

Myotis volans. By Richard M. Warner and Nicholas J. Czaplewski

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Myotis volans (H. Allen), 1866

Long-legged Myotis

[*Vespertilio*]. *volans* H. Allen, 1866:282. Type locality Cabo San Lucas, Baja California, México.

Vespertilio longicrus True, 1886:588. Type locality vicinity of Puget Sound, Washington, U.S.A.

Myotis capitaneus Nelson and Goldman, 1909:28. Type locality San Jorge, 30 mi SW Comondú, Baja California, México.

Myotis altifrons Hollister, 1911:3. Type locality Henry House, Alberta, Canada.

Myotis volans, Goldman, 1914:102. First use of current name combination.

Myotis ruddi Silliman and von Bloeker, 1938:167. Type locality Lime Kiln Creek, 250 ft, southwestern Santa Lucia Mountains, Monterey Co., California, U.S.A.

CONTEXT AND CONTENT. Order Chiroptera, Suborder Microchiroptera, Family Vespertilionidae, Subfamily Vespertilioninae, Genus *Myotis*, Subgenus *Leuconoe*. Findley (1972) placed *M. volans* in the *austrostriparius* species group which also includes *M. austrostriparius*, *M. yumanensis*, *M. albescens*, *M. petax*, and *M. lucifugus*. Four subspecies are currently recognized:

M. v. volans (H. Allen), 1866:282, see above (*capitaneus* Nelson and Goldman a synonym).

M. v. amotus (Miller), 1914:212. Type locality Cofre de Perote, 12,500 ft, Veracruz, México.

M. v. interior (Miller), 1914:211. Type locality 5 mi S Twining, 11,300 ft, Taos Co., New Mexico, U.S.A.

M. v. longicrus (True), 1886:588, see above (*altifrons* Hollister and *ruddi* Silliman and von Bloeker are synonyms).

DIAGNOSIS. *Myotis volans* is readily distinguished in the field from other North American members of the genus by the combination of its short rounded ears that barely reach the nostril when laid forward (Fig. 1), small hindfeet, distinctly keeled calcar (Fig. 2), and fur on the underside of the wing membrane extending from the body to a line joining the elbow and the knee. Several other species of *Myotis* have hair on the underwing, but usually it is not as long, dense, or extensive as in *M. volans*. Additionally, the species is characterized by a skull with a short rostrum, an abruptly elevated forehead profile, and an elevated occiput (Fig. 3). Of short-eared western North American *Myotis*, *M. leibii* and *M. californicus* have keeled calcars, but are much smaller than *M. volans*. *Myotis lucifugus*, *M. velifer*, and *M. yumanensis* do not have a large keel on the calcar nor do they have the densely furred region on the underwing.

GENERAL CHARACTERS. Sexual dimorphism occurs, with females having slightly but significantly larger forearm and condylocanine lengths (Williams and Findley, 1979). Morphologically, the three mainland subspecies show little geographic variation, but the Baja California population of *M. v. volans* is significantly smaller than mainland forms (M. A. Bogan, in litt.). Ranges of measurements (in mm) for selected morphological characters of the mainland subspecies are as follows (Baker and Phillips, 1965; Miller and Allen, 1928): total length, 83 to 106; tail length, 32 to 49; hindfoot length, 5 to 9; ear length, 10 to 15; forearm length, 37.0 to 41.2; greatest length of skull, 13.4 to 15.0; length of maxillary toothrow, 5.0 to 5.6; zygomatic breadth, 8.2 to 9.0; breadth of braincase, 7.0 to 7.6. Similar measurements for *M. v. volans* are (Miller and Allen, 1928): total length, 76 to 85; tail length, 29 to 41; hindfoot length, 7.2 to 7.6; ear length, 11.8; forearm length, 35.2; greatest length of skull, 12.2 to 12.6; length of maxillary toothrow, 4.6 to 4.8; zygomatic breadth, 8.0; breadth of braincase, 6.7 to 7.0.

The hindfoot is about 41% of the length of the tibia. The short ears have a strong basal emargination. The tragus is 6 to 8 mm long and is pointed. Wing membranes attach to the hindfoot at the middle of the metatarsus (Fig. 2). Ears and flight membranes are blackish. Pelage color is variable; dorsally it ranges from the "ochraceous buff" of some *M. v. interior* to the dark, reddish or blackish brown of *M. v. longicrus*. *Myotis v. volans* is reddish buff dorsally with a tinge of cinnamon. Ventral color of the species ranges from pale buffy to cinnamon brown to smoky brown (Miller and Allen, 1928). Bogan (in litt.) noted that some populations exhibited local color adaptations and that *M. v. volans* differed markedly in color from mainland races. The dental formula is $i\ 2/3, c\ 1/1, p\ 3/3, m\ 3/3$, total 38.

DISTRIBUTION. *Myotis volans* inhabits western North America from extreme southeastern Alaska and western Canada to central Mexico (Fig. 4). It occupies an elevational range from 60 m or below to 3,770 m, but is usually found from 2,000 to 3,000 m. Mainland races are typically dwellers of montane habitats and rarely occur in arid lowland areas. *Myotis v. volans*, however, occurs primarily at low altitudes in desert regions of Baja California (Bogan, in litt.).

FOSSIL RECORD. *Myotis volans* has been reported from the Wisconsin glacial (late Pleistocene) of Little Box Elder Cave, Wyoming (Fig. 4) (Anderson, 1968). An early Holocene (7,683 \pm 643 years before present) occurrence was mentioned by Roth (1972) from the Edwards Plateau of Texas, where the species does not occur today (Fig. 4).

FORM. Static flight membrane values for *M. volans* (given as $\bar{X} \pm SE$, with range in parentheses) are: wingspan, 267.37 \pm 1.18 (242 to 286) mm; wing area, 107.85 \pm 0.88 (91.4 to 124.0) cm²; tail area, 18.74 \pm 0.49 (13.0 to 24.0) cm². The aspect ratio, 6.64 \pm 0.04 (5.79 to 7.50), is intermediate for a *Myotis* and summer wing loading, at 0.082 \pm 0.07 (0.065 to 0.102) g/cm², is high compared with that of other North American *Myotis* (Farney and Fleharty, 1969). Hayward and Davis (1964) characterized long-



FIGURE 1. Juvenile male *Myotis volans interior* from Flagstaff, Arizona. Photo by R. M. Warner.

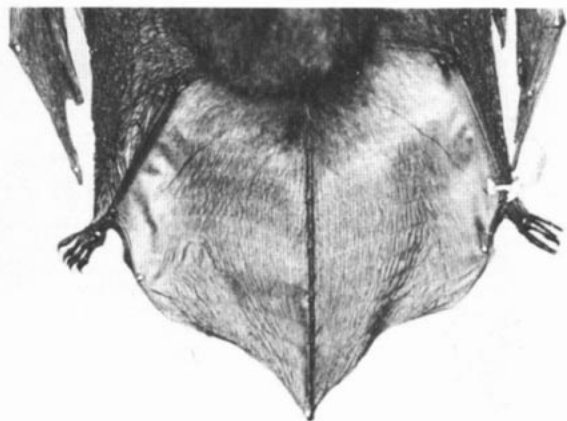


FIGURE 2. Hindlimbs and uropatagium of *Myotis volans* (MVZ 144201). Note the keeled calcar and the attachment of the wing membrane to the middle of the metatarsus.

legged myotis as strong, direct fliers capable of good speed. They estimated the flight speed in a 31-m-long hallway at 15 to 17 km/h.

Reduker (1983) analyzed the masticatory anatomy of *M. volans* and *M. evotis* in an attempt to determine the functional significance of skull and jaw muscle differences between these species. *Myotis volans* appears well suited to use a wide gape followed by forceful jaw closure to capture and subdue insect prey. Freeman's (1981) multivariate analysis of skull and jaw morphology in insectivorous bats placed *M. volans* in a morphological grouping of species designated as soft-bodied insect eaters.

The spermatozoa have a narrow midpiece and a narrow head compared with those of other species of *Myotis* (Forman, 1968).

FUNCTION. Geluso (1978, 1980) found the maximum urine concentration of *M. volans* ($n = 10$) tested under water-denied conditions ranged from 2,125 to 3,525 mosmol/kg ($\bar{X} \pm SD = 2,910 \pm 159$ mosmol/kg). This is relatively poor compared with that of other insectivorous bats studied. Correspondingly, the renal medulla of *M. volans*, as measured by a number of indices, is relatively poorly developed.

O'Farrell and Bradley (1977) found that the mean ($\pm 2 SE$) minimum body temperature at which *M. volans* ($n = 15$) could fly was $25.17 \pm 0.62^\circ\text{C}$. The ability to fly at cool temperatures may enable this species to extend the prehibernation period of activity (Schowalter, 1980).

ONTOGENY AND REPRODUCTION. In New Mexico, spermatogenesis began in August but was depressed during the winter hibernation period. Spermatogenesis followed by spermiation occurred primarily from May to August with peak spermiogenesis during late July. Adult males collected throughout most of the annual cycle had sperm stored in the cauda epididymides. Copulation began in late August and sperm was stored overwinter in the female reproductive tract. Ovulation occurred from March through May, parturition from May through August (Druecker, 1972). Seemingly, there is extensive variation in the timing of female reproductive activity in this species. Pregnant females were captured from 14 April to 15 August in Nebraska (Czaplewski et al., 1979; Jones, 1964), until late July in Wyoming and early August in Colorado (Findley, 1954), from 10 June to 14 July in Nevada (Hall, 1946), as late as 30 June in South Dakota (Jones and Genoways, 1967), 9 July in Montana (Jones et al., 1973), 13 July in New Mexico (Davis and Barbour, 1970), and 4 July in southern California (Dalquest and Ramage, 1946). Some of the observed variation may be related to climatic factors (Druecker, 1972). Druecker (1972) thought males did not become sexually mature until at least their second year but Schowalter (1980) found that most of the fall-captured juvenile males from Alberta were reproductively active. First-year females probably are sexually mature.

Myotis volans is known to live a minimum of 21.0 years based on the recapture of banded individuals (S. Cross, in litt.).

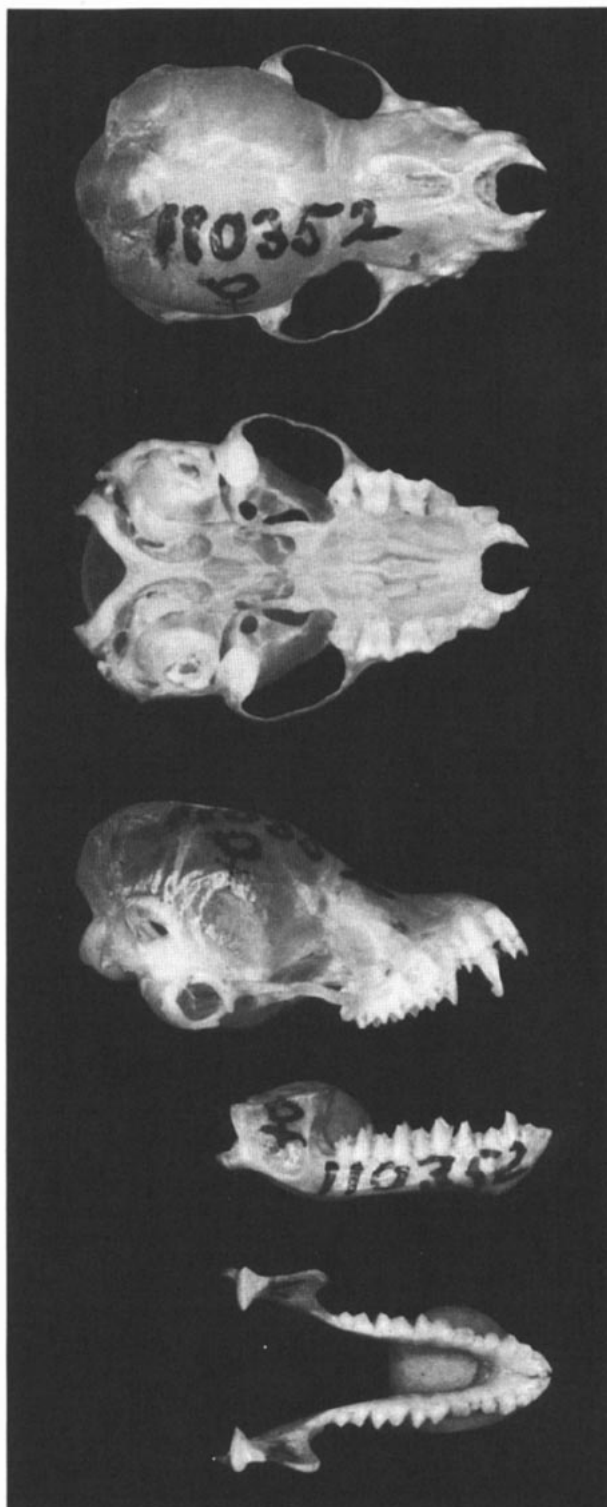


FIGURE 3. Dorsal, ventral, and lateral views of the cranium and lateral and dorsal views of the mandibles of *M. v. volans* (MVZ 110352). Condylbasal length is 12.3 mm.

ECOLOGY AND BEHAVIOR. *Myotis volans* feeds primarily on moths (Lepidoptera) although it is known to consume a variety of other, primarily soft-bodied, invertebrates, including flies (Diptera), termites (Isoptera), lacewings (Neuroptera), wasps (Hymenoptera), bugs (Hemiptera), leafhoppers (Homoptera), and small beetles (Coleoptera) (Black, 1974; Jones et al., 1973; Warner, 1981; Whitaker et al., 1977, 1981). This species is a rapid, direct flier and pursues prey over relatively long distances through, around,

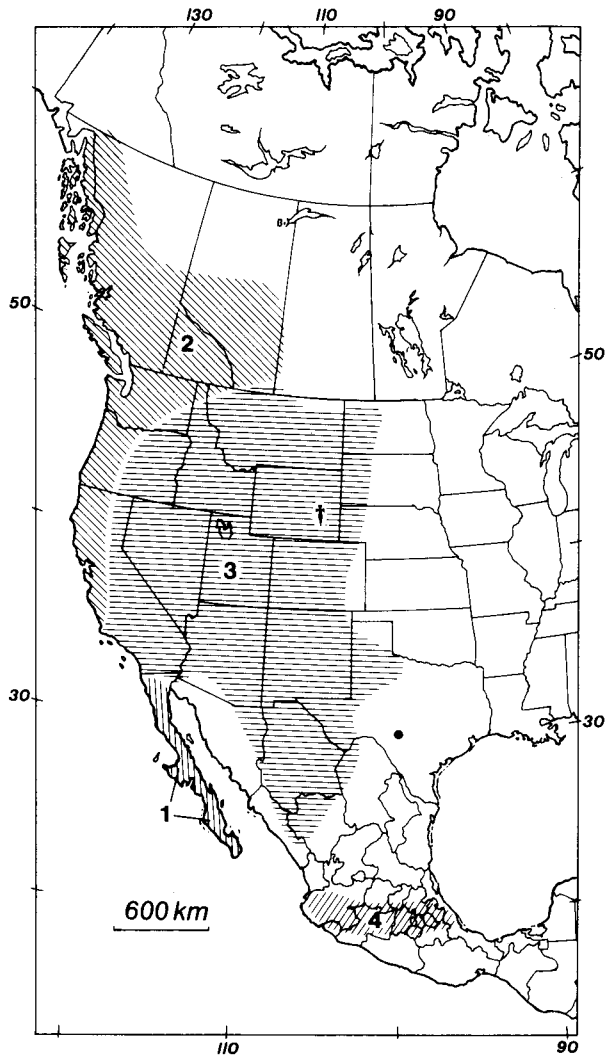


FIGURE 4. Distribution of *Myotis volans*: 1, *M. v. volans*; 2, *M. v. longicrus*; 3, *M. v. interior*; 4, *M. v. amotus*. Pleistocene (dagger) and Holocene (closed circle) records also are indicated.

under, and over the forest canopy (Fenton and Bell, 1979; Fenton et al., 1980; Grinnell, 1918; Warner, 1981). Grinnell's (1918) observations led her to believe that a single individual used the same foraging route every evening. *Myotis volans* consistently responded to artificial (black-light attracted) patches of prey (Bell, 1980) and is suspected of being an opportunistic forager, taking appropriate prey in approximate proportion to their availability in the environment (Warner, 1981).

The echolocation calls of this species are intense frequency modulated (FM)-long constant frequency (CF) signals (Fenton and Bell, 1979, 1981). The FM component sweeps from 89 to 40 kHz, with most of the energy at 46 kHz, and the calls are from 1 to 10 ms in length. The calls are shortened during pursuit and terminal phases by reduction of the length of the CF component. Bats on collision courses may "honk" at each other by lowering the frequency in the terminal part of an FM sweep (Fenton and Bell, 1979).

The long-legged myotis is primarily a coniferous forest bat (Barbour and Davis, 1969; Jones, 1965; Watkins et al., 1972), although it also may be found in riparian and desert habitats in some areas (Barbour and Davis, 1969; Bell, 1980; Bogan, in litt.). They may shift habitat seasonally (Hoffmeister, 1970). This species utilizes a variety of roosts including abandoned buildings (Dalquest and Ramage, 1946), cracks in the ground (Quay, 1948), crevices in a cliff face (Davis, 1978), and spaces beneath exfoliating tree bark (Baker and Phillips, 1965). Caves and mine tunnels are used as hibernacula (Martin and Hawks, 1972; Schowalter, 1980).

Myotis volans is active throughout most of the night (Bell,

1980; Warner, 1981), although there is a peak of activity in the first 3 or 4 h after sunset (Cockrum and Cross, 1964; Warner, 1981). Jones (1965) found this species to be active at temperatures of 12 to 18°C (mean 15°C). Schowalter (1980) found that *M. volans* was more active at colder temperatures than *M. lucifugus* and suggested that this may indicate a greater tolerance of cold temperatures in the long-legged myotis.

In eastern Oregon, DDE, DDT, and DDD residues were found in the carcasses and brains of *M. volans* ($n = 19$), with peak-mean-carcass DDE concentrations of 5.42 ppm reached 1 year after spraying for Tussock moths (*Orgyia pseudotsugata*) (Henney et al., 1982). Pesticide residue levels in tissues decreased for the next 2 to 3 years, almost reaching prespray levels by the third year. No correlation between particular orders of prey used by bat species and concentrations of pesticide residues was found (Henney et al., 1982).

A variety of arthropod ectoparasites was found to infest *M. volans*. These include the mites *Ichoronyssus britannicus* (Furman, 1950), *Pteracarus chalinolobus* (Jameson and Chow, 1952), *Cryptonyssus desultorius*, *Macronyssus crosbi*, macronyssid n. sp., *Spinturnix americanus*, *S. bakeri*, *S. globosus*, *Notoedres* sp., *Acanthophthirus* sp. nr. *gracilis* (Whitaker et al., 1983), and *Spinturnix* sp. (Jones et al., 1973); the chigger *Leptotrombidium myotis* (Andersen and Jones, 1971; Jones and Genoways, 1967; Whitaker et al., 1983); the flea *Myodopsyllus gentilis* (Andersen and Jones, 1971; Jones et al., 1973); the bat bug *Cimex piloselis* (Hansen, 1964); and the nycteribiid flies *Basilia forcipata* (Hansen, 1964; Jones et al., 1973) and *B. calverti* (Fox and Stabler, 1953). Dalquest and Ramage (1946) also listed "crab lice" and "wingless flies" (presumably nycteribiids) among the parasites infecting *M. volans*. Rabies has been recorded in *M. volans* (Constantine, 1979).

GENETICS. The standard and G-banded karyotypes of *M. volans* are indistinguishable from those of most other members of the genus (Baker and Patton, 1967; Bickham, 1979). The diploid number is 44 and the number of autosomal arms (FN) is 50. The X-chromosome is a medium-sized submetacentric and the Y-chromosome is a small acrocentric (Baker and Patton, 1967; Bickham, 1979).

REMARKS. Bogan (in litt.) suggested that *M. v. volans* may be specifically distinct from the three mainland subspecies. If this proves correct then the mainland forms will be recognized as *M. longicrus* (True, 1886).

Koopman (1976) reported that the holotype of *M. volans* consists of an alcoholic specimen, with skull removed, housed at the Academy of Natural Sciences at Philadelphia (ANSP 1834). The skull is in the collections of the U.S. National Museum of Natural History (USNM 5398).

The generic name, *Myotis*, means mouse-eared and the specific epithet, *volans*, means flying. Etymologies of the subspecific names are: *longicrus*, long-legged, a reference to the relatively long tibia of this species; *amotus*, withdrawn or banished, presumably a reference to its isolation from other races; and *interior*, a reference to its distribution in the interior of the continent.

Myotis volans is also known in the vernacular as the hairy-winged myotis.

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