

Lasionycteris noctivagans. By Thomas H. Kunz

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Lasionycteris Peters, 1865

Lasionycteris Peters, 1865:648. Type species *Vespertilio noctivagans* LeConte.

Vesperides Coues, in Coues and Yarrow, 1875:83, same type species.

CONTEXT AND CONTENT. Order Chiroptera, Family Vespertilionidae, Subfamily Vespertilioninae, Tribe Myotini. The genus *Lasionycteris* is monotypic, containing only *Lasionycteris noctivagans*.

Lasionycteris noctivagans (LeConte, 1831)

Silver-haired Bat

[*Vespertilio*]. *noctivagans* LeConte, in McMurtrie, 1831:431. Type locality eastern United States.

Lasionycteris noctivagans Peters, 1865:648. First use of name combination.

CONTEXT AND CONTENT. Context noted in generic summary above. No subspecies are recognized.

DIAGNOSIS. The color is the most distinguishing external feature of *Lasionycteris noctivagans*. Individual hairs are dark brown to black, with silvery-white tips imparting a frosted or silvery appearance. The interfemoral membrane is furred above on the basal half. This species is distinctive and is not likely to be confused with others (Fig. 1).

GENERAL CHARACTERS. External characteristics of adult *L. noctivagans* include black wings, ears and interfemoral membrane. Ears are short, rounded, and naked, with a broad, blunt tragus. The white-tipped dorsal hairs are more conspicuous in young than in adults (Merriam, 1884; Miller, 1897, 1907; Nason, 1948). Older adults may lack the white-tipped hairs (Seton, 1907) or may appear yellowish (Barbour and Davis, 1969).

Measurements of adults (in mm) are: total length, 92 to 115; length of tail, 35 to 45; length of tragus, 5 to 9 (Jackson, 1961; Pearson, 1962). Adult mass ranges from 8.1 to 11 g; females have more subcutaneous fat than males in winter (Layne, 1958). Selected cranial measurements are given in Grinnell (1918), Miller (1897), and Williams and Findley (1979). The skull is flattened with a broad rostrum. The depth of the braincase, including the auditory bullae, is about three-fourths the mastoid breadth. The interorbital region is wide and flattish. The upper surface of the rostrum has a distinct concavity on each side between the lachrymal region and the nares. Other features of the skull are essentially as in *Myotis* except for a general tendency toward broadening and flattening. The dental formula is $i\ 2/2, c\ 1/1, pm\ 2/3, m\ 3/3$, total 36. Illustrations of the skull and dentition are given in Grinnell (1918) and Miller (1897), including a photograph of the skull. Photographs of *L. noctivagans* are shown in Barbour and Davis (1969) and Sealander (1979). The skull is illustrated in Fig. 2.

FOSSIL RECORD. Fossils of *Lasionycteris* are known from the early Blancan at the Beck Ranch locality in Texas (Dalquest, 1978) and the late Pleistocene sites of Little Box Elder Cave and Bell Cave of Wyoming (Anderson, 1968; Kurtén and Anderson, 1980).

DISTRIBUTION. *Lasionycteris noctivagans* occurs in suitable habitat throughout most of North America, ranging from southeastern Alaska, across the southern half of Canada, southward in the United States to Georgia, westward to New Mexico and Arizona, and southward to the Republic of Mexico (Fig. 3). The winter distribution was mapped by Baker (1978) and Izor (1979). Hoffmeister (1970) summarized the winter distribution in Arizona, and Schowalter et al. (1978a) mapped the seasonal distribution for Alberta and British Columbia. Summer distributions were mapped by Baker (1978) and Seton (1907).

FORM AND FUNCTION. Descriptions of skull, dentition, and external morphology were provided by Grinnell (1918), Miller (1897, 1907), and Tate (1942). Lawrence (1943) described the humerus of *L. noctivagans* and compared it with *Myotis*. There are no significant sexual differences in size (head and body length, length of forearm, condylocanine length, and length of maxillary tooththrow) or proportions of these, but females are more variable than males (Williams and Findley, 1979). The baculum of *L. noctivagans* is large among vespertilionids, extending well into the corpus cavernosum (Hamilton, 1949). The head of spermatozoa has a narrowly rounded apex, is nearly symmetrical, and is widest in the basal half. It is distinct in having a narrow neck and lacking a visible helical midpiece (Hirth, 1960).

Various aspects of the functional morphology of wings were treated by Farney and Fleharty (1969) and Poole (1936). The wing area in cm^2 averaged 114.98 (94.6 to 126.0) and wing loading (g/cm^2) averaged 0.081 (0.061 to 0.0105) during July and August (Farney and Fleharty, 1969). Flight speed is relatively slow and deliberate. Hayward and Davis (1964) reported speeds ranging from 10.7 to 11.2 mph (4.8 to 5.0 m/sec) when tested along a straight line course.

Forman (1974) described the organization of lymphoid tissue in the intestinal tract and noted a restricted distribution of Peyer's patch nodules, a feature characteristic of bats having an insectivorous diet. *L. noctivagans* appears to have a relatively poor urine concentrating ability, which corresponds to the relatively large inner medullary zone of the kidney and is characteristic of bats occurring in predominantly mesic habitats (Geluso, 1978).

Echolocation and audition have not been examined in this species, but several authors have commented on some audible sounds produced in specific contexts. Norris-Elye (1951) noted a high pitched and persistent call produced by an isolated newborn. Layne (1958) reported a "sharp raspy buzzy cry" from torpid bats that had been disturbed and a "high pitched bird-like peep note" produced after becoming aroused. Jackson (1961) noted that silver-haired bats squeak and chatter at a lower pitch than do *Myotis*.

ONTOGENY AND REPRODUCTION. As in other temperate zone vespertilionids, mating probably occurs in autumn, followed by sperm storage in females during the winter. In New Mexico, the peak of spermiogenesis occurs in late August



FIGURE 1. Photograph of *Lasionycteris noctivagans* (by T. H. Kunz).

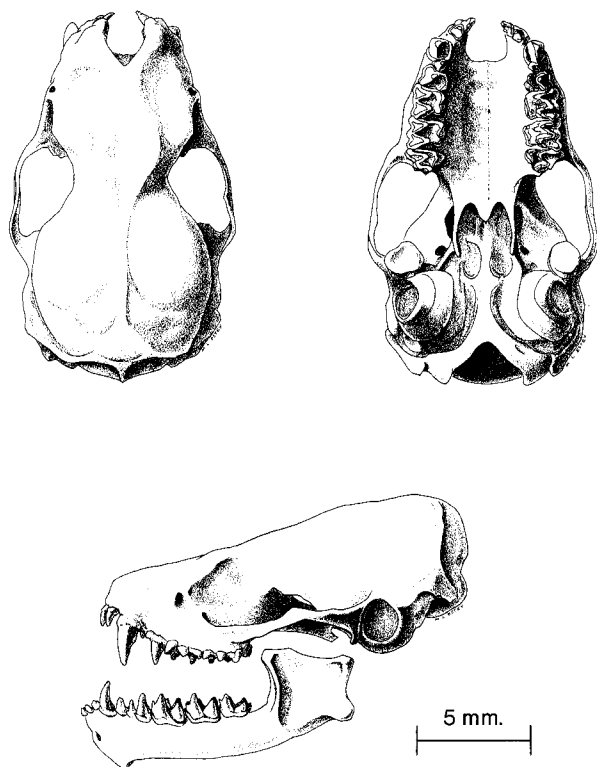


FIGURE 2. The skull of *Lasionycteris noctivagans* (MCZ 7328), Museum of Comparative Zoology, Harvard University.

(Druecker, 1972). Layne (1958) found relatively few sperm in the cauda epididymides of hibernating males in Illinois, but found viable sperm in vaginal smears from females. The peak of ovulation occurs in late April and early May, and a period of approximately 10 days elapses between ovulation and implantation (Druecker, 1972).

A 50 to 60 day gestation period occurs in May and June (Druecker, 1972). Pregnant females have been reported in early June in Minnesota (Bailey, 1929), in mid-June on Long Island (Nichols and Nichols, 1934), and in May and June in New Mexico (Druecker, 1972). Druecker (1972) reported that 36 spring-taken females averaged 1.84 preovulatory eggs or embryos. Females give birth to one or two young with two being the usual number (Druecker, 1972; Kunz, 1971; Seton, 1907; Turner and Jones, 1968). The sex ratio at birth is equal (Kunz, 1971; Merriam, 1884; Schowalter et al., 1978a). Kunz (1971) described the birth of two *L. noctivagans* from a female that had been held in captivity for 3 weeks. On the day of parturition the female refused food (mealworms) and water and assumed a head-up posture during delivery. The female gave birth to one live and one stillborn young by breech presentation. At birth the two young, a male and female, weighed 1.9 and 1.8 g, respectively. Their bodies were hairless and pink with dark membranes, and they had closed eyes and folded ears.

There is no reliable information on where females give birth. Reports of large maternity colonies (Doutt et al., 1966; Merriam, 1884; Seton, 1907) are dubious (Barbour and Davis, 1969; Griffin, 1940). Young are born in late June in Iowa (Easterla and Watkins, 1970; Kunz, 1971), and early July in upstate New York (Merriam, 1884). In Iowa the median parturition date was estimated as 16 June with a lactation period of approximately 36 days (Kunz, 1971). Flying young were first captured on 22 July. Apparently most young males and females mature sexually during their first summer (Druecker, 1972).

ECOLOGY AND BEHAVIOR. Little is known regarding the abundance, population dynamics, mortality, and survivorship of *L. noctivagans*. Barbour and Davis (1969) noted that it is erratic in abundance throughout much of its known range. Merriam (1884) noted that it was the most common bat in the Adirondack region of upstate New York. Early in the present century it was reported as the second most abundant bat, next to *Myotis lucifugus*, in Minnesota (Bailey, 1929). Seton (1907) reported it to be a common bat in Winnipeg in 1905 and 1906 but extremely rare in 1907. In New Mexico it was the fourth most abundant bat out of 19 species taken in mist nets (Jones, 1965, 1966). It was the fourth most abundant bat out of eight species netted in central Iowa; it was outnumbered by *Eptesicus fuscus*, *Lasiurus borealis*, and *Myotis lucifugus* (Kunz, 1971, 1973). Barbour and Davis (1969) suggested that *Lasionycteris* is probably most abundant in the northern Rockies from Wyoming and Idaho, northward to Canada in the United States, although they gave no evidence to support this contention. It appears to be a common resident of Alberta and British Columbia (Schowalter et al., 1978a) but its abundance relative to other species in this region has not been reported.

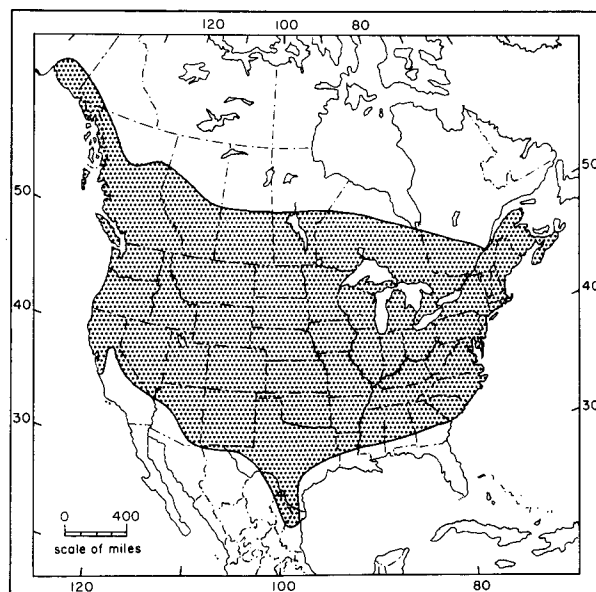


FIGURE 3. The distribution of *Lasionycteris noctivagans* (modified after Hall, 1981).

fugus, in Minnesota (Bailey, 1929). Seton (1907) reported it to be a common bat in Winnipeg in 1905 and 1906 but extremely rare in 1907. In New Mexico it was the fourth most abundant bat out of 19 species taken in mist nets (Jones, 1965, 1966). It was the fourth most abundant bat out of eight species netted in central Iowa; it was outnumbered by *Eptesicus fuscus*, *Lasiurus borealis*, and *Myotis lucifugus* (Kunz, 1971, 1973). Barbour and Davis (1969) suggested that *Lasionycteris* is probably most abundant in the northern Rockies from Wyoming and Idaho, northward to Canada in the United States, although they gave no evidence to support this contention. It appears to be a common resident of Alberta and British Columbia (Schowalter et al., 1978a) but its abundance relative to other species in this region has not been reported.

Although *L. noctivagans* is commonly regarded as a solitary tree-roosting bat there are few reliable records of this bat roosting in trees. Assuming that tree-roosting is the preferred habit, extensive deforestation and forest management practices over the last two centuries may have reduced the roosting sites available. Little is known of its summer roosting habits. In winter, silver-haired bats roost in mines (Layne, 1958; Pearson, 1962), caves (Beer, 1956; Turner, 1974), in hollow trees (Jackson, 1961), under loose bark (Cowan, 1933), in rock crevices (Frum, 1953), and in houses (Bartsch, 1956; Frum, 1953). There are no reliable reports of large winter or summer aggregations (Barbour and Davis, 1969; Griffin, 1940).

Although the migratory patterns of *L. noctivagans* have not been studied by banding, analyses of seasonal distributions based on published observations (Baker, 1978; Izor, 1979) suggest that the northward limit of the species' range shifts to the north in spring and to the south in autumn; females apparently migrate farther than males. The southward shift in autumn appears to be less in western than in eastern North America. Autumn migration appears to be better defined than spring migration in Alberta (Schowalter et al., 1978a). In British Columbia *L. noctivagans* may not be migratory (Dorward et al., 1977; Schowalter et al., 1978a).

In studies where relatively large numbers of *L. noctivagans* have been reported, including upstate New York (Merriam, 1884), Iowa (Kunz, 1971, 1973), New Mexico and Arizona (Jones, 1965, 1966; Jones and Suttus, 1972), and eastern Montana (Jones et al., 1973), summer populations are dominated by females except in the montane west (Jones, 1965, 1966). Males are present throughout the range only during migration. Oceanic observations of spring and fall migrants (Griffin, 1940; Mackiewicz and Backus, 1956) include individuals occurring singly and in small groups.

Known cases of mortality in *L. noctivagans* have resulted from predation by a skunk (Sperry, 1933) and great horned owls (Bond, 1940; Seton, 1907). Bell (1980) reported an aerial attack on *Lasionycteris* by a rabid *Lasiurus cinereus*. Druecker's (1972)

estimate of 1.84 preovulatory eggs or embryos per female and Kunz' (1971) determination of 1.7 volant young per adult female in Iowa suggests that some mortality occurs in the period from conception to fledging. Additional mortality probably occurs during migration. Based on an examination of dental annuli from a series of bats taken in Alberta (Schowalter et al., 1978b), most individuals were estimated as 2 years old but the oldest individual was assigned to a 12-year age class. A comparison of the age structure of *L. noctivagans* with that of *Myotis lucifugus* and *Eptesicus fuscus* based on dental annuli indicated that *L. noctivagans* has the shortest life span.

As in most other insectivorous bats, *L. noctivagans* is opportunistic in its food habits, taking a variety of insects (Jones et al., 1973; Whitaker, 1972; Whitaker et al., 1977). Black (1974) regarded *Lasionycteris* as a "moth strategist," based on feces examined from this bat in New Mexico; however, bats taken in eastern Montana consumed a variety of insects including representatives of the orders Lepidoptera, Hemiptera (Corixidae and Cicadellidae), Coleoptera (Carabidae), Diptera, and Trichoptera (Jones et al., 1973). Whitaker (1972) reported that the stomach contents of two specimens from Indiana contained 100% and 90% Trichoptera, with the remaining 10% consisting of Coleoptera (Scarabidae). The diet of this bat from western Oregon (Whitaker et al., 1977) included predominantly Lepidoptera (32%), Isoptera (15%) and Diptera (25.9%), which accounted for 72.9% of the diet by volume. Representatives of eight other insect orders and two families of arachnids composed the remainder of the diet. Gould (1955) found the remains of a stable fly (*Stomoxys calcitrans*) in the mouth of a bat shot while it foraged over sand dunes in eastern Massachusetts. Based on a diet of mealworms, the daily energy intake of a captive bat averaged 4.86 ± 0.45 (SD) kcal/day. Assimilation efficiency was 88.6% (73.5 to 98.2) (Neuhausser and Brishin, 1969).

Lasionycteris noctivagans is a relatively late flyer, often appearing after other species have begun feeding (Bailey, 1929; Kunz, 1973; Seton, 1907). Whitaker et al. (1977), however, noted that this bat was an early flyer in western Oregon. Seton (1907) observed that upon emerging from its daytime roost, *L. noctivagans* took a direct course to water. In Iowa this bat was characterized by a bimodal pattern of foraging activity, with the major peak occurring 2 to 4 hours after sunset and a second period occurring 6 to 8 hours after sunset (Kunz, 1973). Similar observations were reported for bats taken in eastern Montana although a second peak of activity was less marked (Jones et al., 1973).

Lasionycteris noctivagans typically forages in or near coniferous and/or mixed deciduous forests, adjacent to ponds, streams, and other bodies of water (Davis and Hardin, 1967; Jones, 1965, 1966; Kunz, 1973; Merriam, 1884; Seton, 1907; Turner, 1974; Yates et al., 1979). It is a relatively slow flyer (Hayward and Davis, 1964; Whitaker et al., 1977), foraging along erratic courses and taking many twists and frequent short glides. Each bat may have its own hunting route approximately 46 to 91 m in diameter (Schwartz and Schwartz, 1959).

Where red bats (*Lasiurus borealis*) and hoary bats (*L. cinereus*) occur with *Lasionycteris*, each species appears to be active at a different time (Kunz, 1973; Seton, 1907). Kunz (1973) noted that the first period of activity was intermediate in time between periods of activity for *L. borealis* and *L. cinereus*. In Oregon, Reith (1980) noted that *L. noctivagans* was frequently taken at the same water hole as *Eptesicus fuscus*, but when the latter species was numerically dominant, *L. noctivagans* shifted its activity to a later period. Conversely, when *L. noctivagans* was numerically dominant, it foraged earlier in the evening (Whitaker et al., 1977). From these observations, Reith (1980) suggested that *E. fuscus* may reduce foraging efficiency of *L. noctivagans* when it occurs in relatively large numbers at a feeding site.

Lasionycteris noctivagans has been observed or collected in areas where it forages along with *Myotis lucifugus*, *M. leibii*, *M. thysanodes*, *M. evotis*, *Eptesicus fuscus*, and *Lasiurus cinereus* in eastern Montana (Jones et al., 1973) and South Dakota (Turner, 1974; Turner and Jones, 1968), and with *M. lucifugus*, *M. keenii*, *Lasiurus borealis*, *L. cinereus*, *Eptesicus fuscus*, *Pipistrellus subflavus*, and *Nycticeius humeralis* in Iowa (Kunz, 1973). In New Mexico it has been taken in the same mist nets as most of the above species, but also with *M. californicus*, *M. occultus*, *M. yumanensis*, *Pipistrellus hesperus*, *Idionycteris phyllotis*, *Plecotus townsendii*, *Euderma maculatum*, *Antrozous pallidus*, *Tadarida brasiliensis*, and *T. molossus* (Jones, 1965, 1966).

Ectoparasites of *L. noctivagans* include one mite species each from the families Sarcopidae (Boyd and Bernstein, 1950) and Laelapidae (Jones et al., 1973; Turner, 1974; Turner and Jones, 1968), bat flies of the families Nycteribiidae (Whitaker and

Easterla, 1974) and Streblidae (Turner, 1974), a flea (Jackson, 1961), and two species of bat bugs of the family Cimicidae (Judd, 1950; Usinger, 1966; Whitaker, 1973). No ticks or spinturnicid mites have been reported. Boyd and Bernstein (1950) noted that four of six bats they examined harboured sarcoptid mites, arranged in clusters consisting of adults and their eggs. Most of these mites were located on the ears but in one case they were on a finger on the underside of a wing. Bat bugs from *L. noctivagans* in western North America differ taxonomically from those in the east (Usinger, 1966).

Endoparasites include one species of nematode (Blankespoor and Ulmer, 1970), seven trematodes (Macy, 1933; Webster and Casey, 1973), and three cestodes (Macy and Rausch, 1946; Rausch, 1975; Stunkard, 1961).

Rabies has been reported from *L. noctivagans* in various parts of the United States (Baer and Adams, 1970; Constantine, 1967) and from Canada (Dorward et al., 1977). The incidence of rabies infected bats submitted for diagnosis in California was unimodal; most reports occurred in August (Constantine, 1967). Over a 5 year period (1971 to 1975) the incidence of rabies infection in *L. noctivagans* from Alberta and British Columbia averaged 9.9%, with the highest levels reported for August and September. Over 84% of the rabid bats examined were young of the year (Dorward et al., 1977).

GENETICS. The karyotype of *L. noctivagans* is distinct from that of other vespertilionids in having a $2n$ of 20 and a FN of 28 (Baker and Patton, 1967; Bickham, 1979). The autosomes consist of four pairs of large metacentrics and submetacentrics, one pair of small submetacentrics, and four pairs of small acrocentrics. The X chromosome is a large submetacentric and the Y is a small acrocentric. C-band preparations show that heterochromatin is localized at the centromere (Bickham, 1979). Based on G-band preparations, Bickham (1979) suggested that the karyotype of *L. noctivagans* evolved by centric fusion and translocation from a karyotype like that of *Myotis*.

REMARKS. Vernacular names include silver-haired bat, black bat, silver-black bat, silver bat, and silvery-haired bat (Jackson, 1961). The most frequently used name is the silver-haired bat (Jones et al., 1979). Tate (1942) considered this monotypic genus "essentially a *Myotis* that has become specialized through loss of pm^3 ." Based on the distinctiveness of the baculum (Hamilton, 1949) and the uniqueness of the karyotype, Baker and Patton (1967) suggested a more distant relationship to the genus *Myotis* as well as to other vespertilionids. However, Bickham (1979) postulated that the karyotype of *L. noctivagans* may have evolved from a karyotype like that of *Myotis*. Stegman (1933) described an abnormal left ear from a single specimen in which the tragus was united with the posterior-ventral border of the pinna.

The generic name is derived from the Greek words *lasio* (hairy) and *nycteros* (bat). The specific name combines the Latin words *noctis* (night) and *vagans* (wandering).

I am grateful to Peg Esty for preparing Fig. 2 and to E. R. Hall, who kindly made available a copy of the distribution map for *Lasionycteris* from the 2nd edition (1981) of "The mammals of North America," from which Fig. 3 was prepared.

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