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Lasiurus cinereus.

By Karl A. Shump, Jr., and Ann U. Shump

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Lasiurus cinereus (Palisot de Beauvois, 1796)

Hoary Bat

Vespertilio cinereus Palisot de Veauvois, 1796:18. Type from Philadelphia, Pennsylvania.
Vespertilio villosissimus Geoffroy St. Hilaire, 1806:204. Type locality Paraguay, restricted to Asunción.
Vespertilio pruinosus Say, 1823:167. Type from Engineer Cantonment, Washington Co., Nebraska.
A[talapha] mexicana Saussure, 1861:97. Type locality unknown, probably from Veracruz, Puebla, or Oaxaca.
Lasiurus cinereus Allen, 1864:21. First use of current combination.

CONTEXT AND CONTENT. Order Chiroptera, Suborder Microchiroptera, Family Vespertilionidae, Subfamily Vespertilioninae, Tribe Lasiurini. The genus *Lasiurus* includes 11 extant species (see Shump and Shump, 1982, for key). *Lasiurus cinereus* currently includes three subspecies (Hall and Jones, 1961):

L. c. cinereus (Palisot de Beauvois), 1796:18, see above (*pruinosus* Say and *mexicana* Saussure are synonyms).
L. c. villosissimus (Geoffroy St. Hilaire), 1806:204, see above (*grayi* Tomes, *pallescens* Peters, and *brasiliensis* Pira are synonyms).
L. c. semotus (Allen), 1890:173. Type locality Hawaii.

DIAGNOSIS. *Lasiurus cinereus* is not easily confused with any other lasiurine because of large size and distinctive color. Other members of the genus have a yellowish to reddish pelage, while the hoary bat is mixed dark brownish and grayish, tinged with white to produce a frosty or hoary effect; wrist and shoulder patches are whitish; the throat patch is distinctly yellowish (Barbour and Davis, 1969; Miller, 1897; see Fig. 1).

Hoary bats also differ from other members of the genus by the following dental and skeletal characteristics: talonid on m3 larger; p4 single-rooted instead of double-rooted; hypocone on M1 and M2 smaller; coronoid process lower; ossified part of tympanic ring, which shields petrosal, larger; humerus relatively shorter; forearm relatively longer; first and middle fingers relatively shorter; presternum including keel longer than wide instead of the opposite (Hall and Jones, 1961).

The skull is large, broad and heavy; the rostrum is broad and has wide nasal openings and flaring zygoma. Greatest length of skull is 17.0 to 18.7 mm, and zygomatic breadth varies from 11.8 to 13.9 mm. The skull, in general, resembles that of the red bat but is larger (Hall and Jones, 1961; Miller, 1897; see Fig. 2).

GENERAL CHARACTERS. The hoary bat is large (20 to 35 g) with a heavily-furred interfemoral membrane. The ears do not reach as far as the nostrils when laid forward; they are thick, short, rounded, edged with black. The tragus is short and broad. Hindfoot is one-half as long as tibia; dorsal side has thick fur. Calcar is twice as long as hindfoot, distinctly though narrowly keeled on posterior edge with lobes on tip (Barbour and Davis, 1969; Miller, 1897; see Fig. 2).

Measurements (in mm) reported by Miller (1897) are as follows (n = 4 males): total length, 134.5; length of tail, 57.5; length of tibia, 23.2; length of hindfoot, 10; length of forearm, 50.2; length of thumb, 10.6; length of longest finger, 107; length of ear from notch, 18; width of ear, 17.2; length of tragus, 9. These measurements are comparable to those of Jackson (1961) and Hamilton and Whitaker (1979).

Williams and Findley (1979) found females to average 3.9% larger than males. Size related measurements ($\bar{X} \pm SE$) for males (n = 30) and females (n = 30), in mm, were, respectively: length of head and body, 80.5 ± 0.51 and 83.6 ± 0.46; length of forearm, 52.64 ± 0.251 and 54.22 ± 0.267; condylocanine length, 16.69 ± 0.067 and 17.34 ± 0.066; length of maxillary toothrow, 6.13 ± 0.025 and 6.47 ± 0.027.

The teeth are large and strong, but the minute upper premolars are proportionally smaller than those in *L. borealis* and occasionally absent. Dental formula is i 1/3, c 1/1, p 2/2, m 3/3, total 32 (Miller, 1897).

DISTRIBUTION. Hoary bats are the most widespread of all American bats. They range from near the limit of trees in Canada, southward at least to Guatemala, and in South America from Brazil to Argentina and Chile. They are also found in Hawaii, and there are records of presumed wayward migrants from Southampton Island in northern Canada, Iceland, Bermuda, Hispaniola, and from the Orkney Islands off Scotland. They are uncommon throughout most of the eastern United States and in the northern Rockies, but common in the prairie states and the Pacific Northwest. They winter in southern California, southeastern United States, Mexico (Watkins et al., 1972) and Guatemala, but have been found in Michigan, New York, Connecticut, and Indiana during December and January (Baker and Ward, 1967; Banfield, 1974; Barbour and Davis, 1969; Cabrera, 1958; Hall and Kelson, 1959; K. Koopman, pers. comm.; Sanborn and Crespo, 1957; Whitaker, 1967; Zinn and Baker, 1979). The species range is illustrated in Fig. 3.

FOSSIL RECORD. Although sparse, fossil evidence for *L. cinereus* has been found in late Pleistocene deposits at: Mt. Scott, Meade Co., Kansas; Cragin Quarry, Meade Co., Kansas; Dry Cave, Eddy Co., New Mexico; Schultze Cave, Edwards Co., Texas; San Josecinto Nuevo Leon, Mexico (Dalquest et al., 1969; Hibbard and Taylor, 1960; Kurtén and Anderson, 1980; Martin, 1972). Ancestry can be traced back to the early Blancan species, *Lasiurus fossilis* (Hibbard, 1963), from Fox Canyon, Meade Co., Kansas.

FIGURE 1. *Lasiurus cinereus* (courtesy of M. D. Tuttle).

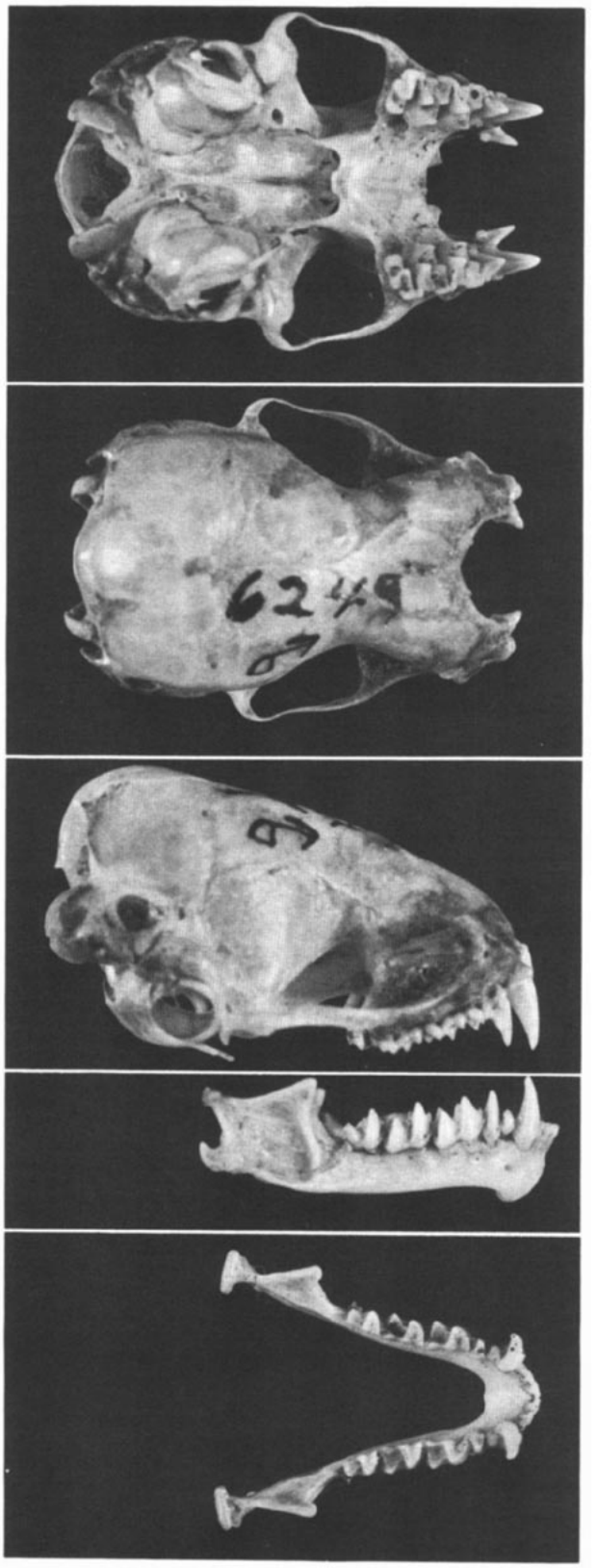

FIGURE 2. Dorsal, ventral, and lateral views of cranium, and lateral and occlusal views of mandible of *Lasiurus cinereus* (Michigan State Univ. no. 6249, male from Angol, Malleco Province, Chile). Greatest length of skull is 17.0 mm.

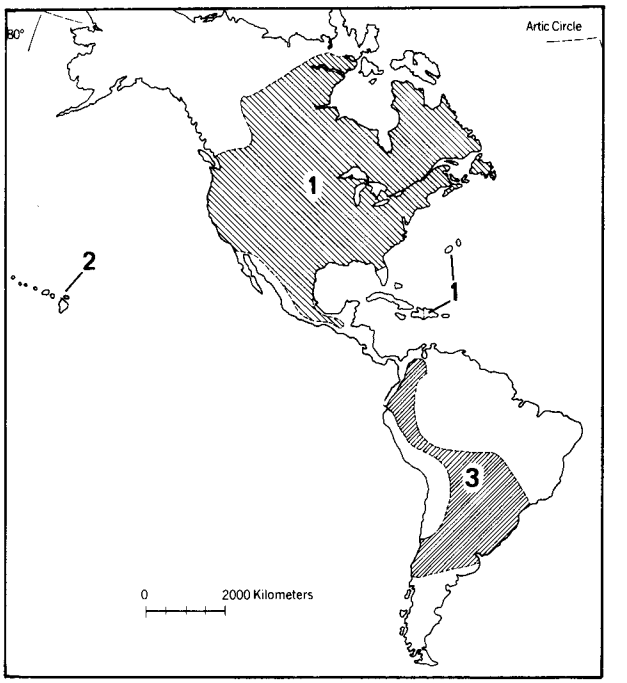

FIGURE 3. Distribution of the hoary bat, *Lasiurus cinereus*: 1, *L. c. cinereus*; 2, *L. c. semotus*; 3, *L. c. villosissimus*.

FORM. The fur is full and soft all over the body. The back has an average fur depth of 6.8 mm, whereas that of the uropatagium is 3.3 mm (Shump and Shump, 1980). The outer portion of the ears are densely furred on the lower two-thirds but sparsely furred on the tip and inner surface. The ears are set low on the head and do not extend much above the dorsal fur line (Miller, 1897; Barbour and Davis, 1969).

The aspect ratio (X = 8.25) and wing loading (X = 0.126) indicate this species is a fast and straight flier (Farney and Fleharty, 1969). Hoary bats are considered one of the fastest fliers among North American bats (Barbour and Davis, 1969).

Four distinct groups of glands are recognized for lasiurines: sudoriferous glands, sebaceous glands, and two groups of different salivary glands—paired submaxillary and paired sublingual (Werner and Dalquest, 1952).

The baculum was described by Hamilton (1949) as being relatively stout and short, the rounded shaft extending into a swollen cylindrical distal portion. This terminates in an elevated point with its tip being higher than the base. At its proximal margin, the base is truncate. Ventrally the bone is convex, except the proximal fifth, which is slightly concave.

FUNCTION. The heavy fur on the uropatagium and the body provide considerable insulation for hoary bats. The coat is significantly more insulative than that of red bats, which in turn is more insulative than the pelage of species of *Myotis* and *Eptesicus*. Insulation ($\bar{X} \pm SE$ in °C $kcal^{-1}$ h^{-1} $m^{2^{-1}}$) was measured as 0.289 ± 0.002 for the body pelage and 0.345 ± 0.001 for body pelage and uropatagium. These values indicate that the uropatagium provides effective insulation, providing a "blanket effect" to shield the bat from the environment (Shump and Shump, 1980).

Lasiurus cinereus seems to tolerate a wide range of temperatures. It has been caught foraging at air temperatures between 0 and 22°C, a range greater than noted for sympatric vespertilionids (Jones, 1965).

Studies on evaporative water loss (Shump and Shump, pers. observ.) show that this species loses less water, under similar environmental conditions, than do *Myotis lucifugus* and *Eptesicus fuscus*. Water loss on a mass-specific basis is less than would be expected. The relatively high insulative value of the pelage is probably an important factor in conserving water. Shump and Watkins (pers. observ.) found *L. cinereus* could lose water composing 28% of its body weight without apparent ill effects; however, its upper limits were not tested.

Bowers et al. (1968) found that a hoary bat in Michigan in a resting (non-torpid) pose had a metabolic rate of 1.19 cc O_2 g^{-1} h^{-1}.

Adrenal weights of *L. cinereus* measured in February, of a male and female respectively, were 2.8 g, 12.7% body weight, and 3.19 g, 14.1% body weight. Adrenal weights should be lowest in midwinter and highest in summer, although data for this species

are not available. Additionally, adrenal weights in relation to body weight (metabolic body size) should be highest in races adapted to the coldest climates, although only sparse data exist for this species (Rudd and Beck, 1969).

ONTOGENY AND REPRODUCTION. Although sexes have been found together in some parts of Nebraska, Montana, and the Dakotas, they are generally separated during the warm months in North America, except during the mating season (Dalquest, 1943; Findley and Jones, 1964; Jones, 1964; Jones and Genoways, 1966; Kunz, 1971). Reports from Indiana (Mumford, 1969) and central Iowa (Constantine, 1966; Kunz, 1971), for instance, record only a few males. Findley and Jones (1964) noted that females seem to be more concentrated in western North America. Vaughan and Krutsch (1954) suggested that an altitudinal separation of sexes occurs in California, with females in lowlands and coastal valleys and males occupying foothills and mountains.

Copulation in *L. cinereus* probably occurs in autumn migration and is followed by delayed implantation, but may take place also on the wintering grounds. Parturition seems to range from mid-May into early July; the usual number of young per litter is two, and ranges from one to four (Barbour and Davis, 1969; Druecker, 1972; Gottschang, 1966; Jackson, 1961; Provost and Kirkpatrick, 1952; Whitaker and Mumford, 1972; Wood, 1922).

Parturition was noted as early as 12 June in Iowa and some young were volant by July (McClure, 1942). Parturition occurs in Indiana from late May through the first half of June (Mumford, 1969; Whitaker and Mumford, 1972); in southern Lower Michigan it probably occurs in June (Kurta, 1980).

Parturition was observed in three captive females with delivery occurring between 0900 and 1300 h. The young grasped the mother with their feet, but did not otherwise assist in the delivery process. Subsequent to birth the young were cradled in the mother's wings while she groomed them until clean and dry. At that time, the young began grooming themselves (Bogan, 1972).

Newborn are covered with fine, silvery-gray hair except on the venter, which is naked. The forearm length of newborn *L. cinereus* is 16 to 20 mm (Munyer, 1967; Mumford, 1969). The ears and eyes are closed at birth but open on day 3 and day 12, respectively. By day 33, purposeful flight is possible (Bogan, 1972). Other details of parturition and development of young were noted by Bogan (1972) and Munyer (1967).

After birth in the wild, young cling to the mother by day but usually are left hanging on a twig or leaf while she forages at night (Barbour and Davis, 1969). In the laboratory, Bogan (1972) found that females carried the young spontaneously in well-controlled flight until the young were 6 to 7 days old.

In central Iowa, Kunz (1971) caught lactating hoary bats from 21 June to 22 July. Volant young were taken beginning 22 July; males outnumbered females 5 to 1. No females were captured in August. Perhaps this was due to differences in foraging behavior or different times of departure to southern wintering sites.

ECOLOGY. *Lasiurus cinereus* is a solitary bat which roosts primarily among foliage in trees, although unusual roosts include a woodpecker hole in British Columbia (Cowan and Guiguet, 1965), caves where it may not find its way out in late summer (Mumford, 1953; Myers, 1960), in the nest of a gray squirrel (Neill, 1952), under a driftwood plank (Connor, 1971), and clinging to the sides of buildings (Bowers et al., 1968). By day hoary bats generally roost 3 to 5 m above ground in trees such as elm, black cherry, plum, box elder, and osage orange. Bats are well hidden from above but visible from below, and they usually prefer the edge of a clearing (Constantine, 1966). In Hawaii, this species has been found during all seasons, ranging from sea level to 4,400 m, in both dry and wet areas, although it seems to prefer a habitat of open or mixed character (Baldwin, 1950).

Although there is much circumstantial evidence to support the assumption that *L. cinereus* migrates, wintering sites are not well documented and no specific migration routes have been plotted. Nevertheless, they often are found flying in large groups in spring and autumn, when they would be expected to be migrating or breeding (Barbour and Davis, 1969; Findley and Jones, 1964; Mumford, 1963). Evidence from Zinn and Baker (1979) suggests that hoary bats migrate through northern Florida from late October to late November and from February to early May, but are essentially absent the remainder of the year. They reported that the autumn migration seemed to occur in waves, whereas the spring migration appeared to be less organized. Some hoary bats probably remain in northern areas and hibernate (Barbour and Davis, 1969; Whitaker, 1967; Whitaker and Mumford, 1972). Findley and Jones (1964), however, suggested that many winter south of the United States.

The swift (about 21.3 km/h), direct flight of these large bats makes them readily identifiable on the wing anywhere in the United States, except where the largest free-tailed bats occur (Barbour and Davis, 1969; Hayward and Davis, 1964). They generally emerge late in the evening to forage, although they may arouse and fly on warm winter afternoons (Barbour and Davis, 1969; Hamilton and Whitaker, 1979). In New Mexico, hoary bats were quite active 1 h 40 min after sundown, just after the appearance of *L. borealis* (Jones, 1965). In Iowa, individuals seemed to forage most 4 to 5 h after sunset (Kunz, 1973). In Missouri, hoary bats were the last vespertilionids to be noted in the sky, about 1 h 15 min after sunset. The greatest success, however, for catches in mist-nets occurred between 3 and 4 h after sunset (Watkins and Shump, pers. observ.). Bell (1980) found *L. cinereus* to be most active in juniper scrub, riparian forest, and desert habitats after midnight in southwestern United States.

Little is known of the food habits of hoary bats, but they appear to have a strong preference for moths (Black, 1972; Ross, 1967). Indications are that the bat approaches a flying moth from the rear, engulfs the abdomen-thorax in its mouth and then bites down, allowing the sheared head and wings to drop to the ground. Hoary bats are also known to eat beetles, flies, grasshoppers, termites, dragonflies, and wasps (Dalquest, 1953; Poole, 1932; Ross, 1967; Zinn and Baker, 1979). Like red bats, however, they seem to forage on relatively few orders of insects, indicating that they are specialists. Whitaker (1967) found grass and a snake skin in the alimentary canal of one found during winter. Even during times of presumed insect abundances, they have been seen attacking pipistrelles (Bishop, 1947; Orr, 1950). In captivity, these bats eat mealworms, moths, and beetles (Jackson, 1961) and muscle and liver of freshly killed mice (Bowers et al., 1968).

The only time hoary bats seem to associate with other species of bats in summer is while foraging. Mumford (1969) reported seeing hoary bats in Indiana feeding with *L. borealis, Eptesicus fuscus, Myotis sodalis, Pipistrellus subflavus, Lasionycteris noctivagans,* and *Nycticeius humeralis.* In areas where *L. borealis* is abundant, however, *L. cinereus* is uncommon, and when *L. cinereus* is abundant, *L. borealis* is uncommon (Kunz, 1973). Hoary bats may forage in groups for insects, but roost separately by day (Mumford, 1969).

No important predators are known for hoary bats, although hawks and owls probably take some from time to time (Barbour and Davis, 1969; Jackson, 1961; Lowery, 1974). There is a report of predation by an American kestrel, *Falco sparverius* (Church, 1967), and by a rat snake, *Elaphe guttata* (Wiseman, 1963). Accidental impalings of hoary bats on barbed wire have been noted on several occasions (Denys, 1972; Iwen, 1958; Hibbard, 1963; Wisely, 1978). Another source of mortality may be females with young being dislodged from trees and falling to the ground, thereby making themselves subject to predators.

Parasites reported for *L. cinereus* are: mites—*Pteracarus chalinolbus, Chiroptonysus americanus* (Radovsky, 1967; Whitaker, 1973; Whitaker and Wilson, 1974); helminths—*Longibucca lasiura, Oochoustica taborensis, Physocephalus sexalatus* (Tromba, 1954); protozoa—*Distoma* sp. (Jackson, 1961).

Lasiurus cinereus has a relatively high incidence of rabies. In Indiana, 25% of the hoary bats collected by citizens from 1965 to 1968 were found to be rabid (Whitaker et al., 1969), and 17.1% collected from 1968 to 1972 were rabid (Whitaker and Miller, 1974). The greatest incidence of rabies was found in the southern part of the state. Other reports of rabid hoary bats from different parts of the United States are found in Bell et al. (1962), Constantine (1967), Enright (1962), Glass (1959), Kough (1954), Maddy et al. (1958), Richardson et al. (1966), Tierkel et al. (1960), Trimarchi (1978), Wiseman et al. (1962), and Witte (1954).

GENETICS. *Lasiurus cinereus* has a karyotype of 2n = 28, FN = 48. There are seven pairs of large metacentric and submetacentric chromosomes, three pairs of medium metacentrics, and three pairs of small acrocentrics. The X-chromosome is a medium submetacentric and the Y-chromosome is a small acrocentric (Baker and Patton, 1967; Bickham, 1979).

REMARKS. The generic name *Lasiurus* means "hairy tail" and the specific name *cinereus* means "grayish" or "ash" colored, referring to the white-tipped, frosty hair coloring.

Bats of this species have survived in captivity for 2 years on mealworms supplemented by a vitamin preparation (Stuart Liquid Formula) at the level of one drop per bat every other day (Orr, 1958). They did not learn to feed by themselves in less than one

month. Bogan (1972) and Orr (1958) remarked that hoary bats were reluctant to take mealworms from dishes. More information on care and maintenance of bats, in general, can be found in Rasweiler (1977).

K. Koopman graciously provided records necessary to approximate the range of *L. cinereus* in South America.

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KARL A. SHUMP, JR., AND ANN U. SHUMP, DEPARTMENT OF BIOLOGICAL SCIENCES, STATE UNIVERSITY OF NEW YORK, BROCKPORT 14420.