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Leptonycteris yerbabuenae.

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Leptonycteris yerbabuenae Martínez and Villa-R., 1940

Lesser Long-nosed Bat

Leptonycteris nivalis yerbabuenae Martínez and Villa-R., 1940: 313. Type locality "Yerbabuena, Estado de Guerrero," Mexico.
Leptonycteris nivalis sanborni Hoffmeister, 1957:456. Type locality "mouth of Miller Canyon, Huachuca Mountains, 10 mi. SSE Fort Huachuca, Cochise County, Arizona."

CONTEXT AND CONTENT. Order Chiroptera, family Phyllostomidae, subfamily Glossophaginae, tribe Glossophagini. *L. yerbabuenae* is monotypic (Simmons 2005).

DIAGNOSIS. *Leptonycteris yerbabuenae* (Fig. 1) is 1 of 4 North American bats with a nose leaf. *L. yerbabuenae* can be distinguished from *Choeronycteris mexicana* and *Macrotus californicus* by the absence of a conspicuous tail and presence of brownish pelage in *L. yerbabuenae* (Arita 1999). Pelage of *L. yerbabuenae* is shorter and denser in comparison to the longer and fluffier pelage of *L. nivalis* (Davis and Carter 1962; Hensley and Wilkins 1988). *L. nivalis* is larger with grayish pelage, narrower uropatagium, and longer wings. *L. yerbabuenae* is smaller (15–25 g versus 18–30 g), has shorter wings (length of forearm 51–54 mm versus 56.5–59.5 mm), and a shorter 3rd finger (92–102 mm versus 106–115 mm) than *L. nivalis* (Arita 1999). Length of head and body of *L. yerbabuenae* averages as much as 10% shorter than that of *L. nivalis* at comparable latitudes (Hoffmeister 1957). Skull of *L. yerbabuenae* (Fig. 2) is smaller than that of *L. nivalis* (Davis and Carter 1962). It is shorter (mean < 27 mm), the condylobasal length is usually ≤ 26.3 mm, and the presphenoid ridge is more prominent and more rounded than in *L. nivalis* (Hoffmeister 1957, 1986). Skull of *L. curasoae* is generally larger than that of *L. yerbabuenae*. Upper incisors of *L. curasoae* are evenly spaced and larger than those of *L. yerbabuenae*. Upper incisors of *L. yerbabuenae* occur in 2 pairs separated by a median gap (Davis and Carter 1962).

GENERAL CHARACTERS. *Leptonycteris yerbabuenae* is a leaf-nosed bat with an elongated snout. Skull has an elongate rostrum bearing a small, triangular nose leaf (Arita 1999). Skull has complete zygomata and molars are elongate with the W-shaped pattern nearly lost (Hall 1981). *L. yerbabuenae* has 3 caudal vertebrae but no externally visible tail (Hoffmeister 1986).

Means and ranges (in mm) of external characters for 10 males and 10 females (in parentheses) from southern Arizona and Mexico are: total length, 81.8, 74–90 (75.8, 73–82); length of tail, 0 (0); length of forearm, 52.9, 51.3–55.0 (52.2, 51.5–53.5); length of 3rd metacarpal, 49.3, 48.4–51.7 (48.6, 48.0–49.5); length of terminal phalanx of 3rd digit, 10.1, 8.8–11.8 (10.7, 9.7–11.3); length of hind foot, 16.4, 15–18 (17.2, 15–19); and length of ear from notch, 17.7, 16–21 (16.8, 15–19). Means and ranges for cranial and dental measurements (in mm) for these same males and females (in parentheses) are: length of skull, 26.8, 26.0–27.3 (26.8, 26.4–27.3); width of braincase, 10.2, 9.8–10.9 (10.0, 9.8–10.2); condylobasal length, 26.5, 25.9–26.9 (26.3, 25.8–26.7); zygomatic width, 11.1, 10.7–11.5 (10.8, 10.6–10.9); interorbital width, 5.1, 4.8–5.3 (5.0, 4.9–5.3); mastoidal width, 10.3, 10.1–10.6 (10.3, 10.1–10.5); distance from palate to alveolus, 14.7, 14.3–15.1 (14.5, 14.1–15.0); length of mandible, 18.6, 18.3–19.0 (18.5, 18.3–18.9); mandibular depth, 2.3, 2.0–2.5 (1.9, 1.7–2.0); and length of maxillary toothrow, 9.6, 9.2–9.8 (9.5, 9.0–9.9). Mean body masses and ranges (in g) for these same males and females (in parentheses) are: 26.2, 23.5–28.7 (24.5, 23.5–28.7). Body masses of adult males and nonpregnant females are 26.4 g and 24.9 g (Ceballos et al. 1997). Sexual dimorphism is absent (Arita 1999).

Measurement (means and ranges in mm) for 5 males and 5 females (in parentheses) are: length of forearm, 53.5, 51.7–55.6 (54.7, 53.9–55.0); length of 3rd metacarpal, 47.3, 45.6–48.5 (48.8, 47.6–49.5); length of 1st phalanx III, 14.1, 13.0–14.8 (14.3, 13.4–14.8); length of 2nd phalanx III, 23.0, 21.5–24.8 (23.9, 22.9–25.0); length of 3rd phalanx III, 11.3, 9.8–12.4 (11.5, 10.6–12.3); length of 3rd digit, 95.6, 92.1–100.3 (98.5, 95.1–101.2); condylobasal length, 25.7, 25.5–26.1 (26.0, 25.7–26.5); zygomatic width, 10.9, 10.8–11.0 (10.8, 10.1–11.3); interorbital width, 4.6, 4.3–4.8 (4.6, 4.4–4.7); mastoidal width, 10.8, 10.7–10.9 (10.9, 10.7–11.1); length of palate from alveolus, 14.2, 14.0–14.5 (14.3, 13.9–14.7); length of maxillary toothrow, 8.6, 8.5–8.8 (8.9, 8.7–9.2); and length of mandible, 18.5, 18.0–18.8 (18.7, 18.1–19.0—Davis and Carter 1962).

DISTRIBUTION. The northern limit of the distribution of *L. yerbabuenae* extends from the Picacho Mountains in southern Arizona southwest to the Agua Dulce Mountains and southeast to the Chiricahua Mountains, and in southwestern New Mexico in the Animas and Pelonicillo mountains (Arita 1991; Cockrum 1991; Fleming and Nassar 2002; Hoyt et al. 1994). The range extends south from Arizona and New Mexico throughout the drier parts of Mexico, including Baja California, to Guatemala, El Salvador, and Honduras (Arita 1991; Arita and Humphrey 1988; Jones and Bleier 1974; Lee and Bradley 1992; Powell et al. 1993; Fig. 3).

Occasional individuals have been recorded outside the northern limits of the range of the species in Arizona (U.S. Fish and Wildlife Service 1997) and in California (Constantine 1998). This species is most common below 1,800 feet in arid and semiarid habitats. *L. yerbabuenae* is a seasonal resident in the northern parts of its range (north of mid-Sonora), arriving somewhat earlier in southern Arizona (early April and departing mid- to late September) than in New Mexico (arriving mid-July to early September—Cockrum 1991). Occasional sightings occur during winter.

Leptonycteris yerbabuenae migrates into northern Sonora and southern Arizona along 2 migration routes (Wilkinson and Fleming 1996). Lesser long-nosed bats arriving in coastal Sonora and southwestern Arizona during the spring migration travel along the western coast of Mexico. Lesser long-nosed bats arriving later in the summer to sites in south-central and southeastern Arizona and southwestern New Mexico fly along the foothills of the Sierra Madre Mountains. Migrants may travel from as far south as Jalisco (1,000–1,600 km—Wilkinson and Fleming 1996).

FIG. 1. Photograph of an adult female *Leptonycteris yerbabuenae* from Mexico. Used with permission of the photographer, M. Tuttle.

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of an adult male *Leptonycteris yerbabuenae* (U.S. National Museum of Natural History [USNM] 554275) from Cochise County, Arizona. Greatest skull length is 25.9 mm.

FOSSIL RECORD. Late Pleistocene fossils are known from Cueva de La Presita, San Luis Potosí (= *L. curasoae*—Arroyo-Cabrales 1992; Arroyo-Cabrales and Polaco 2003). This locality is 21.4 km S of Matehuala, San Luis Potosí (23°29′37″N, 100°37′16″W) at an elevation of 1,540 m.

FORM AND FUNCTION. Body mass in both males and females fluctuates seasonally (Ceballos et al. 1997; Galindo et al. 2004). In central Mexico, total body mass and fat deposits increased June–July in males and August–December in females when they were pregnant or lactating (Galindo et al. 2004).

Almost 40% of the *L. yerbabuenae* examined from the Huachuca Mountains, Arizona, lacked 1 or more lower incisors (Hoffmeister and Goodpaster 1954). Structural modifications to the tongue that facilitate nectar feeding include lateral ridges (5 mm wide and 10 mm long) of long (mean of 0.9 mm), conical-shaped papillae on the tongue (Howell and Hodgkin 1976). Periodontal disease caused by the mite *Radfordiella oricola* is not present in *L. yerbabuenae* (Greenbaum and Phillips 1974) because of continual scraping of the teeth by the hooklike, filiform papillae on the tongue that prevent the attachment of *Radfordiella*.

The large body size of *L. yerbabuenae* and its high wing-loading ratio facilitate energetically efficient, long-distance flight in arid habitats (Sahley et al. 1993). Estimated daily energy requirements for a nonreproductive *Leptonycteris* were ca. 40 kJ and 60–80 kJ for lactating females (Horner et al. 1998). Sexual differences in flight performance and energetics influence migration strategies of males and females (Sahley et al. 1993). Mechanical power expenditure of hovering is comparable to that in slow forward flight (Dudley and Winter 2002).

Lesser long-nosed bats can survive ambient temperatures up to 41°C and do not enter torpor or hibernate (Carpenter and Graham 1967). A lower basal metabolic rate, greater thermal conductance, and higher evaporative water loss permit this species to tolerate high ambient temperatures (Carpenter and Graham 1967). The lower lethal body temperature is >10°C (Carpenter and Graham 1967).

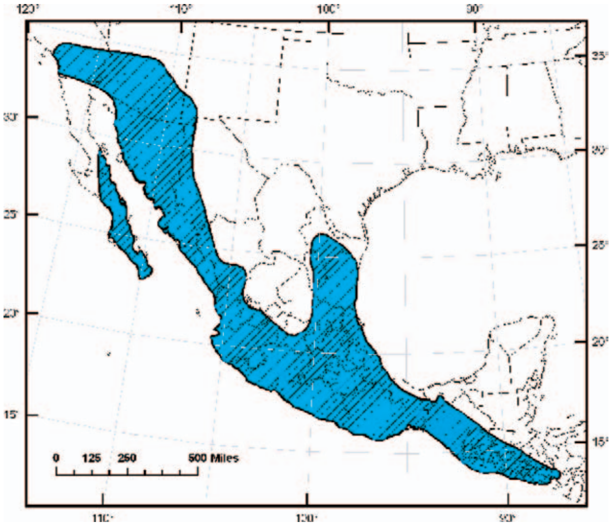

FIG. 3. Geographic distribution of *Leptonycteris yerbabuenae*.

Leptonycteris yerbabuenae feeds on nectar, pollen, and fruit, a diet rich in water but poor in protein and salts (Fleming and Nassar 2002). Renal papilla are very small and the medullary cortex is thick, resulting in copious amounts of very dilute urine. *L. yerbabuenae* normally does not drink, so does not need to roost or feed near water sources within its arid environment (Fleming and Nassar 2002). *L. yerbabuenae* maintains a positive nitrogen balance by ingesting pollen as its primary protein source (Howell 1974). Lesser long-nosed bats tolerate cave and mine environments with high concentrations of ammonia (>1,000 ppm, $n = 1$—Studier et al. 1967).

Lesser long-nosed bats are often covered with pollen. They ingest this pollen in the process of grooming their fur with their feet and then licking the claws to remove the collected pollen (Howell and Hodgkin 1976). The cuticular hair scales are divergent or divaricate versus the more typical appressed condition. Erect hairs covered with these scales that project outward facilitate collection of pollen when lesser long-nosed bats visit flowers in search of nectar.

Lesser long-nosed bats have bimodal hearing with greatest sensitivity at 30–40 kHz and 60–80 kHz.

The external morphology of the brain is characterized by cerebral hemispheres that are short and smooth, with sulci cut deep into the mass of the cerebrum. The internal anatomy includes a short, stubby cerebrum with relatively small olfactory bulbs (McDaniel 1976). Lesser long-nosed bats do not have a dense layer of cell bodies along the margin of the interhemispheric sulcus.

Leptonycteris yerbabuena hosts 2 ectoparasitic flies (*Basilia antrozoi* and *Trichobius sphaeronotus*) and 6 mite genera (*Antricola*, *Ichoronyssus*, *Macronyssus*, *Periglischrus*, *Speleocola*, and *Ornithodoros*—Bradshaw and Ross 1961; Webb and Loomis 1977). *L. yerbabuenae* hosts the fungi that cause candidiasis, cryptococcosis, histoplasmosis, and torulopsosis (Jones 1976; Taylor et al. 2000).

ONTOGENY AND REPRODUCTION. Females give birth to 1 young per year, with the time of mating and parturition varying geographically (Ceballos et al. 1997; Wilson 1973). The sex ratio at birth is 1:1 (Hayward and Cockrum 1971). Two reproductive patterns occur: northern spring births and southern winter births (Ceballos et al. 1997). In either, males and females breed only once per year.

The mean body mass of near-term embryos and newborn young is 4.4 g and 7.3 g, respectively (Hayward and Cockrum 1971). Lengths of forearm and hind foot (in mm) for near-term embryos and newborn young are 18.6, 28.8, and 12.4, 12.7, respectively. A sparse growth of short, grayish hair covers the body but not the head by the time the length of forearm reaches 30 mm (Hayward and Cockrum 1971). The ability to fly is attained when the forearm reaches 46 mm in length. A well-developed pelage exists by the time the forearm reaches 53 mm.

Lactation lasts 4–8 weeks in *L. yerbabuenae* (Jenness and Studier 1976). Milk is high in carbohydrate (4.8 g/100 g as lactose) and relatively high in fat (18.5 g/100 g) and energy (2.1 kcal/g). Despite their noninsectivorous diet, lesser long-nosed bats produce milk with a significant protein content (casein 2.5 g/100 g and whey protein 1.8 g/100 g), thus nursing young are not nutritionally stressed by low levels of milk protein (Jenness and Studier 1976).

In the northern part of their range (north of mid-Sonora), seasonal occupancy is typical of all roosts (Cockrum 1991). Pregnant females arrive in mid- to late April to form large maternity colonies (typically tens of thousands to >100,000 bats) in caves in Arizona and Sonora, typically <1,800 feet and near abundant food sources (Cockrum 1991). Many females return to the same maternity roost in different years (Hayward and Cockrum 1971). *L. yerbabuenae* gives birth at the end of the spring or at the beginning of the summer (Arita 1999; Cockrum 1991). Females and young of both sexes begin leaving the maternity roost by mid-July (Fleming and Nassar 2002). Many of these animals move to nearby transient roosts before migrating south. Unlike females, males live in small groups during the summer in southern Arizona (Cockrum 1991; Hayward and Cockrum 1971). Maternity and transient roosts in the northern part of the species range are typically empty by mid-September.

Many mating and maternity roosts in mainland Mexico are separated geographically. Females at different stages of pregnancy and young of different ages have been found simultaneously in northern maternity roosts (Hayward and Cockrum 1971), thus females conceive at slightly different times, probably in different roosts, before migrating to the maternity roost. Mating takes place in central Mexico in November–December (northern birth schedule) or May–June (southern birth schedule) and young are born ca. 6 months later in northern maternity roosts than in southern maternity roosts (Fleming and Nassar 2002). In both instances, births and nursing occur during peaks in flower and fruit availability in the Sonoran Desert (spring births) or in tropical dry forests (winter births). Males are reproductively active in late fall on San Andres Island, Jalisco (Ceballos et al. 1997), but further south at Las Grutas, Michoacán; peak male reproductive activity occurs in June (Fleming and Nassar 2002). Juveniles start flying after 1 month and exit the caves ca. 2–3 weeks later (Arita 1999).

Leptonycteris yerbabuenae is a year-round resident in southern Baja California with a mid-March birth schedule, roughly midway between the spring and winter birth peaks on the mainland (Fleming and Nassar 2002). Mid-March is when *Agave* flowers are abundant in this area (Wiggins 1980).

Winter maternity roosts occur south of southern Sonora (Gruta Juxtlahuaca in Guerrero and Cueva Tempisque in Chiapas—Fleming and Nassar 2002). Females using these roosts give birth in December or January (Quiroz et al. 1986). Seasonal roost occupancy has been recorded at Cueva Las Grutas, Michoacán (June–August), Cueva de Xoxafi, Hildalgo (February–September), and Gruta Juxtlahuaca, Guerrero (August–February—Fleming and Nassar 2002). Year-round roosts south of southern Sonora typically undergo seasonal fluctuations in size and sexual composition. A balanced sex ratio occurs between June and August when mating occurs, but is skewed toward males in December–January (Fleming and Nassar 2002).

A population of *L. yerbabuenae* at a sea cave roost on Don Panchito Island near Chamela, Jalisco, is in an area that geographically separates the northern migratory populations from the southern nonmigratory populations (Stoner et al. 2003). In this area, *L. yerbabuenae* was present in the cave year-round although significant differences in abundance occurred over time. The population was largest in November–December and smallest in July–August. Reproducing females were most abundant in December–March but also present in July and September. The male population had 2 reproductive periods per year: September–December and May–June (Stoner et al. 2003). However, individual females and males do not have 2 reproductive bouts per year.

Lesser long-nosed bats have been recaptured 4–8 years after banding (Hayward and Cockrum 1971). Predators of *L. yerbabuenae* include owls, carnivores near roost entrances, and snakes. *Bassariscus* and *Mephitis macroura* have been observed in caves occupied by lesser long-nosed bats (Hayward and Cockrum 1971).

ECOLOGY. In the southwestern United States, *L. yerbabuenae* is found mainly in arid grasslands, scrubland, and oak forests (Arita 1999). In this part of the range, seasonal changes in temperature, precipitation, and photoperiod occur. In central and southern Mexico, the preferred habitat includes arid grasslands, tropical thorn and deciduous forests, and pine–oak forests.

Seasonal differences in size and sexual composition are basic features of populations of *L. yerbabuenae* (Ceballos et al. 1997; Cockrum and Petryszyn 1991). In the northwestern part of the range, females arrive at maternity roosts in mid- to late April, numbers peak by mid-May, and the roost is empty by mid-September (Ceballos et al. 1997). Most of the colonies during this time are composed of females and young, and some adult males can be found in temporary roosts ("bachelor roosts") in late summer (Cockrum 1991). In a roost near Chamela, Jalisco, population size began to expand in June–September as males and females returned to the cave, and reached a peak by late November (Ceballos et al. 1997). In December, many males and females leave the roost (Wilkinson and Fleming 1996), thus, the carrying capacity around the Chamela roost is lower in the dry season than in the wet season (Ceballos et al. 1997).

The population dynamics of *L. yerbabuenae* in central Mexico at Tzinacanostoc Cave showed considerable seasonal change in size and composition, but reproductively active females were present throughout the year (Galindo et al. 2004). The colony was largest in February–July (22,000–27,000 adults) with an equal number of males and females. Males mated with females during June–July. The population began to decline in August as males left and between September and December the colony was composed exclusively of pregnant and lactating females (8,000–10,000) and their young; the population had declined by two-thirds from its maximum size. In January, males returned to the cave, increasing the population size. Thus, some populations of *L. yerbabuenae* in central Mexico complete their life cycle without migrating.

Some populations in Mexico are resident throughout the year, linked to food availability (Rojas-Martinez 2001; Rojas-Martinez et al. 1999; Valiente-Banuet et al. 1996). In southern and central Mexico, populations fluctuated seasonally with few residents remaining during spring–summer (Alvarez and González 1970; Alvarez et al. 1999; Ceballos et al. 1997; Herrera 1997; Quiroz et al. 1986; Stoner et al. 2003; Tellez et al. 2000). Two migratory patterns for *L. yerbabuenaeare* (Tellez et al. 2000) are populations that move to the northern deserts in the spring from roosts in dry forests located at latitudes higher than 19°N or populations that move from central Mexican desert roosts (where mating takes place in spring–summer) to roosts in central and southern dry forests where the young are born and raised (fall–winter). A 3rd pattern involves breeding females remaining in the same roost year-round (Galindo et al. 2004).

Leptonycteris yerbabuenae roosts in large and densely packed colonies (typically 1,000 to >100,000 individuals—Fleming and Nassar 2002). Fluctuations in the size and composition of roost populations also are typical (Alvarez and González 1970; Alvarez et al. 1999; Ceballos et al. 1997; Herrera 1997; Quiroz et al. 1986; Stoner et al. 2003; Tellez et al. 2000). Colonies of *L. yerbabuenae* are widely scattered over the landscape (Ceballos et al. 1997).

Significant maternity roost sites include a mine in Organ Pipe Cactus National Monument, Arizona; Bluebird, Copper Mountain, and Old Mammon mines, Arizona; Pinacate Cave, Pinacate Biosphere Reserve, Sonora; Cueva del Tigre, Carbo, Sonora; Sierra Kino–Isla Tiburon caves, Bahia Kino, Sonora; Santo Domingo Mine, Aduana, Sonora; Cueva La Capilla, cave near Buenavista, Baja California Sur; San Andres Island, Jalisco; Don Panchito Island, Jalisco; Cueva La Mina, Jalisco; Gruta Juxtlahuaca, Guerrero; Cueva Tempisque, Ocozocoautla, Chiapas; Tzinacanostoc, Puebla, Guerrero; and a cave near Tuxtla Guttierez, Chiapas (Arita and Humphrey 1988; Ceballos et al. 1997; Cockrum 1991; Galindo et al. 2004; Horner et al. 1998; Stoner et al. 2003). Significant nonmaternity roosts include Patagonia Bat Cave, Manila Mine, Star of Texas Mine, and Hilltop Mines, Arizona; a cave near Alamos, Sonora; Cueva Las Grutas, Michoacán; and Cueva de Xoxafi, Hildalgo (Arita and Humphrey 1988; Ceballos et al. 1997; Cockrum 1991).

Most of the range of *L. nivalis* is included within the range of *L. yerbabuenae* (Arita and Humphrey 1988). However, *L. nivalis* occurs more frequently in upland pine–oak or tropical deciduous forests and *L. yerbabuenae* occupies lowland tropical and subtropical dry forests. The 2 species spatially segregate along altitudinal and mean annual temperature gradients with *L. yerbabuenae* occupying lower and warmer areas than *L. nivalis* (Arita 1991). This segregation is not complete and the ranges overlap at some altitudes.

The diet of *L. yerbabuenae* consists mainly of nectar, pollen, and fruit (Gardner 1977; Hoffmeister and Goodpaster 1954). Insect remains occur in some stomachs, but these may have been consumed accidentally during nectar feeding (Howell 1974). Much of the pollen is probably ingested coincidental to nectar feeding or during grooming (Howell and Hodgkin 1976). Nectar and pollen dominate the diet but cacti fruits may be taken, especially when females are lactating (Fleming and Nassar 2002). Lesser long-nosed bats are opportunistic foragers and their diet correlates with the availability of local plant resources.

Leptonycteris yerbabuenae consumes nectar and pollen from paniculate agave flowers and nectar, pollen, and fruit produced by columnar cacti, especially saguaro (*Cereus giganteus*) and organpipe (*Stenocereus thurberi*) cacti in southern Arizona and Sonora (Fleming et al. 1993; Hayward and Cockrum 1971; Howell 1979; Howell and Roth 1981; Wilson 1985). Winter populations in southern Mexico feed on flowers of a variety of plants (Agavaceae, Bombacaceae, Cactaceae, Convolvulaceae, and Leguminosae) based on their temporal availability (Alvarez and Gonzalez 1970; Gardner 1977; Quiroz et al. 1986). Pollen from species of Bombacaeae is a crucial dietary resource year-round in Jalisco, Mexico (Stoner et al. 2003). These food resources are patchily distributed and the nectar is only seasonally available. Lesser long-nosed bats time their movements and feeding to the flowering of these cacti and agaves.

Seasonal changes in the diets of migrant *L. yerbabuenae* were documented through carbon stable isotope analysis (Fleming et al. 1993). *L. yerbabuenae* feeds exclusively on plants with a crassulacean acid metabolism photosynthetic pathway (CAM; Agavaceae and Cactaceae) during migration and in the northern part of the range of the species. In the southern part of its range, it feeds primarily on C_3 plants (all other plants visited by *L. yerbabuenae*). *L. yerbabuenae* is a CAM specialist in Baja California, where it is a year-round resident. It feeds primarily on C_3 plants throughout the year near Chamela, Jalisco, where cacti and agave densities are low (Ceballos et al. 1997). *L. yerbabuenae* is a CAM specialist in the most arid parts of its range but a CAM-C_3 generalist in the more mesic areas (Fleming and Nassar 2002).

Lesser long-nosed bats follow a "nectar corridor" composed of CAM species that provide nectar during their migrations to and from the Sonoran and Chihuahuan deserts (Fleming et al. 1993). In spring, lesser long-nosed bats feed on at least 4 night-blooming columnar cacti species and an *Agave* species during their journey north. The timing for peak flowering in the cacti species is asynchronous, providing an extended period of abundant nectar (Fleming et al. 1993). In fall, the nectar corridor for the migration south is provided by a series of *Agave* species. *L. yerbabuenae* and species of Cactaceae and Agavaceae are effectively mutualists over a large geographical area (Fleming et al. 1993; Waser and Real 1979). In *Agave macroacantha*, fruits originating from flowers pollinated by *L. yerbabuenae* yield significantly more seed than those exposed to *Choeronycteris mexicana* or to the whole pollinator guild collectively (Arizaga et al. 2000).

Leptonycteris yerbabuenae is a major pollinator of Cactaceae and Agavaceae and disperser of cactus seeds (Alcorn et al. 1961; Alvarez and Gonzalez 1970; Fleming et al. 1996; Godínez-Alvarez and Valiente-Banuet 2000; Howell and Roth 1981; McGregor et al. 1962). *L. yerbabuenae* is a potential pollinator of species of Bombacaeae and is the principal pollinator of *Ceiba grandiflora* (Stoner et al. 2003). *L. yerbabuenae* visited flowers found in trees in disturbed habitats less frequently than trees found in undisturbed habitats. Habitat disruption has a negative effect on lesser long-nosed bats in tropical dry forest ecosystems as well as negative consequences for the plants they pollinate (Quesada et al. 2003).

Seed set in *Agave palmeri* was reduced by >95% of the maximum potential in the absence of *L. yerbabuenae* (Howell and Roth 1981). *L. yerbabuenae* is an excellent pollen vector for self-incompatible, widely spaced desert cacti (Horner et al. 1998). Lesser long-nosed bats disperse cacti seeds, but the rate of cactus seed dispersal by lesser long-nosed bats is lower than that by birds in the same area (U.S. Fish and Wildlife Service 1997). Because of its role as an important pollinator of columnar cacti and agave, lesser long-nosed bats are a keystone mutualist and the Sonoran Desert ecosystem might be harmed by the decline of populations of *L. yerbabuenae* (U.S. Fish and Wildlife Service 1997). Disappearance of lesser long-nosed bats from the Sonoran Desert would reduce fruit and seed set in columnar cacti and paniculate agaves with economic and ecological impacts (Arita and Wilson 1987; Valiente-Banuet 2002).

Although roosts may contain thousands of lesser long-nosed bats during the day, when they leave the roost at night and disperse over the landscape, local densities within cactus patches can be low (0.5 bats/ha—Fleming et al. 2001) leading to low flower visitation rates (Fleming et al. 1996). Overharvesting of agaves in Mexico, collection of cacti in the United States, and habitat conversion for development, agriculture, and livestock grazing may cause populations of *L. yerbabuenae* to decline.

ANIMAL HUSBANDRY. *Leptonycteris* bats have been maintained in the laboratory for extended periods (Greenhall 1976). The artificial nectar diet approximated the nutritional content of a natural diet dominated by nectar and pollen. A diet recipe is available (Greenhall 1976). Care should be taken to maintain protein content at 9–11% and sugar content at 14–20%.

BEHAVIOR. Long, nightly commuting flights are a basic component of the foraging ecology of *L. yerbabuenae* (Horner et al. 1998). They roost gregariously and live in a few large, widely scattered colonies. In Sonora, individual bats leave their day roost shortly after sunset and fly continuously during the early evening with little feeding, scouting out and assessing availability of food sources (Horner et al. 1998). In Arizona, small groups forage together, mainly between 2400 and 0200 h (Howell 1979).

Most individuals visited many flowers spread over many plants growing in a large area, far more than necessary to meet energy and nutrient needs (Horner et al. 1998). In southeastern Arizona, the lesser long-nosed bat diet is primarily nectar and pollen from *Agave palmeri* (Ober and Steidl 2004). Conservation management strategies targeted at *L. yerbabuenae* must consider the spatial distribution and temporal variation in flowering of *A. palmeri*.

Visitation rates varied with time of night, distance and orientation from the roost, and the number and relative position of flowers on the inflorescence (Ober and Steidl 2004). Flower visits were clumped among plants and flowers (Horner et al. 1998). Lesser long-nosed bats visited most flowers <5 times and obtained ca. 0.1 ml per visit. The energy budget of *L. yerbabuenae* is estimated to be at least 40 kJ/day and lesser long-nosed bats make roughly 80–100 visits to cactus flowers to obtain this energy. When lactating, a female's energy budget is estimated to increase by 50–100%. Examination of radiotracking data indicates that bats spend almost 5 h in flight each night and fly ca. 100 km. Time in flight represents 21% of the daily time budget but 44% of the energy budget. Day roosting represents 75% of the time budget but only 50% of the energy budget. Food supply is not limited during the spring.

During the day *L. yerbabuenae* roosts in abandoned mines and caves, forming colonies that range in size from a few to >10,000 individuals (Arita 1999). At night when not foraging, lesser long-nosed bats typically roost in caves, abandoned buildings, mines, rock crevices, trees, and shrubs (Cockrum 1991; Hoyt et al. 1994). They are gregarious and night-roosting colonies may contain a few thousand to >100,000 bats (Ceballos et al. 1997; Cockrum and Petryszyn 1991; Wilkinson and Fleming 1996).

In Arizona, *L. yerbabuenae* is typically the single occupant of caves or mines, although it sometimes roosts with *Choeronycteris mexicana*, *Corynorhinus townsendii*, *Macrotus californicus*, *Myotis velifer*, *M. thysanodes*, and *Tadarida brasiliensis* (Hayward and Cockrum 1971; Hoffmeister 1986; U.S. Fish and Wildlife Service 1997). In Mexico, *L. yerbabuenae* roosts with 10 species of bats from 5 families (Mormoopidae, *Mormoops megalophylla* and *Pteronotus davyi*; Phyllostomidae, *Glossophaga morenoi* and *G. soricina*; Natalidae, *Natalus stramineus*; Vespertilionidae, *Myotis velifer*; and Molossidae, *Tadarida brasiliensis*—U.S. Fish and Wildlife Service 1997). When occupying a cave or mine with other species, *L. yerbabuenae* tends to roost separately by moving deeper into the cave or mine tunnel (U.S. Fish and Wildlife Service 1997).

At birth, the hind feet of young are roughly adult size, enabling them to hang from the roost ceiling while the adults are foraging (Hayward and Cockrum 1971). When beginning flight, lesser long-nosed bats bring their body into a horizontal position with several wing beats before releasing their grip (Barbour and Davis 1969). When hovering the downward stroke of the wings is directed forward and the up stroke backward (Hoffmeister 1986).

Leptonycteris yerbabuenae from the Chamela roost in Jalisco shares haplotypes or high levels of genetic similarity with individuals from northern roosts in Baja California and southern Arizona (Wilkinson and Fleming 1996). Close genetic similarities were not found for bats from roosts in Guerrero and Chiapas. Thus, lesser long-nosed bats from the Chamela area migrate northward to establish maternity roosts in Baja California, Sonora, and southern Arizona. These migrants come from multiple rather than a single southern source (Wilkinson and Fleming 1996).

GENETICS. *Leptonycteris yerbabuenae* has a diploid number of 32 and a fundamental number of 60 (Baker 1967). All autosomes are biarmed and vary in size. One pair of smaller chromosomes approaches subtelocentric centromere placement; the other chromosome pairs have metacentric (8 pairs) or submetacentric centromeres (6 pairs). The X chromosome is a medium–small submetacentric and the Y is a minute acrocentric (Baker 1967). Gene flow is high among populations of *L. yerbabuenae* distributed over a range of distances (Wilkinson and Fleming 1996). Nucleotide sequences for unique haplotypes are available (Wilkinson and Fleming 1996).

CONSERVATION STATUS. *Leptonycteris yerbabuenae* is considered an endangered species throughout its range in the United States and Mexico, and a recovery plan for this species has been approved (U.S. Fish and Wildlife Service 1997). *L. yerbabuenae* was added to the U.S. Endangered Species List in 1988 (Shull 1988). It is also on the list of endangered and threatened species for Mexico (Secretaría de Desarrollo Social 1994). *L. yerbabuenae* is listed in the International Union for the Conservation of Nature Red List of Threatened Species as vulnerable because of declining populations resulting from apparent range restrictions (Hutson et al. 2001). In the United States, numbers in some locations are relatively stable from year to year, but disagreement on population estimates exists (Cockrum and Petryszyn 1991; U.S. Fish and Wildlife Service 1997; Wilson 1985). No critical habitat is designated. The seasonal cycle of migration within the northern part of the range of the species must be carefully considered when determining population estimates (Cockrum and Petryszyn 1991). Acknowledging this, Fleming et al. (2003:65) suggested, "Our data do not indicate that this species is uncommon or is experiencing a secular decline in numbers in the U.S., as implied by its 'endangered' status." Threats include harvesting of the lesser long-nosed bat's food plants, loss of cave-roosting sites through destruction, recreational caving, sealing abandoned mine entrances, and killing for pest control.

A conservation strategy for *L. yerbabuenae* should protect migratory corridors and all northern maternity roosts (Stoner et al. 2003). This species is sensitive to human disturbance and may not return to a roost once disturbed (Cockrum and Petryszyn 1991). Four priority areas for conservation of lesser long-nosed bats in Mexico are western Sierra Madre, Balsas Basin, southern Sierra Madre, and the southeastern lowlands (Arita and Santos-del-Prado 1999). Protecting all locations of breeding colonies and roosting areas for resident (nonmigratory) populations, not just high-diversity caves, in the southern part of the species range is equally important (Arita 1993). The endangered tropical dry forest that extends from western Mexico south into Central America is an important habitat for this species and should be protected (Ceballos and Garcia 1995). Protection of food plants within a radius of 50 miles (81 km) around known roosts as well as along migratory paths is recommended (U.S. Fish and Wildlife Service 1997).

REMARKS. The name *Leptonycteris* is from the Greek *leptos*, meaning slender, and *nycteris*, meaning bat, in reference to the slender rostrum of this genus (Hensley and Wilkins 1988). The specific epithet refers to the type locality, near the small town of Yerbabuena, in the state of Guererro, Mexico. The original type series actually came from a cave a short distance south of Yerbabuena, somewhat higher than 1,800 m elevation, and near a locality called Laguna Honda (Martínez and Villa-R. 1940).

Although *L. yerbabuenae* was described in 1940, a considerable amount of literature devoted to this species can be found under the junior synonym *L. sanborni*, which dates from 1957. *L. yerbabuenae* is more abundant and has a much wider distribution than the other species in the genus (Arita and Humphrey 1988). Arita and Humphrey (1988) documented that *L. nivalis* is rarer than previously believed and indicated that several published reports regarding *L. nivalis* actually refer to *L. yerbabuenae*. The taxonomy of this genus was confused for many years because most of the type series of *L. nivalis yerbabuenae* was lost shortly after the description. Arita and Humphrey (1988) examined 3 remaining paratypes and concluded that *L. n. yerbabuenae* was based on a composite series of specimens that included both *nivalis* and *yerbabuenae*. They argued for including *yerbabuenae* in the synonymy of *L. curasoae*, a species otherwise known only from South America and the nearby Caribbean. However, subsequent workers, including Koopman (1994) and Simmons and Wetterer (2002), separated *yerbabuenae* and *curasoae*, returning to the prior arrangement of 3 species (*curasoae*, *nivalis*, and *yerbabuenae*).

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