MAMMALIAN SPECIES No. 547, pp. 1–6, 5 figs.

Myotis leibii.

By Troy L. Best and Jason B. Jennings

Published 9 May 1997 by the American Society of Mammalogists

Myotis leibii (Audubon and Bachman, 1842)

Eastern Small-footed Myotis

Vespertilio leibii Audubon and Bachman, 1842:284. Type locality "Erie county, Michigan" (=Ohio—Miller and Allen, 1928: 172).

Myotis winnemana Nelson, 1913:183. Type locality "Plummers Island [Montgomery Co.—Hall, 1981:188], Maryland (in Potomac River 10 miles above Washington)."

CONTEXT AND CONTENT. Order Chiroptera, Suborder Microchiroptera, Family Vespertilionidae. The genus *Myotis* contains 84 species (Koopman, 1993). *Myotis leibii* is monotypic (van Zyll de Jong, 1984, 1985).

DIAGNOSIS. *Myotis leibii* (Fig. 1) is recognized by its short hind foot (<8 mm), short ears (<15 mm—Bogan, in press; McDaniel et al., 1982), dark-brown pelage (Bailey, 1933), black facial mask, black ears, absence of a dark shoulder patch (Godin, 1977), overall small size (length of forearm, ca. 32 mm—Bailey, 1933), obviously keeled calcar, and small, flattened skull (Bogan, in press; Fig. 2). When laid forward, the ears extend slightly beyond the nose (Godin, 1977).

The range of *M. leibii* is allopatric with that of *M. californicus* and *M. ciliolabrum*, the other species of *Myotis* in North America that have small feet and keeled calcars (Bogan, in press). Compared with *M. leibii*, *M. californicus* has dull, dark-brown, or reddish-brown pelage, which is paler and does not contrast with the snout and facial hair. In addition, the pelage of *M. californicus* has no pronounced sheen and the skull has a rounded braincase and a steeply sloping forehead. In *M. ciliolabrum*, the braincase is vaulted and the width of the upper incisors is relatively narrower than in *M. leibii* (van Zyll de Jong, 1984, 1985). The baculum of *M. ciliolabrum* was first reported to differ strongly from that of *M. leibii* (Krutzsch and Vaughan, 1955), but subsequent analyses of a larger number of specimens revealed no consistent differences between bacula of these taxa (van Zyll de Jong, 1984).

In general, color of *M. leibii* resembles *Myotis lucifugus*, but differs in its golden-tinted, almost yellowish, pelage (Godin, 1977). *M. leibii* is distinguished easily by its much shorter forearm, blackish muzzle, and distinctly shorter ears and feet. The forearm of *M. leibii* is ca. 4–8 mm shorter than that of *M. lucifugus*. In addition, the skull of *M. leibii* is smaller and more flattened (Nelson, 1913).

Myotis leibii and *Pipistrellus subflavus* are similar in size. *P. subflavus* can be distinguished from *M. leibii* by its blunt, rather than pointed, tragus (Bogan, in press), lack of a keel on the calcar, larger feet (Barbour and Davis, 1969), paler color, especially the pale-pinkish forearms, and lack of a keeled sternum (Godin, 1977).

GENERAL CHARACTERS. The face (Allen, 1939; Nelson, 1913), ears, wings, and interfemoral membrane are black. The pelage is dark yellowish-brown dorsally and cinereous ventrally. The pelage on the back is black from the roots to near the end of the hairs, where it is so slightly tipped with pale brown as to give it a dark yellowish-brown appearance (Audubon and Bachman, 1842). The underparts are dull grayish-brown (Nelson, 1913).

Myotis leibii is one of the smallest North American members of the genus *Myotis* (McDaniel et al., 1982). Average external measurements (n = 30–40; in mm) are: total length, 83; length of tail, 36; length of hind foot, 7; length of ear, 13; length of forearm, 32.2 (van Zyll de Jong, 1985). In Ontario and Quebec, average mass was 3.8 g (range, 3.2–5.5—van Zyll de Jong, 1985), but average mass in January was 5.0 g (range, 4.1–5.5 g—Hitchcock, 1965).

The skull is small and delicate, the braincase is flattened, and the forehead slopes gradually upward from the rostrum (Fig. 2). The prominent forehead of many species of *Myotis* is lacking (Barbour and Davis, 1969; McDaniel et al., 1982; van Zyll de Jong, 1985). Average cranial measurements (n = 32; in mm) are: greatest length of cranium, 13.6; mastoid width, 7.1; least interorbital width, 3.3; orbital width at the lacrimal foramina, 4.4; rostral width immediately posterior to the canines, 3.2; maxillary width at M3, 5.1; width of the upper incisors, 2.4; length of the maxillary toothrow, 5.1; length of the P4-M3 series, 3.6; length of M2, 1.2; width of M2, 1.5; basal width of upper canine at the cingulum, 0.7; depth of cranium, 4.2; height of the coronoid process, 2.8 (van Zyll de Jong, 1984).

DISTRIBUTION. The eastern small-footed myotis is one of the rarest bats in North America (Barbour and Davis, 1969; Davis et al., 1965; Gates et al., 1984; Griffin, 1940; Mohr, 1932*a*, 1934), but it may be common in some areas (M. B. Fenton, in litt.; A. Hicks, in litt.). It ranges from Ontario and New England southward to Georgia and Alabama and westward into Oklahoma (Barbour and Davis, 1969; Fig. 3). *M. leibii* occurs at elevations of 300–780 m in Pennsylvania (Mohr, 1932*b*), 750 m in Virginia (Johnson, 1950), 1,125 m in Kentucky (Barbour, 1951), and ca. 240–675 m in Georgia (Baker, 1967).

FOSSIL RECORD. *Myotis leibii* is known from Big Bone Cave, Van Buren Co., Tennessee (Wisconsinan Land-mammal Age of the Pleistocene—Corgan, 1975), and Cumberland Cave, Maryland (middle Pleistocene—Martin, 1972). Specimens that resemble *M. leibii* were recovered from middle or late Pleistocene deposits at Conrad Fissure, Arkansas (Brown, 1908).

FORM AND FUNCTION. The pelage of adults is long (McDaniel et al., 1982), soft, and downy (Audubon and Bachman, 1842). The shiny tips of longer hairs give the pelage a golden

FIG. 1. An adult *Myotis leibii* in New York. Photograph by J. S. Altenbach.

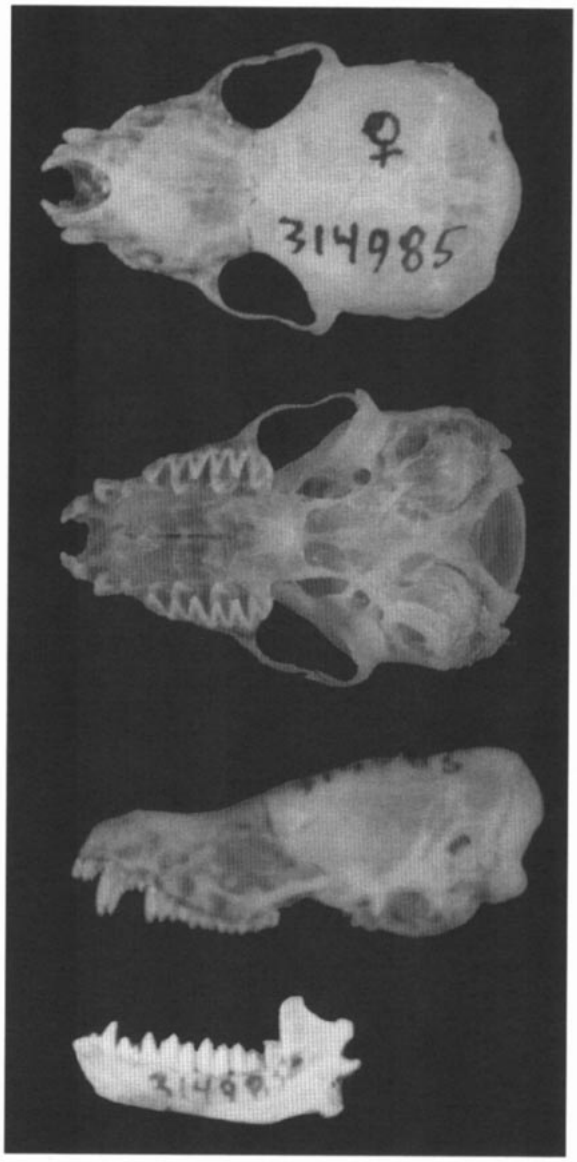

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Myotis leibii* from Breathing Cave, Bath Co., Virginia (female, United States Museum of Natural History 314985). Greatest length of cranium is 12.8 mm. Photographs by J. C. Rainey.

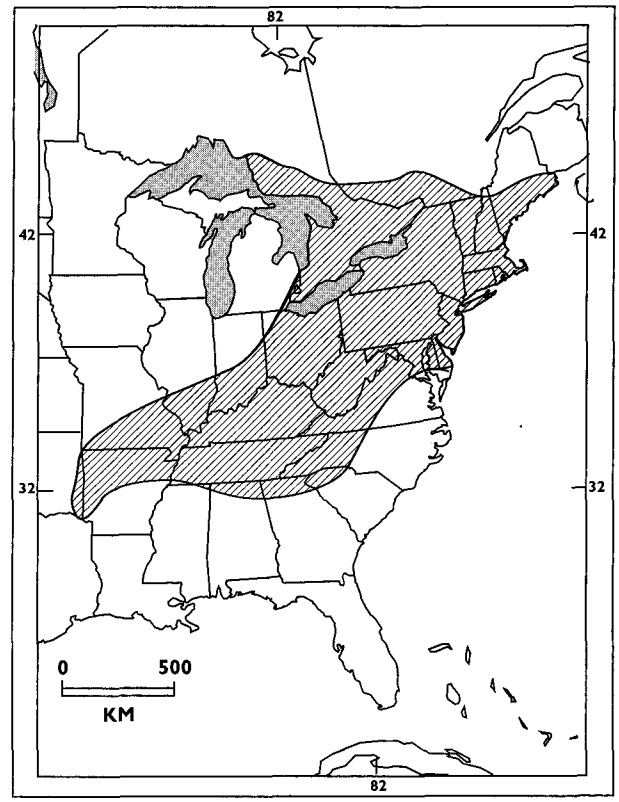

FIG. 3. Distribution of *Myotis leibii* in North America (Hall, 1981; van Zyll de Jong, 1984).

sheen. The ears and flight membranes are blackish (van Zyll de Jong, 1985).

The head is short, the nose is blunt, and the ears are erect, broad at the base (Audubon and Bachman, 1842), relatively long, and reach or exceed the tip of the nose when laid forward. The tragus is slender, tapering, and about one-half as long as the ear (van Zyll de Jong, 1985).

The feet are small and less than one-half as long as the tibia (van Zyll de Jong, 1985), the toes are short and slender, and the claws are sharp and curved (Audubon and Bachman, 1842). The calcar is about as long as the free border of the uropatagium and has a prominent keel. The metacarpals are subequal (van Zyll de Jong, 1985). The tail extends beyond the interfemoral membrane, which is naked (Audubon and Bachman, 1842). *M. leibii* has a wingspan of 210–250 mm (Nelson, 1913; van Zyll de Jong, 1985). For two individuals, mass was 3.2 and 4.1 g, the area of the wing was 61 and 62 cm^2 (Poole, 1936).

The dental formula is i 2/3, c 1/1, p 3/3, m 3/3, total 38 (Miller, 1907). The anterior upper incisors are bilobate (Audubon and Bachman, 1842).

Myotis leibii tolerates colder temperatures than *M. lucifugus*, arousing from torpidity below −9°C, compared with −4°C in *M. lucifugus*. Loss of mass during hibernation from December to April in a combined sample of males and females (n = 9–23) was 4.7–5.6 g or 16% (Fenton, 1972).

The immunoreactive fibers of luteinizing hormone-releasing hormone are rare in the external zone of the median eminence of the hypothalamus, but these fibers are densely distributed in the internal zone. This dense accumulation of fibers projects caudoventrally through the infundibular stalk and enters the neural lobe. The number of immunoreactive fibers decreases suddenly where the stalk widens to form the neural lobe. The majority of fibers of luteinizing hormone-releasing hormone that enter the neural lobe parallel the posterior border of the pars intermedia and extend ca. 25% of the dorsoventral extent of the pituitary (Anthony et al., 1984).

The baculum is small and deeply sculptured (Fig. 4). The slender distal part terminates in a slight knob. Proximally, the dorsal and lateral extensions are separated by a prominent notch (Hamilton, 1949). The bone is somewhat saddle-shaped, concave ventrally, and has a dorsal prominence. Average and range of measurements (in mm) of the baculum (n = 5) are: length, 0.80 (0.72–0.89); width, 0.35 (0.30–0.40); height, 0.34 (0.26–0.40—van Zyll de Jong, 1984, 1985).

ONTOGENY AND REPRODUCTION. Females have two mammae (Godin, 1977). In Arkansas, a reproductively active male, as indicated by epididymides that extended into the uropatagium, was present on 14 September (Saugey et al., 1993). Apparently, one young is produced each year (Barbour and Davis, 1969; Godin, 1977); offspring probably are born in May or June (Peterson, 1966). In Ontario, a summer colony of ca. 12 bats was behind a sliding barn door on 6 July (Hitchcock, 1955). *M. leibii* may live 6–12 years (Hitchcock, 1965; Mohr, 1952).

ECOLOGY. The eastern small-footed myotis usually occurs in mountainous regions (Adams, 1950; Baker, 1967; Barbour, 1951; Johnson, 1950; McDaniel et al., 1982; Neuhauser, 1971; Schwartz, 1954; Tuttle, 1964), but not always (M. B. Fenton, in litt.). It has been found in buildings (Barbour, 1963; Hitchcock, 1955; Neuhauser, 1971; Peterson, 1966), on the face of rock bluffs (McDaniel et al., 1982), in turnpike tunnels (Mohr, 1942*b*), and beneath slabs

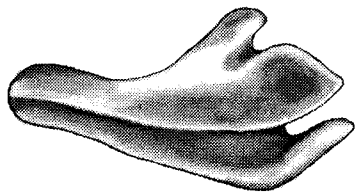

FIG. 4. Lateral view of the baculum of *Myotis leibii* (modified from Hamilton, 1949).

of rock and stones (Barbour and Davis, 1969; Krutzsch, 1966; Tuttle, 1964). *M. leibii* usually is encountered during hibernation (Barbour and Davis, 1969). The only known hibernation sites are caves and old mines (Davis, 1955; Fenton, 1972; Hall, 1962; Hitchcock, 1946; Krutzsch, 1966; Mohr, 1933, 1936; Schwager and Benton, 1956), where it often occupies narrow crevices, hangs on the wall or from the ceiling, or is on the floor of the hibernaculum in crevices or under rocks (Allen, 1939; Davis, 1955; Martin et al., 1966; McDaniel et al., 1982).

The largest known group of hibernating *M. leibii* was in Fourth Chute Cave, Renfrew Co., Ontario. In the drafty passage at Fourth Chute Cave, *M. leibii* usually hibernated in narrow cracks in the wall or ceiling (Hitchcock, 1949). On 5 April, 30 were present, on 6 January, there were 76, on 25 and 26 February, there were 85 and 142, respectively (Hitchcock, 1946). In one small fissure, 35 were present on 4 January. They were packed so solidly that it appeared almost impossible for those farthest in to get air. On 29 November, few *M. leibii* were present (Hitchcock, 1949).

In New York, *M. leibii* was present 5 m inside a cave in dim light (Trapido, 1942). It also occurred in a mine shaft located along a large creek that passed through a tract of hemlock-beech-hard maple forest. The shaft extended ca. 25 m horizontally into the side of a steep hill, and in winter, the temperature was nearly freezing throughout its length (Schwager and Benton, 1956). In Pennsylvania, the eastern small-footed myotis occurs in caves located in heavily wooded areas including hemlock forests (Mohr, 1932*b*, 1933, 1936); 52% of hibernacula occupied were small caves <150 m in length (Dunn and Hall, 1989).

In Tennessee, *M. leibii* was present in Little Mammoth Cave, Campbell Co., on 27 March. Outside the cave, the temperature was 21°C, the temperature 135 m inside, where two *M. leibii* were encountered, was 9°C, and 220 m inside, where a third individual was encountered, it was 11°C. The cave was 315 m long and located on the side of a steep hillside in a mature deciduous forest. The entrance to the cave was ca. 2 m wide and 3 m high. The pelage of these three bats was entirely dry, indicating they probably had been active. Although torpid, the bats became active quickly. On 4 March, another was 3 m back under a ledge and 0.3 m above the floor. The temperature was 4°C and the bat was torpid (Tuttle, 1964).

In North Carolina, one male and one female were present on 19 January in man-made tunnels, which had been constructed for mining of talc. The tunnels in which the bats were found were ca. 25 m deep, and both were moist. One bat was flying and the other was hanging from the wall ca. 20 m inside the mouth of the tunnel. Because the bats were easily disturbed, it is possible they were not hibernating (Schwartz, 1954).

In Arkansas and southeastern Oklahoma, *M. leibii* may hibernate in rock glaciers, also known as rock rivers, found on mountains composed of sandstone. These rock glaciers probably were formed in peri-glacial conditions (permanent snow fields during glacial epics) and may be 8–16 ha in area and attain depths of 15 m to bedrock. The insulating effect of these massive structures and the numerous openings that may lead to talus caves could provide suitable hibernating habitat in areas devoid of fracture or solution caves (Saugey et al., 1993).

The eastern small-footed myotis is fairly common in late summer in the flocks of migrating bats, but the whereabouts of these individuals at other seasons is unknown (Barbour and Davis, 1969). Relative to other species of bats in its distributional range, *M. leibii* is uncommon. The reasons for the relative rarity are not known, but it may be the result of a relatively low rate of survival (van Zyll de Jong, 1985).

Although the sex ratio has been reported as 1:1 (Hitchcock, 1949, 1965; Mohr, 1936, 1939, 1952), the rate of survival for males is considerably greater than that of females (estimated average annual survival is 0.757 and 0.421, respectively). The lower rate of survival of females in northern populations may be a result of a combination of factors: the greater demands of reproduction on females; the higher metabolic rates and longer sustained activity during the day in summer (i.e., less time spent in daytime lethargy); the greater exposure to possible disease-carrying parasites in maternity colonies (Hitchcock et al., 1984).

In Ontario and Quebec, *M. leibii* occurs in the same caves as *Eptesicus fuscus, Pipistrellus subflavus, M. lucifugus,* and *M. septentrionalis* (Hitchcock, 1949). In Ontario, *M. leibii* is known to hibernate in physical contact with *E. fuscus,* usually in small clusters of less than five bats, but it was not observed close to or in physical contact with *M. lucifugus* (Fenton, 1972). In Vermont, *M. leibii* was hibernating in a cave with *E. fuscus, M. lucifugus, M. septentrionalis, M. sodalis,* and *P. subflavus* in late January. Instead of hanging by the hind feet, *M. leibii* was tucked away singly or rarely two together, in small depressions or crannies of the rock, lying down flat on their venters (Allen, 1939). Elsewhere, *M. leibii* occurs in caves and mines with *Corynorhinus rafinesquii, E. fuscus, M. lucifugus, M. septentrionalis, M. sodalis,* and *P. subflavus* (Allen, 1939; Baker, 1967; Mohr, 1936; Schwartz, 1954; Tuttle, 1964).

The eastern small-footed myotis has been kept in captivity (Gates, 1936), but nothing is known about its diet. However, in the laboratory, a 3.7-g individual captured 1.7–9.5 mosquitos/min (Griffin et al., 1960).

Ectoparasites include the chiggers *Euschongastia hamiltoni* (Brennan, 1947) and *Trombicula myotis* (Neuhauser, 1971). No endoparasites are known.

Bands and ear tags have been used to mark individuals (Griffin, 1936; Mohr, 1936). Hand nets and mist nets have been used to capture *M. leibii* (Barbour and Davis, 1969; Davis et al., 1965; Fenton, 1972; Hall, 1985; McDaniel et al., 1982).

In commercializing Fourth Chute Cave, construction eliminated the circulation of cold air in one of the unvisited passages of the cave where the largest known population of *M. leibii* in eastern North America hibernated. These bats were totally dispossessed as a result of the warmer microclimate produced (Mohr, 1972). A mine ca. 10 km from this cave, which had been flooded from 1918 to 1964, was drained in 1964. In winter 1965–1966, 57 hibernating *M. leibii* were counted in the mine, and 22 were present in winter 1966–1967. The small-footed myotis hibernated in areas of the mine with good air flow, lower humidity, and lower temperatures than other parts of the mine (M. B. Fenton, in litt.).

In Pennsylvania, most groups of *M. leibii* reported in caves prior to 1979 have disappeared. However, 21 new hibernacula have been reported from an eight-county area; 17 of these were new localities for hibernating *M. leibii.* Most populations contained fewer than five individuals per site; the largest group in a cave contained 29 individuals (Dunn and Hall, 1989).

In Pennsylvania, the eastern small-footed myotis has been listed as threatened (Dunn and Hall, 1989; Hall, 1985) and at risk (Kirkland and Krim, 1990). The United States Fish and Wildlife Service listed *M. leibii* as a Category 2 species (Bogan, in press; Drewry, 1991; Harvey et al., 1991).

BEHAVIOR. The eastern small-footed myotis emerges at dusk shortly after sunset (van Zyll de Jong, 1985). It flies slowly, erratically, or regularly, usually at heights of 0.3–3 m (Barbour and Davis, 1969; Davis et al., 1965; van Zyll de Jong, 1985). It apparently uses the ceilings of caves, ca. 3 m above the floor, as night roosts (Davis et al., 1965). *M. leibii* can be seen flying in and out of caves (Bailey, 1933; Barbour and Davis, 1969), and in open fields (Neuhauser, 1971), and can be captured easily with a dip net (Barbour and Davis, 1969; Davis et al., 1965).

This tiny bat occurs in drafty open mines and caves, and hangs near the entrance where the temperatures drop below freezing. At these roost sites, humidity is relatively low (Barbour and Davis, 1969; Fenton, 1972) and subject to greater fluctuation than deeper in the cave or mine (Fenton, 1972). Distribution, however, varies with temperature; during cold weather, this bat moves to more sheltered places away from the entrance. Its hibernating habits are similar to those of *E. fuscus,* but it may not be as tolerant of cold and dry conditions (Barbour and Davis, 1969; Hitchcock, 1965).

Myotis leibii is among the last to move into caves in autumn,

seldom appearing before mid-November and leaving by March or early April (Bailey, 1933; Barbour and Davis, 1969; Fenton, 1972; Gunier and Elder, 1973; Hitchcock, 1965; Mohr, 1945). It can withstand severe weather and is almost continually active throughout winter (Mohr, 1933, 1936, 1942*a*). Furthermore, *M. leibii* may move in and out of caves during the milder parts of winter (Hitchcock, 1965; Mohr, 1936), returning when it becomes colder. No shifting from one cave to another has been noted, except for one individual, which after its original hibernating site was closed during a rock fall, took up winter quarters in a cave several hundred meters away (Mohr, 1936).

Some individuals hibernate horizontally (Godin, 1977), beneath stones or in crevices on the floor of caves and mines (Davis, 1955; Martin et al., 1966). One was found in the floor of Schoolhouse Cave, Pendleton Co., West Virginia, on 26 January. It was in a small crevice in the clay floor, well out of sight, and it was vocalizing and active when uncovered. The crevice contained an accumulation of feces, indicating the bat may have lived there in an active state for some time. Another was observed under loose rocks on the floor of Greenville Saltpeter Cave, Monroe Co., West Virginia, on 27 December. It was ca. 15 cm below the surface and there was a considerable amount of feces among the rocks near the bat (Davis, 1955).

The use of floor crevices as hibernacula may be attributable more to selection of a stable cooler temperature and greater protection from disturbance than from small size of feet. The cooler temperature of the ceiling fluctuates more during hibernation than the temperature under the rocks on the floor, which remains comparatively stable (Martin et al., 1966).

Myotis leibii deserts the caves long before other hibernating bats. This may indicate migratory movement in late winter (Mohr, 1933). Departures occur while *M. lucifugus* and *M. sodalis* are still in hibernation (Mohr, 1936).

During copulation, the male mounts the female, grasps the hair of the female at the base of the skull with his teeth and pulls her head far back, usually at a right angle to her body. The male strengthens his grip by using his thumbs to hold her body in place, and then pushes his hind quarters backward and downward around the rump of the female, bringing his protruded penis beneath her interfemoral membrane. By a forward movement at this moment, the penis is brought close to the vaginal orifice. During this preliminary phase of copulation, the penis becomes erect, and the glans becomes bulbous and noticeably hyperemic. After mounting the female, the male probes the vaginal orifice with the erect penis. With some effort, the male gains access to the vagina, and the penis appears to move vigorously and relatively independently of any essential movements of the hind quarters of the animal. With the penis in the vagina, both animals remain quiet, except for a quivering of the hind quarters of the female reminiscent of rapid breathing. Thus, the male initiates copulation and the role of the female is passive. The presence of the interfemoral membrane of the female does not seem to inhibit the male as might be expected in the posterior approach, because the free movements of the penis carried this organ around and beneath the membrane (Wimsatt, 1945).

Myotis leibii shows a definite homing ability. Marked bats were present in the same cave in different seasons, and when moved they returned to the original cave (Mohr, 1936). Furthermore, movements of banded individuals indicate that *M. leibii* may move as far as 19 km away from the banding site (Hitchcock, 1955, 1965). This information suggests that this species may hibernate near its summer range (van Zyll de Jong, 1985).

Myotis leibii often is a solitary species (Allen, 1939; Dunn and Hall, 1989; Martin et al., 1966; Mohr, 1936). However, groups of ≤30 (Martin et al., 1966) and sometimes >50 individuals occur together, packed in so tightly and so deeply that they are easily overlooked (Barbour and Davis, 1969).

The eastern small-footed myotis vocalizes (Davis, 1955), but specific attributes of its vocalizations are unknown. In tests conducted on bat detectors, the echolocation calls of *M. leibii, M. lucifugus,* and *P. subflavus* were more audible to humans than those of *M. septentrionalis* (Forbes and Newhook, 1990).

GENETICS. The diploid number of chromosomes is 44 and the fundamental number of chromosomal arms is 52. G-bands of this species reveal a metacentric autosome that presumably resulted from addition of a heterochromatic short arm to the typical acrocentric chromosome present in *Myotis nigricans.* This is not confirmed by C-bands. In all other respects the G-band karyotype is identical to that of *M. nigricans* (Bickham et al., 1986; Fig. 5).

FIG. 5. G-banded karyotype of a female *Myotis leibii* from Renfrew Mine, Renfrew Co., Ontario (Bickham et al., 1986).

Electrophoretic examination of 20 proteins was conducted to compare *M. ciliolabrum* and *M. leibii.* Fixed allelic differences at the adenylate kinase and diaphorase loci between *M. ciliolabrum* and *M. leibii* suggest that no introgression occurs between these taxa and that they are distinct species (Herd, 1987).

REMARKS. There has been considerable confusion regarding the taxonomy of *M. leibii* (Glass and Baker, 1965, 1968). The specific epithet *subulatus* has been used for *M. leibii.* This is confusing because prior to 1928 (Miller and Allen, 1928), the specific epithet *subulatus* was applied to *M. keenii* (McDaniel et al., 1982).

Myotis c. ciliolabrum and *M. c. melanorhinus* until recently were regarded as subspecies of *M. leibii* (van Zyll de Jong, 1984, 1985), but morphometric (van Zyll de Jong, 1984) and biochemical (Herd, 1983) evidence has demonstrated that this view is no longer tenable. Multivariate craniometric comparisons show that *M. ciliolabrum* and *M. leibii* are as distinct from one another as each is from the other member of the *leibii* group, *M. californicus* (van Zyll de Jong, 1984, 1985). Specimens from the alleged zone of intergradation between the eastern and western small-footed myotis in Oklahoma (Glass and Ward, 1959; van Zyll de Jong, 1984) did not show any evidence of intermediacy. To the contrary, they could be assigned unequivocally to either the western (*M. ciliolabrum*) or eastern form (*M. leibii*—van Zyll de Jong, 1984, 1985). Electrophoretic comparison of *M. c. melanorhinus* and *M. leibii* (Herd, 1983) showed differences greater than that expected between subspecies of one species and as great as those observed between some species of bats and rodents, thus confirming the morphometric evidence (van Zyll de Jong, 1985).

Myotis is from the Greek *mys* meaning "mouse" and *ot* "ear" (Jaeger, 1955). The specific epithet *leibii* is in honor of G. C. Leib who collected the type specimen (Audubon and Bachman, 1842; Miller and Allen, 1928). We have followed Jones et al. (1992) in using the common name of eastern small-footed myotis. Additional common names include Leib's bat (Audubon and Bachman, 1842), least brown bat (Mohr, 1934), Leib masked bat, least bat (Hitchcock, 1949), and chauve-souris pygmée (Peterson, 1966).

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. E. Rodriguez for preparing Figs. 3 and 4, M. B. Fenton for providing access to unpublished data, and M. K. Causey, J. L. Dobie, M. B. Fenton, W. R. Gannon, and R. S. Lishak for critically evaluating an early draft of the manuscript. This is journal article 15-965207 of the Alabama Agricultural Experiment Station.

LITERATURE CITED

ADAMS, D. A. 1950. *Myotis subulatus leibii* in North Carolina. Journal of Mammalogy, 31:97–98.

ALLEN, G. M. 1939. Bats. Harvard University Press, Cambridge, Massachusetts, 368 pp.

ANTHONY, E. L. P., J. C. KING, AND E. G. STOPA. 1984. Immunocytochemical localization of LHRH in the median eminence, infundibular stalk, and neurohypophysis: evidence for multiple sites of releasing hormone secretion in humans and other mammals. Cell and Tissue Research, 236:5–14.

AUDUBON, J. J., AND J. BACHMAN. 1842. Descriptions of new species of quadrupeds inhabiting North America. Journal of the Academy of Natural Sciences of Philadelphia, series 1, 8:280–323.

BAILEY, V. 1933. Cave life of Kentucky: mainly in the Mammoth Cave region. The American Midland Naturalist, 14:385–635.

BAKER, W. W. 1967. *Myotis leibii leibii* in Georgia. Journal of Mammalogy, 48:142.

BARBOUR, R. W. 1951. The mammals of Big Black Mountain, Harlan County, Kentucky. Journal of Mammalogy, 32:100–110.

———. 1963. Some additional bat records from Kentucky. Journal of Mammalogy, 44:122–123.

BARBOUR, R. W., AND W. H. DAVIS. 1969. Bats of America. The University Press of Kentucky, Lexington, 286 pp.

BICKHAM, J. W., K. MCBEE, AND D. A. SCHLITTER. 1986. Chromosomal variation among seven species of *Myotis* (Chiroptera: Vespertilionidae). Journal of Mammalogy, 67:746–750.

BOGAN, M. A. In press. Eastern small-footed myotis, *Myotis leibii*. *In* Complete book of North American mammals (D. E. Wilson and S. Ruff, eds.). Smithsonian Institution Press, Washington, D.C.

BRENNAN, J. M. 1947. New species of chiggers (Acarina, Trombiculidae) from bats of the Nearctic region. The Journal of Parasitology, 33:245–252.

BROWN, B. 1908. The Conrad Fissure, a Pleistocene bone deposit in northern Arkansas: with descriptions of two new genera and twenty new species of mammals. Memoirs of the American Museum of Natural History, 9:155–208.

CORGAN, J. X. 1975. Pleistocene bats of Tennessee. The American Midland Naturalist, 93:503.

DAVIS, W. H. 1955. *Myotis subulatus leibii* found in unusual situations. Journal of Mammalogy, 36:130.

DAVIS, W. H., M. D. HASSELL, AND C. L. RIPPY. 1965. *Myotis leibi leibi* in Kentucky. Journal of Mammalogy, 46:683–684.

DREWRY, G. 1991. Endangered and threatened wildlife and plants; animal candidate review for listing as endangered or threatened species. Federal Register, 56(225):58804–58836.

DUNN, J. P., AND J. S. HALL. 1989. Status of cave-dwelling bats in Pennsylvania. Journal of the Pennsylvania Academy of Science, 63:166–172.

FENTON, M. B. 1972. Distribution and overwintering of *Myotis leibii* and *Eptesicus fuscus* (Chiroptera: Vespertilionidae) in Ontario. Royal Ontario Museum, Life Sciences Occasional Papers, 21:1–8.

FORBES, B., AND E. M. NEWHOOK. 1990. A comparison of the performance of three models of bat detectors. Journal of Mammalogy, 71:108–110.

GATES, J. E., G. A. FELDHAMMER, L. A. GRIFFITH, AND R. L. RAESLY. 1984. Status of cave-dwelling bats in Maryland: importance of marginal habitats. Wildlife Society Bulletin, 12:162–169.

GATES, W. H. 1936. Keeping bats in captivity. Journal of Mammalogy, 17:268–273.

GLASS, B. P., AND R. J. BAKER. 1965. *Vespertilio subulatus* Say, 1823: proposed suppression under the plenary powers (Mammalia, Chiroptera). The Bulletin of Zoological Nomenclature, 22:204–205.

———. 1968. The status of the name *Myotis subulatus* Say. Proceedings of the Biological Society of Washington, 81:257–260.

GLASS, B. P., AND C. M. WARD. 1959. Bats of the genus *Myotis* from Oklahoma. Journal of Mammalogy, 40:194–201.

GODIN, A. J. 1977. Wild mammals of New England. The Johns Hopkins University Press, Baltimore, Maryland, 304 pp.

GRIFFIN, D. R. 1936. Bat banding. Journal of Mammalogy, 17: 235–239.

———. 1940. Notes on the life histories of New England cave bats. Journal of Mammalogy, 21:181–187.

GRIFFIN, D. R., F. A. WEBSTER, AND C. R. MICHAEL. 1960. The echolocation of flying insects by bats. Animal Behaviour, 8: 141–154.

GUNIER, W. J., AND W. H. ELDER. 1973. New records of Myotis leibii from Missouri. The American Midland Naturalist, 89: 489–490.

HALL, E. R. 1981. The mammals of North America. Second ed. John Wiley & Sons, New York, 1:1–600 + *90*.

HALL, J. S. 1962. A life history and taxonomic study of the Indiana bat, *Myotis sodalis*. Reading Public Museum and Art Gallery, Scientific Publications, 12:1–68.

———. 1985. Small-footed bat *Myotis leibii* (Audubon and Bachman). Pp. 360–362, *in* Species of special concern in Pennsylvania (H. H. Genoways and F. J. Brenner, eds.). Special Publication of Carnegie Museum of Natural History, 11: 1–430.

HAMILTON, W. J., JR. 1949. The bacula of some North American vespertilionid bats. Journal of Mammalogy, 30:97–102.

HARVEY, M. J., J. R. MACGREGOR, AND R. R. CURRIE. 1991. Distribution and status of Chiroptera in Kentucky and Tennessee. Journal of the Tennessee Academy of Science, 66:191–193.

HERD, R. M. 1987. Electrophoretic divergence of *Myotis leibii* and *Myotis ciliolabrum* (Chiroptera: Vespertilionidae). Canadian Journal of Zoology, 65:1857–1860.

HITCHCOCK, H. B. 1946. Myotis subulatus leibii in Ontario. Journal of Mammalogy, 26:433.

———. 1949. Hibernation of bats in southeastern Ontario and adjacent Quebec. The Canadian Field-Naturalist, 63:47–59.

———. 1955. A summer colony of the least bat, Myotis subulatus leibii (Audubon and Bachman). The Canadian Field-Naturalist, 69:31.

———. 1965. Twenty-three years of bat banding in Ontario and Quebec. The Canadian Field-Naturalist, 79:4–14.

HITCHCOCK, H. B., R. KEEN, AND A. KURTA. 1984. Survival rates of *Myotis leibii* and *Eptesicus fuscus* in southeastern Ontario. Journal of Mammalogy, 65:126–130.

JAEGER, E. C. 1955. A source-book of biological names and terms. Third ed. Charles C Thomas Publisher, Springfield, Illinois, 323 pp.

JOHNSON, D. H. 1950. *Myotis subulatus leibii* in Virginia. Journal of Mammalogy, 31:197.

JONES, J. K., JR., R. S. HOFFMANN, D. W. RICE, C. JONES, R. J. BAKER, AND M. D. ENGSTROM. 1992. Revised checklist of North American mammals north of Mexico, 1991. Occasional Papers, The Museum, Texas Tech University, 146:1–23.

KIRKLAND, G. L., JR., AND P. M. KRIM. 1990. Survey of the statuses of the mammals of Pennsylvania. Journal of the Pennsylvania Academy of Science, 64:33–45.

KOOPMAN, K. F. 1993. Order Chiroptera. Pp. 137–241, *in* Mammal species of the world: a taxonomic and geographic reference (D. E. Wilson and D. M. Reeder, eds.). Second ed. Smithsonian Institution Press, Washington, D.C., 1206 pp.

KRUTZSCH, P. H. 1966. Remarks on silver-haired and Leib's bats in eastern United States. Journal of Mammalogy, 47:121.

KRUTZSCH, P. H., AND T. A. VAUGHAN. 1955. Additional data on the bacula of North American bats. Journal of Mammalogy, 36:96–100.

MARTIN, R. A. 1972. Synopsis of late Pliocene and Pleistocene bats of North America and the Antilles. The American Midland Naturalist, 87:326–335.

MARTIN, R. L., J. T. PAWLUK, AND T. B. CLANCY. 1966. Observations on hibernation of *Myotis subulatus*. Journal of Mammalogy, 47:348–349.

MCDANIEL, V. R., M. J. HARVEY, R. TUMLISON, AND K. N. PAIGE. 1982. Status of the small-footed bat, *Myotis leibii leibii*, in the southern Ozarks. Proceedings of the Arkansas Academy of Science, 36:92–94.

MILLER, G. S., JR. 1907. The families and genera of bats. Bulletin of the United States National Museum, 57:1–282.

MILLER, G. S., JR., AND G. M. ALLEN. 1928. The American bats of the genera Myotis and Pizonyx. Bulletin of the United States National Museum, 144:1–218.

MOHR, C. E. 1932*a*. Myotis subulatus leibii and Myotis sodalis in Pennsylvania. Journal of Mammalogy, 13:160–161.

———. 1932*b*. The seasonal distribution of bats in Pennsylvania. Proceedings of the Pennsylvania Academy of Science, 6: 189–194.

———. 1933. Pennsylvania bats of the genus Myotis. Proceedings of the Pennsylvania Academy of Science, 7:39–43.

———. 1934. Marking bats for later recognition. Proceedings of the Pennsylvania Academy of Science, 8:26–30.

———. 1936. Notes on the least brown bat *Myotis subulatus leibii*. Proceedings of the Pennsylvania Academy of Science, 10:62–65.

———. 1939. Bat tagging in Pennsylvania. Proceedings of the Pennsylvania Academy of Science, 13:43–45.

———. 1942*a*. Results of ten years' bat marking in Pennsylvania. Proceedings of the Pennsylvania Academy of Science, 16: 32–36.

———. 1942*b*. Bat tagging in Pennsylvanian turnpike tunnels. Journal of Mammalogy, 23:375–379.

———. 1945. Sex ratios of bats in Pennsylvania. Proceedings of the Pennsylvania Academy of Science, 19:65–69.

———. 1952. A survey of bat banding in North America, 1932–1951. Bulletin of the National Speleological Society, 14:3–13.

———. 1972. The status of threatened species of cave-dwelling bats. Bulletin of the National Speleological Society, 34:33–47.

NELSON, E. W. 1913. A new bat from the eastern United States. Proceedings of the Biological Society of Washington, 26:183–184.

NEUHAUSER, H. N. 1971. *Myotis leibii leibii* in the Great Smoky Mountains National Park. Journal of the Tennessee Academy of Science, 46:79.

PETERSON, R. L. 1966. The mammals of eastern Canada. Oxford University Press, Toronto, Ontario, 465 pp.

POOLE, E. L. 1936. Relative wing ratios of bats and birds. Journal of Mammalogy, 17:412–413.

SAUGEY, D. A., V. R. MCDANIEL, D. R. ENGLAND, M. C. ROWE, L. R. CHANDLER-MOZISEK, AND B. G. COCHRAN. 1993. Arkansas range extensions of the eastern small-footed bat (*Myotis leibii*) and northern long-eared bat (*Myotis septentrionalis*) and additional county records for the silver-haired bat (*Lasionycteris noctivagans*), hoary bat (*Lasiurus cinereus*), southeastern bat (*Myotis austroriparius*), and Rafinesque's big-eared bat (*Plecotus rafinesquii*). Proceedings of the Arkansas Academy of Science, 47:102–106.

SCHWAGER, H., AND A. H. BENTON. 1956. *Myotis subulatus liebii* in eastern New York. Journal of Mammalogy, 37:441.

SCHWARTZ, A. 1954. A second record of *Myotis subulatus leibi* in North Carolina. Journal of the Elisha Mitchell Science Society, 70:222.

TRAPIDO, H. 1942. The least brown bat, Myotis subulatus leibii, in New York. Journal of Mammalogy, 23:218.

TUTTLE, M. D. 1964. *Myotis subulatus* in Tennessee. Journal of Mammalogy, 45:148–149.

VAN ZYLL DE JONG, C. G. 1984. Taxonomic relationships of Nearctic small-footed bats of the *Myotis leibii* group (Chiroptera: Vespertilionidae). Canadian Journal of Zoology, 62:2519–2526.

———. 1985. Handbook of Canadian mammals: bats. National Museums of Canada, Ottawa, Ontario, 2:1–212.

WIMSATT, W. A. 1945. Notes on breeding behavior, pregnancy, and parturition in some vespertilionid bats of the eastern United States. Journal of Mammalogy, 26:23–33.

Editors of this account were DUKE S. ROGERS, ELAINE ANDERSON, and KARL F. KOOPMAN. Managing editor was BARBARA H. BLAKE.

T. L. BEST AND J. B. JENNINGS, DEPARTMENT OF ZOOLOGY AND WILDLIFE SCIENCE AND ALABAMA AGRICULTURAL EXPERIMENT STATION, 331 FUNCHESS HALL, AUBURN UNIVERSITY, ALABAMA 36849–5414.