman, 1992), and the cingulum forms a lengthened posterior shelf (Allen, 1893). The small PM3 lies lateral to the interval between the canine and the PM4. The PM4 has a prominent paracone and large expanded heel to receive the protoconid of m1. The third commissure of M3 is one-fourth the length of the second, which is different from the rudimentary third commissure of M3 in the similarly-sized *E. underwoodi* (Eger, 1977; Freeman, 1981*a*). Lower incisors are compressed and bilobed, and premolars are slightly crowded. The commissure at the lingual base of the heel of pm3 is deeply emarginate in the middle. The heel of the M3 is somewhat compressed bucco-lingually, the lingual cusp being higher (Allen, 1893).

Comparison of jaw proportions with dentary length shows that *E. perotis* has thin jaws for a bat its size. It also has well-developed jaw muscles and relatively large teeth (Freeman, 1981*a*).

The ears are large and rounded (Hoffmeister, 1986), united across the forehead, 1.6 times as wide as high (Vaughan, 1966), and project ca. 10 mm beyond the snout (Davis, 1974), which is obliquely truncated (Elliot, 1901). The auricle of the ear is broadly convex anteriorly and posteriorly, and slightly convex on top. The tragus is small, truncate, and nearly concealed by the semi-oval antitragus, which is ca. 10 mm in length and 7 mm in greatest height. The antitragus is separated posteriorly from the auricle by a deep notch. Ears are haired along the margin, but the greater portion of the keel, both externally and internally, is naked. The folds of the ears directly above the nostrils are heavily haired on both upper and lower surfaces (Grinnell, 1918).

In general, the wings are well-adapted for rapid, prolonged flight (Findley et al., 1972; Vaughan, 1959). Species of *Eumops* have among the narrowest wings of all molossids (Freeman, 1981*a*). This wing structure is adapted to high-speed flight in open areas; high-speed flight apparently is correlated with high aspect-ratios (Findley et al., 1972). *E. perotis* was the fastest molossid and had the highest aspect-ratio in a study of *E. perotis, Tadarida brasiliensis,* and *T. molossa* (Vaughan, 1966).

The wings of *E. perotis* are long and slender. The fifth metacarpal is >50% of the length of the third metacarpal. The dorsal surface of the wing membrane, as well as the interfemoral membrane, is furred to a distance of ca. 12 mm from the body. There is a small patch of hair on the dorsal surface of the antebrachial membrane that extends inward from the edge of the radius, except at the bottom of the angle formed by the junction of the radius with the humerus. Another group of hairs extends along the distal 75% of the posterior edge of the forearm, which widens and occupies the angle between the forearm and fourth metacarpal. A third small group of hairs is at the distal end of the third metacarpal. A small patch of fur on the ventral surface of the antebrachial membrane occupies the angle between the anterior edge of the membrane and proximal one-half of the humerus. A line of fur extends from this patch across the humerus and along its posterior edge and unites with a small patch on the lateral membrane immediately posterior to the distal end of the humerus. The interfemoral membrane is not haired, except for a narrow border along the proximal margin of its dorsal surface, and a few scattered hairs along the edge of the postcalcarial lobe (Grinnell, 1918).

Flight membranes are tough and leathery (Vaughan, 1959). The wings extend from the juncture of the middle and distal one-third of the tibia (Elliot, 1901). The second phalanx of the fourth digit is ca. 6 mm in length (Davis, 1974) and is believed to be indicative of a narrow wingtip (Freeman, 1981*a*). Average ratios of wings are: area of chiropatagium/area of plagiopatagium, 0.83; length of chiropatagium/length of plagiopatagium, 1.58; greatest width of wing/length of wing, 0.36; aspect ratio: wingspan^2, 9.98. Average aerodynamic characteristics of the wings are: wingspan, 516 mm; area of wing, 199.22 cm^2; aspect ratio (wingspan^2/area), 11.9; ratio of proximal to distal segment of wing (area), 68.8; uropatagial loading (g/cm^2), 2.15 (Vaughan, 1959, 1966). Minimum flight speed is 23.5 km/h. High-speed dives made when approaching a roosting place in a cliff may be made possible partly by the narrowing of the plagiopatagium when the wing is partly flexed (Vaughan, 1966).

Because drag increases in proportion to surface area and as the square of the speed, *E. perotis* probably is subject to ca. 3× the drag faced by *Myotis evotis.* This explains why features that tend to minimize drag, such as low camber of the wing and short ears, which present their most streamlined aspect to the airstream, are of greater importance in the large *E. perotis* than in smaller, relatively slow-flying bats. Even the short, velvety pelage may be an adaptation to reduce drag during flight (Vaughan, 1966).

The legs and feet are short and stout, the feet are twice as long as wide (Grinnell, 1918), and the ratio of foot to tibia is ca. 60 (Davis, 1974). The mechanical arrangement of the hind limbs do not favor quadrupedal locomotion. Nevertheless, because of the strength of the musculature of the pectoral girdle, the greater mastiff bat can crawl rapidly for long distances. While it crawls, the body remains parallel to the ground and the ventral surface is elevated slightly above the substrate. The tail curves upward at an angle to the substrate of ca. 45° and probably serves as a sensory organ when the bat is moving either forward or backward in a crevice. The head is held low, in line with the body (Vaughan, 1959).

There is no keel on the sternum. There are 13 ribs; the 12th and 13th are widely deflected and have larger interspaces than the others. The sacrum has three elements. The innominate has a concave dorsum anchylosed to the sacrum and to each other at the pubis. The internal trochanter of the femur has a minute spine. The external trochanter has a rugose longitudinal ridge extending on the proximal one-fourth of the shaft. The tibia has a globose spine and the posterior surface of the shaft near the condyle is depressed for flexion of the toes. The proximal end of the fibula has a globose extremity; the distal end is largest and the malleolus is well defined (Allen, 1893).

The axis of the cervical vertebrae has a long transverse process that has a foramen to the outside of the foramen for the vertebral artery. There is a keel on the ventral surface of the centrum ending in a tubercle. The atlas has a tubercle on the anterior arc and there is a large spine on the anterior border of the wide transverse process. The scapula is coracoid-deflected posteriorly and narrowed at the end (Allen, 1893).

Hibernating abilities are unknown, but *E. perotis* may enter torpor (Barbour and Davis, 1969). In laboratory and field studies of temperature regulation conducted in California, this species maintained high body temperatures during the day from March through October. During December, January, and February, however, bats entered a daily torpor, even when kept in the laboratory at room temperatures. They remained in torpor from early morning until late afternoon or evening, when they aroused spontaneously. In the attic of a heated building, bats always were in daily torpor from December through February, but they regularly aroused at night and left their roost to feed. Only on nights when temperature at dusk was <5°C did bats fail to emerge. In laboratory experiments, this species maintained a high body temperature when exposed to air temperatures over the range of 0–40°C. Neutral temperature for the species seems to be 30°C, as measured by oxygen consumption and heart rate; shivering increased at temperatures above and below this point (Barbour and Davis, 1969; Leitner, 1966). Another study determined that individuals placed into a refrigerator at 10°C quickly became torpid; they remained inactive until exposed to higher temperatures 10 days later (Krutzsch, 1955*a*). Differences between these studies may be due to seasonal variation in responses (Barbour and Davis, 1969).

Body temperature at rest is 34–35°C, and is somewhat lower than body temperatures maintained by most mammals. As air temperature increases >30°C, body temperature increases. Body temperature always is higher than ambient temperature, and the animals apparently cannot regulate their temperature by cooling. They can tolerate ambient temperatures of 38–39°C for ≥1 h without heat stress (Barbour and Davis, 1969; Leitner, 1966).

Males have a dermal gland that is enlarged during the mating season (Davis, 1974; Hoffmeister, 1986; Villa-R., 1967). This gland is on the ventral surface of the throat region, just cephalad to the anterior edge of the sternum in both sexes, but is indistinct in young individuals of both sexes and in adult females. When enlarged, this gland produces a thick, oily secretion with a strong odor that may serve to attract females (Cockrum, 1960; Krutzsch, 1955*a*). The gland is most active in early spring (March) when it measures ca. 14 mm across and 4 mm in depth, but by mid-April activity has subsided greatly; one greater mastiff bat had an active gland on 5 December (Howell, 1920*a*). In a male with enlarged testes examined 17 April, the gland was enlarged, nearly circular in outline, 11 mm in diameter, extended 5 mm above the level of the skin, and the central pore was slit-like, 4 mm in length, and 1.5 mm in width. No hair was present on the gland (Cockrum, 1960).

Unlike other species of *Eumops*, *E. perotis* does not have a baculum (Brown, 1967; Ryan, 1991). The glans penis of *E. perotis* is not significantly different from that of *E. auripendulus* or *E. glaucinus*. At its base, the glans penis of *E. perotis* is oval in cross-section, but at midlength the glans widens and is dorsoventrally compressed. From its widest point (ca. 66% of the distance from the prepucial junction) the glans tapers sharply and terminates bluntly. Along the ventral surface of the glans there is a prominent medial ridge that encloses the urethra. This urethral ridge terminates by forming a collar around the ventral rim of the urinary meatus (Ryan, 1991).

ONTOGENY AND REPRODUCTION. Unlike vespertilionid bats of North America, reproductive activity does not begin in males until spring, probably shortly before time of ovulation in females (Cockrum, 1960). Sperm production and copulation occur in early spring when the gular gland of the male is most functional (Barbour and Davis, 1969; Easterla, 1972; Krutzsch, 1955*a*). In the southwestern United States, testes of adult males are enlarged and capable of producing sperm in March and April, they have regressed in some individuals by mid-April, and testes of adult males are small and presumably inactive in late summer and autumn (Cockrum, 1960; Krutzsch, 1955*a*). In Arizona, an adult male had enlarged testes on 27 March, another had small testes on 17 April, another had enlarged testes (4 by 10 mm) on 17 April, and another had small testes on 22 October (Cockrum, 1960). In Hidalgo, Mexico, testes of four males were 11–16 mm in length on 20 March (Polaco et al., 1992).

Nursery colonies often contain adult males. Time of ovulation and length of gestation are unknown. Parturition dates vary more extensively in this species than any other bat in the United States, and are recorded for June, July, August, and probably September (Barbour and Davis, 1969; Easterla, 1972). Time of birth within a colony is variable (Cockrum, 1960). In California, juveniles nearly ready to fly and small, naked young were found together in July (Krutzsch, 1955*a*), and a juvenile was present 11 November. This animal was very young, with cartilaginous gaps of ca. 2 mm at finger joints. Although nothing is known of rates of growth in this species, it seems unlikely that such a bat could be >2 months old (Barbour and Davis, 1969).

One young per female ordinarily is produced, but one female had two embryos (one was 20 mm in crown-rump length and the other 15 mm) on 10 April. In the southwestern United States, embryos or young have been observed 6 April–10 August (Barbour and Davis, 1969; Cockrum, 1955, 1960; Cox, 1965; Grinnell, 1918; Hoffmeister, 1986; Howell, 1920*a*; Howell and Little, 1924; Krutzsch, 1955*a*; Ohlendorf, 1972). In Big Bend National Park, Texas, 12 pregnant females were observed 10–27 June and one on 21 July. Each contained one embryo. From 22 June to 7 August, 12 lactating females were observed as well as another on 11 June. Flying juveniles were not observed until 30 August. Some 16 nonreproductive females were present in June, July, and September. Most parturition occurs here in June and July (Easterla, 1972). In Hidalgo, Mexico, a pregnant female was observed on 20 March (Polaco et al., 1992).

In Arizona, a female was found clinging to a cactus clump at 1639 h on 10 August. She was giving birth to a single young. Young are born naked, except for some tactile hairs on the feet and face, and the throat gland is evident. Eyes may be open (Cockrum, 1960) or closed. On young bats, particularly those that are almost naked, the gland on the ventral throat is conspicuous as a small swelling slightly cephalad to the sternum (Krutzsch, 1955*a*).

Two greater mastiff bats were recovered 2 years after being banded in southern California (Howell and Little, 1924). The lifespan of *E. perotis* is unknown.

FIG. 4. Habitat occupied by *Eumops perotis californicus* at Guadalupe Canyon, Cochise Co., Arizona. Photograph courtesy of B. J. Hayward.

ECOLOGY. Colonies of *E. perotis* are small, usually <100, and adult males sometimes are found in maternity colonies (Barbour and Davis, 1969). In California, the greater mastiff bat has been found in cultivated areas, in rocky places where chaparral (*Ceanothus*, *Adenostoma*) and live oak (*Quercus agrifolia*) intermingle, and in more arid, rocky situations where vegetation is sparse (Krutzsch, 1955*a*). In southern California, type of vegetation limits choice of roosting sites. Most roosts are in semiarid sites that support low-growing chaparral; most conspicuous constituents of which are California buckwheat (*Eriogonum fasciculatum*), greasewood (*Adenostoma fasciculatum*), black sage (*Salvia mellifera*), white sage (*Salvia apiana*), and coastal sagebrush (*Artemisia californica*). In these areas, plants are low-growing and do not significantly obstruct approaches to cliffs and outcrops of rock (Vaughan, 1959). In southwestern New Mexico, *E. perotis* occurs where vegetation is a mixture of elements characteristic of xeric scrubland and riparian woodland (Rowlett, 1972). In Texas, it has been observed over ponds that were surrounded by dense stands of mesquite (*Prosopis juliflora*) and willow (*Salix*; Walton and Kimbrough, 1970). In Zacatecas, Mexico, it occurs in tropical habitat along the Río Juchipila (Matson and Patten, 1975). In Argentina, the greater mastiff bat apparently is a typical inhabitant of mountainous zones, cities, and subtropical forests (Barquez et al., 1993; Mares et al., 1989; Redford and Eisenberg, 1992).

Greater mastiff bats live in high, dry places (Freeman, 1981*a*), and they have special flight requirements for launching themselves for takeoff. Usually, they cannot get airborne from the ground, but will scramble to a post or a tree to gain height for launching. They usually need a height >2 m for a sufficient drop when taking off, so all roosts are in locations that allow the bat to drop >2 m to launch into flight (Hoffmeister, 1986; Howell, 1920*a*; Krutzsch, 1955*a*; Little, 1920; Vaughan, 1959). In the southwestern United States, it is most common in rugged rocky canyons and cliffs, where crevices provide its favored daytime retreats (Barbour and Davis, 1969; Dalquest, 1946). Sheltered crevices occupied by a colony usually can be recognized by massive urine stains on the cliff below, and droppings, which are larger than those of other bats (Barbour and Davis, 1969). Odor of the roost site is detectable by humans at a distance of ca. 50 m (Ohlendorf, 1972).

In Arizona (Fig. 4), the greater mastiff bat roosts in crevices and shallow caves on sides of cliffs and rock walls, e.g., 45–100 of these bats hung in large crevices in a cave on the east face of a 100-m cliff (Cockrum, 1960; Cox, 1965), 15–20 individuals roosted in a narrow crevice in a 6-m deep, 9-m wide, and 13–15-m tall grotto at the base of a 60–100 m cliff (Cox, 1965), and several occupied a crevice in the roof of the cave that housed the cliff dwelling at Tonto National Monument (Johnson and Johnson, 1964). Roosts have large openings below, although they may narrow above to a few centimeters. This permits the bat to leave the roost by dropping a few meters from its resting spot and then exiting from the crevice (Vaughan, 1959). The actual resting spot within the crevice is high above ground and usually quite inaccessible to predators (Krutzsch, 1955*a*).

In southern California, *E. perotis* also seeks diurnal refuge in crevices in rocks that form vertical or nearly vertical cliffs, or that are situated on steep slopes. Usually, it roosts in crevices that are high above the ground and have unobstructed approaches. Occupied crevices were >30 cm in depth and had entrances ≥5 cm in width and 15 cm in length; larger crevices seem to be preferred, but some slitlike openings were 2–3 m in length. Several crevices were >3 m in depth. Large, exfoliating slabs of rock often form crevices suitable for these bats. Because granitic rocks and consolidated sandstones are likely to weather by exfoliation and form deep, vertical crevices suitable for retreats, this species is most common in broken terrain where extensive exposures of these rocks occur. Of the roosting sites examined, all had moderately large openings that could be entered from below, and entrances usually were oriented horizontally and faced downward. All roosts were crevices that became narrow enough at some point to enable bats to wedge themselves into the space and have their dorsal and ventral surfaces against rock surfaces. When frightened, they may force themselves into narrow spaces (Vaughan, 1959).

In Texas, a colony of greater mastiff bats was in a crevice formed by exfoliation of a nearly vertical rimrock. There were openings on the lower and upper sides of the slab. The crevice was about in the middle, vertically, of the rimrock that was ca. 40 m in height. There was a steep slope from the base of the rim with no tall vegetation that might obstruct approach to the crevice (Ohlendorf, 1972).

Eumops perotis has adapted to manmade shelters and is now found in such cities as Tucson, Arizona, and Los Angeles, California. In California, nearly as many day roosts are known in buildings as in natural crevices (Barbour and Davis, 1969). It has been found hanging from a black acacia (*Acacia*) tree (von Bloeker, 1932), behind signboards (Stephens, 1906), under the window awning of an office building (Krutzsch, 1955*a*), hanging on ledges over doors (Grinnell, 1918), in attics, large warehouses, and cracks in masonry walls (Howell, 1920*a*, 1920*b*). Occasionally, *E. perotis* may be found hanging from a rafter in the open (Howell, 1920*a*); this species probably moves out into the open in response to excess heat (Barbour and Davis, 1969). One was hanging from the ledge of a window, swinging back and forth and knocking against the window at ca. 2000-2100 h in December (Grinnell, 1918).

Eumops perotis is insectivorous (Barquez et al., 1993; Vaughan, 1959), and feeds on small to large insects of soft to intermediate hardness (Freeman, 1981*a*, 1981*b*). Habits of insects on which it feeds (low-flying, weak-flying insects) indicate that *E. perotis* usually feeds from near ground level (ca. 1 m above the surface) to treetop level (Ross, 1961), but presence of a variety of diurnal insects in the diet may indicate that it feeds upon insects that have been carried by air currents to altitudes of ≤1,000 m (Vaughan, 1959). In one study conducted in Arizona, diet consisted of Odonata (Aeschnoidea—1%), Orthoptera (Acrididae—10%), Hemiptera (Miridae—10%), Coleoptera (Scarabaeidae, *Cremastocheilus*, Tenebrionidae, Curculionidae—11%), Lepidoptera (moths—10%), Hymenoptera (Halictidae, 36%; Formicidae, 12%; Megachilidae, 5%; Anthophoridae, 5%—58%). Thus, diurnal hymenopterous insects made up 58% of the diet (Easterla, 1972; Easterla and Whitaker, 1972; Ross, 1961, 1967). In another study in Arizona, *E. perotis* primarily consumed abdomens of large hawk moths (Lepidoptera; Sphingidae) ≤60 mm in length, but some Homoptera (Cicadellidae, Cicadidae, and Fulgoridae) were present in the intestine of one individual (Ross, 1967). In Big Bend National Park, Texas, its diet consisted of Lepidoptera (79.9%), Orthoptera (Gryllidae, Tettigoniidae—16.5%, Acrididae—2.8%), and unidentified Insecta (0.7%). The orthopterans may have been picked from cliff walls where the species roosts (Easterla, 1972; Easterla and Whitaker, 1972).

The diet of *E. perotis* differs from that of *E. underwoodi* (Ross, 1967). Difference in jaw structure between *E. perotis* and *E. underwoodi* may be related to type of prey eaten. The long thin jaws of *E. perotis* are suited for large, soft-bodied insects such as moths, whereas the thick jaws of *E. underwoodi* are suited for hard items such as beetles (Freeman, 1981*a*, 1981*b*; Strait, 1993). Further, the finely-wrinkled, skirt-like lips aid manipulation of large prey by *E. perotis* (Freeman, 1981*a*).

In the southwestern United States, other species of chiropterans occupying the same habitat or roost site as *E. perotis* include *Myotis californicus, M. thysanodes, M. velifer, Eptesicus fuscus, Pipistrellus hesperus, Antrozous pallidus* (Walton and Kimbrough, 1970), *Lasiurus borealis, Tadarida brasiliensis*, and *Nyctinomops femorosacca* (Rowlett, 1972), but *E. perotis* usually does not cluster with these smaller species (Barbour and Davis, 1969; Cockrum, 1960; Howell, 1920*a*). In some areas of Mexico, associated species include *N. femorosacca, N. macrotis, Mormoops megalophylla, Myotis yumanensis, M. velifer, M. californicus, P. hesperus, A. pallidus, T. brasiliensis* (Easterla, 1970), *Pteronotus parnellii, Rhogeessa parvula* (Jones et al., 1972), *Glossophaga soricina, Artibeus jamaicensis, Dermanura tolteca*, and *Desmodus rotundus* (Polaco et al., 1992).

In California, *E. perotis* and *Nyctinomops femorosacca* occurred in the same crevice, but *E. perotis* occupied the lower wider end of the crevice and *N. femorosacca* occupied the upper narrower end. Although in the same crevice, they never were observed to come into contact (Krutzsch, 1945). In Arizona, the greater mastiff bat may cohabit crevices with white-throated swifts (*Aeronautes saxatalis*), but the swifts seem not to be in direct contact with the bats because the swifts occupy the back part of the crevices (Cox, 1965; Johnson and Johnson, 1964).

In southwestern Texas, one *E. perotis* released in the morning was stooped upon (unsuccessfully) by a peregrine falcon (*Falco peregrinus*) while the bat was spiraling upward in a large circle. The peregrine falcon circled, gained considerable height, and stooped again, this time easily catching the bat. After the capture an American kestrel (*F. sparverius*) chased the peregrine falcon for a short distance before the peregrine falcon perched and began eating the bat. Previous to being attacked by the peregrine falcon, the bat had been chased and harassed by several white-throated swifts; the bat reacted several times by diving away from the swifts. Another released greater mastiff bat was stooped upon twice, unsuccessfully, by a red-tailed hawk (*Buteo jamaicensis*). Later the bat was harassed by white-throated swifts (Easterla, 1972). In Morelos, Mexico, remains of *E. perotis* were found in pellets of the barn owl (*Tyto alba*; Sanchez H. et al., 1993).

Eumops perotis has not tested positive for rabies (Eads et al., 1957; Wiseman et al., 1962). Ectoparasites include the polyctenids *Hesperoctenes angustatus* (Ohlendorf, 1972) and *H. eumops* (Krutzsch, 1955*a*, 1955*b*). No endoparasites are known.

The greater mastiff bat apparently does not detect mist nets, and is readily taken in them. This species has never been taken over the little woodland ponds that often are so productive for netting other species of bats. Apparently, *E. perotis* prefers a large pool in the open with plenty of open space for the approach. When first captured, *E. perotis* is quite pugnacious and will bite viciously, but it quickly becomes docile after handling (Barbour and Davis, 1969). Greater mastiff bats can adapt to captivity (Constantine, 1961), but it is difficult to induce them to feed (Grinnell, 1918; Leitner, 1966).

BEHAVIOR. *Eumops perotis* can be detected by listening for its high-pitched calls (Barbour and Davis, 1969), which are loud and distinctive (Cockrum, 1960). Vocalizations can be heard >200 m from a roost (Ohlendorf, 1972) and when these bats are flying ≤300 m above ground (Vaughan, 1959). A softer call with a longer interval between "cheeps" than usual calls, characteristically is uttered by a bat just before it drops from its roost (Cox, 1965). When flying in the open, the greater mastiff bat emits a high-pitched piercing cry every 2–3 s as it flies high above the ground, away from obstacles. Intervals between cries are not always constant, and as the bat approaches the ground the intervals decrease, until, as the bat nears some obstacle or makes its approach to the roost crevice, the cries no longer are separate, but blend together in a high buzz (Vaughan, 1959). In Arizona, a greater mastiff bat flew down a canyon with high cliffs on either side; its calls and echoes could be heard ≥0.4 km (Cockrum, 1960).

Eumops perotis is colonial (Grinnell, 1933), sexes occur together through the year (Howell, 1920*a*; Krutzsch, 1955*a*; Ohlendorf, 1972), and it probably is a permanent resident throughout its range (Easterla, 1972), e.g., in Arizona, the greater mastiff bat is present in every month, except possibly January (Cockrum, 1960;

Hoffmeister, 1986). Some roost sites are occupied throughout the year, but most are not occupied year round (Barbour and Davis, 1969; Cockrum, 1960; Howell, 1920*a*; Howell and Little, 1924; Krutzsch, 1955*a*; Leitner, 1966). The four seasons usually are spent in different roosts (Easterla, 1972). Numerous records of individuals at temporary roosting sites in autumn and winter suggest that dispersal of summer colonies is common, but nothing is known about extent of movements or whether there are seasonal migrations (Barbour and Davis, 1969).

Greater mastiff bats move among alternate daytime roosts. In California, bats in one colony used three crevices on the face of a cliff. The bats used only those portions of crevices that were ≥5 m above ground, showed no preference between vertical and horizontal openings, and never used shallow crevices that extended only 30–60 cm into the cliff. The colony would shift freely among the main roost and two other crevices. Sometimes, the main roost would be deserted, except for the young; adults were in other crevices. When young were unable to fly, adults always returned to them within 24 h. After young were independent, the colony often shifted from one site to another without apparent provocation. Such shifting probably is influenced by temperature, other local conditions, and disturbance by humans (Krutzsch, 1955*a*).

Eumops perotis appears to have a daily activity pattern (Krutzsch, 1955*a*). It may move about in its roost at any hour of the day, but is most active in early morning and late afternoon, at which times it is fairly vocal. In the morning, it occupies deeper parts of crevices, but in the afternoon some bats usually are near the entrance. Greater mastiff bats become increasingly active as darkness approaches. When poised at the mouth of the crevice, shortly before launching into flight, they chatter loudly and emit loud "smacking" noises; as a bat launches itself, it gives a series of piercing, high-pitched cries. The bat drops from the mouth of the crevice and dives rapidly downward until sufficient air speed is gained to allow the bat to begin level flight. The wings usually give several powerful strokes as soon as the animal drops clear of the mouth of the crevice, and the bat dives at an angle of ca. 45° for ca. 3–7 m before it pulls upward in a wide arc and assumes level flight. Character of the terrain adjacent to roost sites seems to affect the way this species takes flight; bats usually emerge from roosts beneath which there is relatively little space by diving only 2–3 m and then pulling sharply upward (Vaughan, 1959).

Time of emergence from the roost varies; generally, greater mastiff bats begin leaving their roosts 40–50 min after sunset, but many leave ca. 1–1.5 h after sunset (Barbour and Davis, 1969; Easterla, 1972; Vaughan, 1959). In Arizona, *E. perotis* begins leaving colonies for foraging at ca. 2000 h in late July. Most bats at one colony exited within 5 min, and within 3 min at another. A few stragglers remained and then left at later times. At one roost, activity continued throughout the night, with bats returning, leaving, and flying about the roost. Bats started to return ca. 0400 h on one night and slightly later on another. When bats returned for the day, they came in almost simultaneously and at a rapid rate (Cox, 1965).

In Texas, greater mastiff bats were vocalizing at sunset (1815 h) on 30 January. The first bats emerged at 1845 h; within 10 min, 30 had flown. By 1900 h, 49 had emerged and were clearly visible as they flew. They emerged from the upper side of the crevice, dropped 6–8 m, and then flew away. They flew at an altitude of several hundred meters over the open terrain. Bats emerged from one large crevice and 8–10 came from two smaller ones higher up on the rimrock. By 1910 h, when the first stars were visible, 61 individuals had flown; by 1935 h, no more bats left the roost and no sounds came from the crevice (Ohlendorf, 1972).

Eumops perotis returns to the roost early in the morning. The occasional individuals that return to the crevice in the night and stay for a short time usually are females with young in the roost. In mid-summer, small groups generally begin returning to the immediate vicinity of the colony site ca. 2.5 h before sunrise. The groups circle around the area and bats periodically dive near the crevice; often, after staying near the roost for a few minutes, the group will leave the immediate area. The first bats usually enter the crevice at ca. 0200 h, and most have entered by 0300 h (Vaughan, 1959). It seems probable that individuals of a colony must keep some contact with each other during the 6–8 h they are foraging and away from the roost (Hoffmeister, 1986).

Early observations indicated that the greater mastiff bat had a relatively short foraging period (Howell, 1920*a*); however, the foraging period usually is ca. 6.5 h in length, and throughout this time most *E. perotis* fly continuously. *E. perotis* probably does not rest for long periods during the night, but it will return to the roost for short times (<30 min) during the night. There does not seem to be a peak period of activity. The greater mastiff bat may forage 10–25 km from roost sites; perhaps moving from coastal areas inland to desert habitats of southern California (Vaughan, 1959). It forages from near ground level (Ross, 1961) to considerable elevation (≤1,000 m). Character of the terrain and weather conditions probably influence the elevation at which these bats forage. Over broken country, they seem to fly higher than over level sections (Vaughan, 1959). Intermittent rain does not appear to reduce activity (Cox, 1965) and they are active during bad weather, e.g., foggy nights, rainy nights, and violent thunderstorms (Vaughan, 1959).

FIG. 5. Karyotype of a male *Eumops perotis californicus* from Alamos, Sonora, Mexico (Baker, 1970).

GENETICS. The karyotype of *E. perotis* (Fig. 5) has a diploid number of 48 chromosomes; fundamental number is 56. The X chromosome is submetacentric and the Y is acrocentric; sex chromosomes appear identical to those of *E. underwoodi* (Baker, 1970; Warner et al., 1974).

REMARKS. Sanborn (1932) and Cabrera (1958) considered *E. dabbenei* to be conspecific with *E. perotis*. Subsequent authors have listed this taxon as a distinct species (e.g., Eger, 1977; Freeman, 1981*a*; Koopman, 1993).

Eumops is from the Greek prefix *eu-* meaning "good" or "true" and the Malayan *mops* meaning "bat." The specific epithet *perotis* is from the Latin prefix *per-* meaning "through" or "complete" and the Greek *ōta* meaning "ear" (Jaeger, 1955). Additional common names include California mastiff bat (Bryant, 1891), western mastiff bat (Hoffmeister, 1986), moloso de orejas anchas (Eisenberg, 1989), moloso gigante (Mares et al., 1989; Redford and Eisenberg, 1992), and moloso oréjon gigante (Barquez et al., 1991).

We thank L. L. Thornton, A. M. Coffman, and other personnel in the Interlibrary Loan Department at Auburn University R. B. Draughon Library for assistance in obtaining articles from other institutions, T. Rodriguez for preparing Fig. 3, R. Toomey for providing a copy of Arroyo-Cabrales (1992), J. C. Rainey for translating Spanish documents, and J. L. Dobie, J. L. Eger, R. E. Mirarchi, and J. M. Ryan for critically evaluating an early draft of the manuscript. This is journal article no. 15-955017 of the Alabama Agricultural Experiment Station.

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Editors of this account were DUKE S. ROGERS, ELAINE ANDERSON, AND KARL F. KOOPMAN. Managing editor was ALICIA V. LINZEY.

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