

Myotis lucifugus. By M. Brock Fenton and Robert M. R. Barclay

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Myotis lucifugus (LeConte)

Little Brown Bat, Little Brown Myotis

[*Vespertilio*]. *lucifugus* LeConte, in McMurtrie, 1831:431. Type locality Georgia, probably the LeConte Plantation, near Riceboro, Liberty County.

Vespertilio gryphus Cuvier, 1832:15. Type locality New York.

?*Vespertilio salarii* Cuvier, 1832:18. Type locality New York.

?*Vespertilio crassus* Cuvier, 1832:18. Type locality New York.

Vespertilio domesticus Green, 1832:290. Type locality western Pennsylvania.

?*Vespertilio lanceolatus* Wied-Neuwied, 1839:364. Type locality Bethlehem, Pennsylvania.

Vespertilio carolii Temminck, 1840:237. Based on specimens from Pennsylvania and New York.

Vespertilio virginianus Audubon and Bachman, 1841:93. Type locality mountains of Virginia.

Vespertilio brevirostris Wied-Neuweid, 1860:19. Type locality Freiburg, Pennsylvania.

Vespertilio affinis Allen, 1864:53. Type locality Fort Smith, Arkansas.

Myotis (Leuconoë) carissima Thomas, 1904:383. Type locality Lake Hotel, Yellowstone National Park, Wyoming.

Myotis occultus Hollister, 1909:43. Type locality west side of Colorado River, 10 mi. above Needles, San Bernardino County, California.

Myotis baileyi Hollister, 1909:44. Type locality base of White Mountains, 7,500 ft., near Ruidosa, Lincoln County, New Mexico.

Myotis pernox Hollister, 1911:4. Type locality Henry House, Alberta.

CONTEXT AND CONTENT. Order Chiroptera, Suborder Microchiroptera, Family Vespertilionidae, Subfamily Vespertilioninae. The genus *Myotis* now includes approximately 80 species. Six subspecies of *Myotis lucifugus* are currently recognized.

M. l. alascensis Miller 1897:63. Type locality Sitka, Alaska.

M. l. carissima Thomas 1904:383, see above (*altipetens* Grinnell and *albicinctus* Allen are synonyms).

M. l. lucifugus (LeConte, in McMurtrie, 1831:431), see above (*gryphus* Cuvier, *salarii* Cuvier, *crassus* Cuvier, *domesticus* Green, *lanceolatus* Wied, *carolii* Temminck, *virginianus* Audubon and Bachman, *brevirostris* Wied, and *affinis* Allen are synonyms).

M. l. occultus Hollister, 1909:43, see above (*baileyi* Hollister is a synonym).

M. l. pernox Hollister, 1911:4, see above.

M. l. relictus Harris, 1974:598. Type from Keeler, 3,600 ft., Inyo County, California.

DIAGNOSIS. The lack of a keel on the calcar and the presence of hairs on the hind foot that extend beyond the toes are useful field characters for distinguishing *M. lucifugus* from *M. sodalis*. The shorter tibia, the absence of a keel on the calcar, and the lesser amount of fur on the undersurface of the wing permit field separation of *M. lucifugus* from *M. volans* (see Barbour and Davis, 1969). This species can be distinguished from *M. septentrionalis* (= *M. keenii septentrionalis*; van Zyll de Jong, 1979) in the field by the long sharply pointed tragus and ears which extend well beyond the nose (>2 mm) when laid forward in the latter species. In most areas where they are sympatric, *M. lucifugus* may be distinguished from *M. yumanensis* by glossy versus dull fur, respectively (but 'intermediate' individuals have been reported from some areas, Barbour and Davis, 1969; Harris, 1974; Parkinson, 1979). Other North American *Myotis* can be separated from *M. lucifugus* in the field by relative size of hind feet, length of ears, or the location of insertion of wing membranes on the hind limbs (see Barbour and Davis, 1969). *Myotis lucifugus* can be distinguished from the tropical *M. fortidens* by

the shape of the baculum; but the presence of a keel on the calcar and reduction in the number of upper and lower premolars (more typical of *M. fortidens*) are less dependable characters (Findley and Jones, 1967). *Myotis daubentoni* is the Palearctic equivalent of *M. lucifugus*, and the former can usually be separated from the latter which has elongated claws with enlarged toes, wing membranes which insert on the basal half rather than the terminal half of the metatarsi, and fur on the venter which is not conspicuously glossy and which is paler and contrasts more with that of the dorsum (Miller and Allen, 1928).

GENERAL CHARACTERS. Females average slightly larger than males, and this is reflected in significant differences in winter weight (Fenton, 1970a) and lengths of forearms and head and body (Williams and Findley, 1979). The range of measurements (in mm) for selected characters is: forearm 33 to 41; ear 11.0 to 15.5; tragus 7 to 9; hind foot 8 to 10; greatest length of skull 14.0 to 15.9; zygomatic breadth 8.1 to 10.5; breadth of braincase 7.0 to 8.2; maxillary toothrow 5.0 to 6.9, and the mean values for selected characters are presented by Williams and Findley (1979). The fur has a glossy appearance and ranges in color on the dorsum from dark sooty brown through paler golden brown and pallid, to yellowish or olive brown. Partially albino specimens have been reported from some areas (Walley, 1974). The tragus is medium in height and blunt; the hind foot is about 55% of the length of the tibia. The calcar is about 17 mm long and usually lacks a keel. The skull has a relatively short rostrum and in profile the forehead has a graded upslope; the braincase is somewhat flattened and subcircular in dorsal view (Fig. 1). Most populations of *M. lucifugus* lack sagittal crests, but this is often well developed in *M. l. occultus* where it is associated with larger teeth and skull (Findley and Jones, 1967; Barbour and Davis, 1970), which in turn coincides with an increase in the number of sympatric species of *Myotis* (Findley and Jones, 1967).

DISTRIBUTION. The range of the species and subspecies (Fig. 2) covers most of North America (Jones et al., 1977). Specimens from the state of Mexico and the Distrito Federal in Mexico (Alvarez and Ramirez-Pulido, 1972) are from higher elevations in forested areas (Findley and Jones, 1967). Most of the specimens from the northern edge of the range are males, although nursery colonies of *M. l. pernox* are known from the Yukon (Youngman, 1975). Records from Iceland (Koopman and Gundmundsson, 1966) and Kamchatka (Hahn, 1905) probably represent ship-transported individuals. The fossil record consists of recent cave deposits (Jelga, 1963).

FORM AND FUNCTION. Since *M. lucifugus* has been 'the bat' for many studies, there is a wealth of information available about many aspects of its form and function. A detailed review of the circulatory systems of bats (Kallen, 1977) includes a great deal of data about *M. lucifugus* on a broad spectrum from penile erection to the incidence of cardiac glycogen in the heart as hibernation progresses. The heart beat rate in *M. lucifugus* ranges from 20 beats per minute (bpm) at 7°C rectal temperature, through 100 bpm (25°C), to 210 bpm (35°C) for non-flying bats. The highest rate recorded was 1368 bpm, and the lowest 8 bpm in a supercooled bat with a rectal temperature of -5°C (Kallen, 1977). The blood volume on a yearly average is 13.0 ml/100 g, while for active females during pregnancy and lactation this value is 11.1 ml/100 g (Kallen, 1977). In a review of blood physiology, Riedesel (1977) pointed out that those who have studied the formed elements in the blood of bats would agree to several points: bats are susceptible to dehydration, site of blood collection affects results, activity of the spleen influences circulating elements, circadian differences may be strong, and there are often considerable differences between species. A reflection of some of these variations is provided by the data of several workers (Bruce and Wiebers, 1969; Studier and Ewing, 1971) on sodium levels in the blood of *M. lucifugus*. Other comprehensive reviews which include data on *M. lucifugus* cover the central nervous

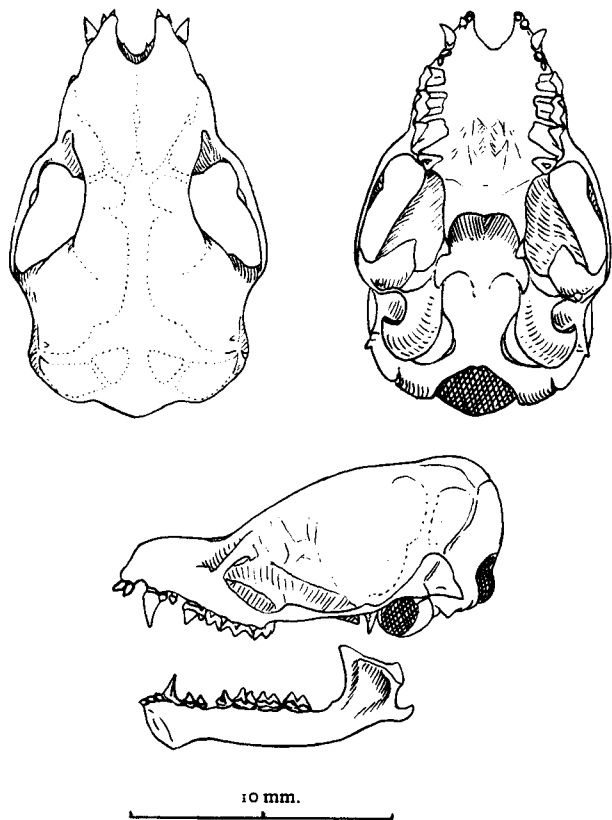


FIGURE 1. The skull of *Myotis lucifugus lucifugus* (Royal Ontario Museum no. 10563 ♂) from Peterson (1966) by permission of R. L. Peterson and Oxford University Press.

system (Henson, 1970a), the peripheral nervous system (Quay, 1970a), the auditory system (Henson, 1970b), and the integument and its derivatives (Quay, 1970b). *Myotis lucifugus* has been shown to efficiently filter ammonia by respiratory mucous; 84.5% removed at 1330 ppm, 77.5% at 3010 ppm, performing at a level well beyond that of *Mus musculus* (76.9% at 870 ppm), but below that of *Tadarida brasiliensis* (Studier, 1969). In his review of the urinary system in bats, Rosenbaum (1970) included a variety of data on the anatomy, histophysiology and renal physiology of *M. lucifugus*. There is variation in the urine concentrating abilities of different subspecies of *M. lucifugus*, with *M. l. occultus* producing urine at 2000 to 3000 milliosmols/kg, and *M. l. lucifugus* at 1100 to 2200 milliosmols/kg; in both subspecies urine was more concentrated after feeding (Bassett and Wiebers, 1979). The breast muscles of *M. lucifugus* show high oxidative capacities and low glycolytic potentials, as well as high levels of myofibrillar ATPase, suggesting the capacity for fast contraction; all features that should reflect aerobic generation of muscular power. During hibernation there is significant decline in the oxidative capacity, but none in the glycolytic potential (Armstrong et al., 1977). There appear to be different enzyme forms for normothermic versus hibernating *M. lucifugus* (Moon and Borgmann, 1976) and the enzyme pyruvate kinase from muscle and liver was different for normothermic and hibernating bats (Borgmann and Moon, 1976). The pinealocytes show nucleolar and nuclear changes in diameter throughout the year with a peak in March and the nadir in September. This pattern is the inverse of the pituitary luteinizing hormone secreting cells (Quay, 1976), and of the production of testosterone (Gustafson and Shemesh, 1976).

The amount of brown fat in *M. lucifugus* also shows seasonal variation. There are 13 topographically distinct deposits of brown fat in this species, situated to transfer heat to the blood efficiently and rapidly during arousal from hibernation (Rauch and Hayward, 1969, 1970). When the ambient temperatures fall below their thermal neutral zone (32 to 36°C winter; 39 to 42°C summer; Stones and Wiebers, 1967), little brown bats readily enter torpor as a means of conserving energy rather than as a reflection of poor thermoregulatory ability. Summer torpor is physiologically distinct from winter torpor, since in winter the animals sponta-

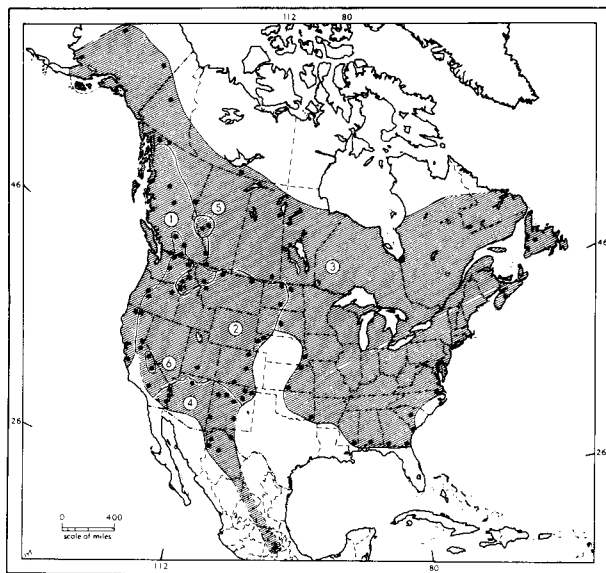


FIGURE 2. The distribution of *Myotis lucifugus* according to Hall and Kelson (in press), and showing the subspecies: 1, *M. l. alascensis*; 2, *M. l. carissima*; 3, *M. l. lucifugus*; 4, *M. l. occultus*; 5, *M. l. pernox*; and 6, *M. l. relictus*. There is some question about the distribution of subspecies, for example Youngman (1975) reported that *M. lucifugus* from the Yukon and Alaska were referable to *M. l. pernox*. Parkinson (1979) suggested that some specimens from parts of Oregon and California were intermediate between *M. l. carissima* and *M. yumanensis sociabilis*, and a similar situation may occur in other locations. Barbour and Davis (1969) indicated that *M. lucifugus* is not as widely distributed in Arizona and Nevada as suggested here. This figure is reproduced from Hall (in press) by permission of E. R. Hall and John Wiley and Sons, Inc.

neously (endogenously) arouse, while in summer the animals require some exogenous stimulation (Menaker, 1961). Little brown bats survive hibernation with about half as much stored energy as non-chiropteran heterotherms by strictly limiting the number of times that they arouse from torpor. Menaker (1964) demonstrated that torpid *M. lucifugus* go as long as 90 days without arousing. This factor is critical to the hibernating bat, for the energetically expensive part of hibernation is arousal, and increased frequency of arousal by hibernating *M. lucifugus* increases the weight loss suffered by these animals (Fenton, 1970a). Because torpid *M. lucifugus* arouse in response to a variety of physical stimuli (sound, touch, temperature change, etc.), the mechanical stimuli associated with disturbances in hibernacula may cause decreased survival rates. Hibernating bats do not feed, although they drink water during arousals. During the hibernation season *M. lucifugus* loses 25% of its autumnal weight (Fenton, 1970a).

The olfactory system is well developed (Bhatnagar, 1975), although the vomeronasal organ is absent (Cooper and Bhatnagar, 1976). The paired parhinal glands, which are largest and most conspicuous in *M. lucifugus* during the mating season (see Behavior), appear to produce behaviorally significant secretions (Thomas et al., 1979). Relatively little is known about the taste discrimination shown by *M. lucifugus*, but they find some insects distasteful and will reject them (Dunning, 1968; Coutts et al., 1973).

The eyes of *M. lucifugus* function better in dim than in bright light (Bradbury and Nottobohm, 1969; Masterson and Ellins, 1974). They lack the choroidal papillae and folded retinas characteristic of the Megachiroptera, and exhibit no eyeshine (Suthers, 1970). The fact that their eyes function better in dim than in bright light explains their poor performance in visual discrimination experiments conducted under bright lights.

ONTOGENY AND REPRODUCTION. Fertilization occurs after ovulation in the spring when females leave hibernation. The timing of these events is influenced by local conditions, resulting in earlier dates for parturition in more southerly parts of the range. The gestation period is 50 to 60 days (Wimsatt, 1945),

again depending upon local conditions, as torpor can prolong gestation in temperate vespertilionids (Racey, 1973). Pregnant females offset the influence of cool temperatures by selecting roosts that are consistently warmer than ambient (Davis and Hitchcock, 1965; Fenton, 1970a; Humphrey and Cope, 1976), but births in any area are staggered, with most occurring in a three week period (Cagle and Cockrum, 1943; Smith, 1954; Fenton, 1970a; Humphrey and Cope, 1976; Schowalter et al., 1979), a feature suggesting variation in the timing of fertilization, and hence, departure from hibernation. There is evidence that females approaching term lose their ability to thermoregulate (Studier et al., 1973). Energy demands on females are greatest during lactation, but higher towards the end of pregnancy than earlier in pregnancy (Studier et al., 1973; Anthony and Kunz, 1977).

Births occur in nursery colonies comprised almost entirely of females, although occasional adult males have been reported at these sites, particularly early in the season. During birth females reverse their normal head down hanging posture so that the neonate is born into the interfemoral membrane. In this species females bear a single young. It is flesh colored and covered with fine silky hair (Wimsatt, 1945); the eyes and ears usually open within a few hours of birth (Gould, 1971), and the deciduous teeth are almost fully erupted at birth (Fenton, 1970b). The young use the deciduous incisors, along with the large thumbs and hind feet, to cling to the female. Growth is rapid and allometric, with the thumbs and feet increasing little in size, while the wings and ears increase greatly in size. By day 9.5 young are capable of thermoregulation (Studier and O'Farrell, 1972), and by week 3 they can fly. At this time the permanent teeth are almost fully erupted, and insect remains first appear in the digestive tracts of the young (Fenton, 1970b). Weaning appears to take place around week 3 after birth, coinciding with a drop in weight of the young (Anthony and Kunz, 1977; Schowalter et al., 1979), but the details of mother-young interactions at this time remain relatively unknown (Gould, 1971).

By the time that the young are volant they have reached adult proportions of forearm and metacarpal lengths, but through their first summer they weigh significantly less than adults. In the earlier part of the summer young may be distinguished from adults by their pelage, which is noticeably darker, and by their unossified metacarpal-phalanges joints (Davis and Hitchcock, 1965). By the latter part of the summer, however, these characters are unreliable. At this time subadult females can usually be identified by small nipples and the absence of a worn patch around them, and subadult males can be readily distinguished from adults by the condition of the testes and epididymis (Racey, 1974; Thomas et al., 1979). Spermatogenesis starts in May and continues to late August (Gustafson and Shemesh, 1976).

Almost from birth *M. lucifugus* produce vocalizations, including high frequency sounds typical of echolocation pulses (Gould, 1971). In another species (*M. velifer*), baby bats can hear sounds from day 2, and by day 13 they have hearing sensitivity that is virtually the same as that of adults (Brown and Grinnell, 1980). Young *M. lucifugus* are clumsy in their first flights, and Buchler (1980) has found that initial attempts to catch prey involve sitting on a perch and waiting for a suitable target to come within range.

ECOLOGY. Little brown bats roost in a variety of situations, depending upon season and setting. In general, three types of roosts may be distinguished: day roosts, night roosts, and hibernation sites. Day and night roosts are used by active bats in spring, summer, and fall, while hibernacula are used as overwintering sites. Each roost has different characteristics appropriate for the place that it fills in the animals' requirements.

Day roosts occupied by *M. lucifugus* include sites in buildings, trees, under rocks, in piles of wood and occasionally in caves. Nursery roosts are usually located in and around buildings, but they may also be found in hollow trees or other natural crevices and hollows with appropriate temperature regimes. Ambient temperature and shelter appear to be the factors of greatest importance for bats in day roosts, and especially for those in nurseries. The sites must be warm enough to foster rapid growth of the young, whether before or after birth. Youngman (1975) found nursery colonies of *M. lucifugus* under sheet metal roofs of trappers' caches in the Yukon; attics of buildings often harbor nursery colonies of this species (Davis and Hitchcock, 1965). Little brown bats usually seek out dark or dimly lighted sites for day roosts, but open areas sheltered from predators may also be used. Temperature and water vapour pressure in the roosts significantly influence rates of water loss by the bats (Procter and Studier,

1970). *M. lucifugus* can tolerate diurnal weight losses up to 25% of their pre-emergence weights, and small clusters do not appear to ameliorate these rates of water loss in the laboratory (Studier et al., 1970). Most of the diurnal water loss occurs across the lungs (Herreid and Schmidt-Nielson, 1966) and through the sweat glands, which are not controlled by conditions of evaporation (Sisk, 1957).

Adult males and nonparous females usually occupy day roosts away from the nurseries; these individuals often occur alone or in small groups. A variety of physical sites is used, ranging from spaces within piles of stacked lumber or behind sheets of tarpaper, to small spaces under stones on hillsides, and occasionally caves. Ambient temperature and shelter are important, but the sites chosen by males and nonparous females tend to be cooler than the sites used for nurseries, and the bats in these roosts are frequently torpid. Little brown bats commonly use day roosts with southwestern exposures which provide exogenous heat for arousal from daily torpor (Fenton, 1970a).

Little brown bats customarily congregate in night roosts just after the initial feeding period in the evening. The sites selected are usually confined spaces into which many bats pack themselves, resulting in an increase in roost temperatures (T. H. Kunz, pers. comm.). The function of the night roosts remains unclear. They are often located in the same buildings as day roosts, but at different places suggesting that proximity to feeding sites and associated energy savings are not their main functions. The fact that night roosts are usually situated in confined spaces suggests that temperatures in night roosts are energetically beneficial to the bats. In this context the expenditure of body heat to warm a small cavity is smaller than that required to warm a larger one (Kunz, pers. comm.) and it is clear that active bats digest food more rapidly than inactive ones (Buchler, 1975). Night roosting could result in an accumulation of feces away from the day roosts, perhaps making the latter less conspicuous to predators. Pregnant females commonly use night roosts, but lactating ones do not; after the young have been weaned, young of both sexes and adult females use night roosts. A further indication of the importance of temperature in these roosts is the fact that *M. lucifugus* rarely occupies night roosts when night temperatures are above 15°C (R. M. R. Barclay, unpublished observations).

With the dispersal of the nursery colonies, which begins in midsummer, *M. lucifugus* start to appear in many types of day roosts. At this time it is common to find young of the year roosting on the sides of buildings or trees, completely in the open, and these bats frequently enter buildings which at other times of the year harbor no bats, leading to a peak in the number of contacts between bats and people (Barclay et al., 1980). It is clear that *M. lucifugus* are catholic in their roosting habits, taking shelter in any sites with appropriate microclimates, and quickly locating and exploiting new roosts.

Little brown bats hibernate in suitable sites throughout their range, usually in caves or abandoned mines. We have not found records of them hibernating in buildings. High levels of humidity ($\geq 90\%$) and temperatures above freezing characterize the sites most commonly used as hibernacula (Hitchcock, 1949, 1965; Fenton, 1970a; Humphrey and Cope, 1976), but there are records of *M. lucifugus* hibernating at sites where ambient temperatures are below freezing (Fenton, 1972). Laboratory data indicate that these bats become super-cooled (Davis and Reite, 1967), but there are no field data to support this and the status of super-cooling in *M. lucifugus* remains unclear (compare Davis, 1970, and Lyman, 1970). Hibernacula are rarely used by *M. lucifugus* as day roosts in summer (occasional nonparous females and males excepted), presumably because of the low ambient temperatures therein; but near the end of August in Ontario, and somewhat later farther south, some individuals (usually adult males) spend the day in hibernacula. They become torpid and appear to be aroused during the night by the activity of other bats at the site. The hibernacula act as centers for swarming activity which lasts from early to late August or into October, depending upon the location (see Behavior).

At the northern edge of their range in Ontario, hibernation lasts from early September until early or mid-May, while populations in more southern locations may not enter the hibernacula until sometime in November, and may leave by the middle of March. Departures from the hibernacula depend upon local weather conditions and the frequency of arousal from torpor.

Various workers have compared the prey captured by *M. lucifugus* with the available insects in areas where they feed (Belwood and Fenton, 1976; Buchler, 1976; Anthony and Kunz, 1977). Other studies have determined food habits by analysis of feces or stomach contents (Ross, 1961, 1967; Whitaker, 1972). It is

clear from laboratory (Griffin et al., 1960) and field studies (Fenton and Bell, 1979) that little brown bats are catholic in the food they eat and that they are effective at feeding in patches of insects. In the laboratory, *M. lucifugus* captured up to 12 fruit flies per minute (Griffin et al., 1960). In the laboratory and in the field they appeared to fix on their insect targets at short range (≤ 1 m) (Griffin et al., 1960; Fenton and Bell, 1979). The combination of rapid feeding and short range detection of food, coupled with attempts to capture several insects over a short distance produces a mosaic of both selective and generalized (by taxon) prey selection. *Myotis lucifugus* feeding in a mating swarm of insects appear to feed selectively on one or two species of insects (Buchler, 1976), but when foraging in a group of insects that has accumulated around a light or in the lee of some vegetation they have a heterogeneous diet by taxon, but select prey by size. In northern parts of its range, little brown bats show great variation in diet, similar to that of young of the year in more southerly locations (Belwood and Fenton, 1976). In northern latitudes the variation probably reflects the shorter time available for hunting and the patchy distribution of prey, while the variability in the diets of young is most likely the result of their inexperience (Belwood and Fenton, 1976; Anthony and Kunz, 1977).

In all areas studied, *M. lucifugus* prey heavily on aquatic insects; in southern Ontario, New Hampshire, and Nova Scotia, chironomids are the staple diet (Belwood and Fenton, 1976; Anthony and Kunz, 1977). In the course of an evening, however, little brown bats often vary their hunting patterns. They may feed initially along the margins of lakes and streams, zig-zagging in and out of the vegetation 2 to 5 m above the ground; later in the evening they usually forage in groups over water staying within 2 m, and often within 1 m of the surface (Fenton and Bell, 1979). There is no evidence of territorial behavior by individuals or groups from a colony while over feeding areas, although frequently individuals return time after time to the same feeding sites (Hough, 1957).

Lactating bats tend to select larger insects than males or nonparous females, but chironomids are still their staple food. Little brown bats tend to take insects from 3 to 10 mm in length (Anthony and Kunz, 1977). The rapid rate of mastication (seven jaw cycles per second; Kallen and Gans, 1972), short time for passage of food through the digestive tract (35 to 54 min; Buchler, 1975), and feeding rapidly in clumps of insects, appear to be specializations for minimizing inter-capture intervals and maximizing the rate of turnover of food.

The ability of *M. lucifugus* to exploit a wide range of roosts and food probably contributes to large populations of this species in many parts of its range. Although the rate of reproduction is low (one young per year), individuals may live a long time; the 1979 record is over 31 years for a male banded as an adult in southeastern Ontario by H. B. Hitchcock. Records of bats over 10 years old are common (Humphrey and Cope, 1976). Population age structure and survival rates are not clearly defined. Humphrey and Cope (1976), using data from band recoveries, calculated survival rates of 1.55 years for males and 1.17 to 2.15 years for females. Mortality is highest over the first winter, probably because young of the year weigh significantly less than adults when they enter hibernation. There are no records, however, of mass die-offs at hibernacula, other than those associated with natural disasters such as floods (DeBlase et al., 1965) or vandalism (Gould, 1970).

Banding studies show that female *M. lucifugus* often move several hundred kilometers between summer roosts and hibernacula (Davis and Hitchcock, 1965; Griffin, 1970; Fenton, 1970a; Humphrey and Cope, 1976). Less is known about movements of males as they do not congregate in large colonies in the summer. The disappearance of winter-banded male *M. lucifugus* in the summer and of summer-banded female *M. lucifugus* in winter has been documented for some time (Griffin, 1940), and is more marked in northern parts of the range. In Ontario many more little brown bats hibernate in abandoned mines than in the scattered caves, and males comprise over 75% of the mine populations but usually 65% of those in caves (Fenton, 1970a).

The fidelity of individuals for specific nurseries or hibernacula could result in isolation of populations, but studies of allozyme variation have not supported this hypothesis. The mixing of populations occurs during swarming (Fenton, 1969) and results in no apparent genetic isolation (Carmody et al., 1971) (see also Behavior).

The flexibility of roosting and feeding habits, and the rapidity with which *M. lucifugus* finds new roosts, strongly suggest that their populations are limited by the availability of roosts, rather

than by food. Further support for this is provided by the fact that *M. lucifugus* clearly cue on the calls of others to find roost sites (see Behavior).

A variety of predators feed on *M. lucifugus*, but none specializes on them. The list of predators is long and includes small carnivores, birds, mice, and snakes (Gillette and Kimbrough, 1970). In most instances the predator appears to take advantage of opportunities associated with concentrations of bats. Some house cats become adept at catching little brown bats (or other species), but this appears to be an individual pattern of behavior; cats may or may not eat their catch (Humphrey and Cope, 1976).

Myotis lucifugus hosts a range of parasites (Ubelaker, 1970) from cestodes (Rausch, 1975), helminths (Nickel and Hansen, 1967), to many arthropod ectoparasites (Anciaux de Faveaux, 1971, 1976). The most common ectoparasites are fleas, bed bugs, and mites. The incidence of infection by ectoparasites varies seasonally and by sex and age group (Fenton, 1970a). It is possible that high levels of infestation cause the deaths of some individuals (Hitchcock, 1965), but there is no evidence of this.

Accidents probably contribute to more mortality in populations of *M. lucifugus* (Manville, 1963) than either predators or parasites. Examples include bats impaled on barbed wire and on burdocks, and animals killed in hibernacula by flood waters. Exposure to pesticides also causes mortality in *M. lucifugus* populations, regardless of whether the poisons are applied directly to control bats or indirectly to their insect food (Kunz et al., 1977). At times of weaning, of migration, and at the end of the hibernation period, bats may be poisoned by high levels of insecticides released by metabolism of fat deposits where pesticides have accumulated (Geluso et al., 1976).

Since *M. lucifugus* is the common house bat in many parts of North America, it has been the target of a variety of control operations. Pesticides, including DDT, do not work effectively to control these bats (Kunz et al., 1977; Barclay et al., 1980); changing the illumination in the colony (Laidlaw and Fenton, 1971) and sealing out the bats (Barclay et al., 1980) are more effective alternatives. Furthermore, the application of pesticides to bat colonies may increase contact between bats and people (Barclay et al., 1980).

A common rationalization for using pesticides to control populations of *M. lucifugus* is that they may carry and transmit rabies. Several studies (see Trimarchi and Debbie, 1977) have shown that the incidence of rabies in *M. lucifugus* is less than 1%, and that there is no clear relationship between rabies in these bats and the incidence of the disease in sylvatic carnivores (Trimarchi, 1978).

Populations of *M. lucifugus* have drastically declined in numbers in many parts of its range, attributable in part to the use of pesticides (whether directly or indirectly applied), control measures in nursery colonies, collecting of bats for experimentation, and disturbance of hibernating individuals. The effect of disturbance on hibernating bats is very important, as it causes them to lose weight, thus decreasing their chances of survival. Curtailing of winter banding operations (already largely accomplished) during the hibernation season could alleviate this problem.

BEHAVIOR. *Myotis lucifugus* produce high intensity (110 decibels sound pressure level reference to 10 micropascals at 10 cm), frequency modulated (FM) calls that last from less than one millisecond (ms) to about 5 ms and sweep from about 80 to 40 kHz, with most of their energy at 45 kHz (Fenton and Bell, 1979; Griffin, 1958). The echoes of these calls are used to detect obstacles and food. During the approach phase (Simmons et al., 1979a), second and third harmonics are present in the calls, but during the feeding buzz or terminal phase, most energy is in the fundamental frequency (47 kHz). There is no sign of the second harmonic although the third is pronounced in the feeding buzz. The rate of call production varies; a cruising bat may produce about 20 pulses per second; while chasing insects or approaching an obstacle, the pulse repetition rate increases to over 50 per s (Griffin, 1958).

Stimulation of the dorsal part of the reticular formation in the midbrain or the lateral part of the central gray matter, using a train of pulses, causes a train of short FM sounds to be produced (Suga et al., 1973). The muscular arrangement of the middle ear (Henson, 1965) and a neural mechanism in the nucleus of the lateral lemniscus produces a synchronized attenuation of the outgoing pulses, as perceived in the central nervous system of the bat (Suga and Shimozaawa, 1974). The attenuation is synchronized between the muscles of the middle ear and the larynx so that a 3 millisecond delay occurs between contraction of the middle ear

muscles and those of the larynx. An incoming pulse has the reverse effect (Jen and Suga, 1976). Neurons in the lateral lemniscus show very short recovery times and facilitation by a second tone burst, suggesting specialization for echo detection. Those in the inferior colliculus show a broader spectrum of recovery times, suggesting a scaling of echo to distance measure. The neurons in the lateral lemniscus and those in the inferior colliculus, as well as some in the auditory cortex, function to process FM signals received by the bats, providing information about direction, range, and speed of the frequency sweep (Suga and Schlegel, 1973). The directional sensitivity of sound reception by *M. lucifugus* is influenced by frequency, with maximum sensitivity to 15° lateral to the median plane at 55 kHz, and 2.5° lateral to this plane at 95 kHz. Interaural pressure shows a linear change with azimuth angle which is also influenced by frequency (Shimozawa et al., 1974).

Little brown bats use the echoes of FM calls to locate and track insects, and the comparison of the echoes to the original calls presumably also allows them to gain information about the surface details of their targets (Webster and Brazier, 1965; Griffin, 1958). Bats are more effective at detecting moving than stationary targets (Jen et al., 1980). The high rates of pulse repetition associated with obstacle avoidance or attempts to catch insects may serve to appraise bats of the last millisecond changes in the position of the target (Fenton and Bell, 1979). Examination of the frequency-time structure of the echolocation calls often permits identification of *M. lucifugus* in the field. It is possible to distinguish little brown bats from other species, including other species of *Myotis*. This is accomplished by using the display from a zero-crossing period meter (Simmons et al., 1979b). Differences in the pattern of the call, more particularly the nature of the FM sweep in time, and the presence and duration of the constant frequency (CF) components are useful characters in this context (Fenton and Bell, 1979).

When on a collision course, feeding *M. lucifugus* will vocalize (honk) at one another (Fenton and Bell, 1979; Barclay et al., 1979) in a manner similar to that described for *Noctilio* by Suthers (1965). These are the only nonecholocation sounds used by this species when feeding in the field. The vocalizations (honks) involve lowering the terminal portion of the FM sweep from 40 to about 25 kHz.

There is evidence that little brown bats use the echolocation calls of conspecifics to locate roost sites (Fenton, 1980). These calls are typically used by males calling from mating sites within hibernacula (Thomas et al., 1979).

Although *M. lucifugus* uses echolocation to find food and to detect obstacles, experiments involving homing by blinded individuals suggest that visual cues are also used for orientation (Mueller, 1968). However, Mueller (1968) noted that day flying bats were very vulnerable to predation by raptors, a situation which could partially explain the poor homing performance of blinded bats. Visual cues are probably important for orientation by little brown bats, as they are for other chiroptera (Williams and Williams, 1970). Nightly departure from day roosts appears to be influenced, at least in part, by changes in light intensity. *Myotis lucifugus* departed significantly earlier from artificially illuminated colonies than from dark colonies (Laidlaw and Fenton, 1971); apparently the difference in light intensity between illuminated roosts and the outside made it seem darker outside.

Congregations of large numbers of individuals in roosts and hibernacula appear to result from the localization of a critical resource rather than from some underlying social structure. There are relatively complex and variable vocalizations associated with mother-young interactions (Gould, 1971; Barclay et al., 1979), but the vocal repertoire of this species is not large (Barclay et al., 1979). Furthermore, despite considerable individual variation in the calls (Fenton, 1977; Barclay et al., 1979), there is no evidence suggesting highly organized social structure within aggregations. The relative lack of interactions between individuals feeding in groups, aside from occasional honks, suggests little social structure in feeding assemblages. Within a colony, individuals are often attracted to the squawk calls of others, but there is no evidence of an alarm or distress call that serves to frighten away or to attract conspecifics (Fenton et al., 1976; Barclay et al., 1979). Social displays that obviously involve visual components have not been observed (Barclay et al., 1979; Thomas et al., 1979); visual displays have been reported from other Microchiroptera (Bradbury, 1977).

During mating the male mounts the female from the rear and, in response to her struggles, may produce a copulation call which appears to appease the female (Barclay and Thomas, 1979).

In Ontario there are two phases to mating activity; an active period when both participants are normothermic, and a passive phase when active males move around the hibernacula attempting to copulate with torpid partners of either sex (Thomas et al., 1979). Most matings occur during the active phase, corresponding roughly to the peak in testosterone levels in plasma (Gustafson and Shemesh, 1976), and implying that active females can store viable sperm (Thomas et al., 1979). Data from studies of sperm stored by females from fall mating until spring fertilization, suggested that active females did not store sperm (Guthrie, 1933; Wimsatt, 1944); but these data do not agree with those from studies of the incidence of mating behavior (Thomas et al., 1979). This question must still be resolved.

The mating system of *M. lucifugus* appears to be random, unstructured, and promiscuous, because neither males nor females can protect any investment made in choosing mates. Males cannot prevent other males from mating with 'their' females while they are torpid; and torpid females are often inseminated by other males during the passive phase. Males appear to mate with as many females as possible, while females also appear to mate more than once (Thomas et al., 1979).

Mating starts in Ontario around the middle of August. There is a peak in mating during the active phase, but the passive phase continues throughout the winter. It is not clear just how much of the mating observed by people banding bats in hibernacula is the result of disturbance and how much occurs naturally. Mating involves adult males and females and subadult females, but subadult males are not sexually mature in their first year (Gustafson and Shemesh, 1976; Thomas et al., 1979).

The active mating period begins during the middle of the swarming period which begins with the arrival of bats at the hibernacula, about an hour after dark. Little brown bats usually feed before arriving at hibernacula, and spend a variable amount of time flying around inside (Davis and Hitchcock, 1965; Hall and Brenner, 1968; Fenton, 1969). During the latter part of July, bats arriving at hibernacula are adult males and nonparous females, but early in August the population includes adult females and subadults of both sexes. At this time, the bats are particularly responsive to calls of conspecifics (Fenton, 1969; Thomas et al., 1979). Bats which swarm at a site may or may not hibernate there, and the recovery rate of banded individuals from swarming to hibernation, or from season to season at any particular site, is usually low (Fenton, 1969). Swarming appears to serve a pre-nuptial function, and may also familiarize young of the year with the locations of suitable hibernacula. The hibernacula may also serve as rendezvous sites for migrating bats. During swarming, individuals may travel considerable distances (Fenton, 1969). Swarming clearly results in a mixing of the populations of bats from different areas, as reflected by studies of allozyme variation conducted in Ontario (Carmody et al., 1971).

When approaching a roosting site, these bats frequently make short circling flights that involve a close approach to, or brief touch down on, the potential landing site. This pattern of behavior is also exhibited by males during the mating season (Thomas et al., 1979), and has been observed in other species of bats. These bats spend a considerable amount of time each day grooming themselves. They use the claws of their hind feet to comb the fur and their tongues and teeth to clean the wing membranes. Grooming behavior commonly takes place in day and night roosts, and is also typical of bats arousing from hibernation. During hibernation, the grooming activity of one individual may dislodge neighbors, leading to falls and possible injury. *Peromyscus* spp., which are common in some hibernacula, often eat injured bats (Trevor-Deutsch, 1973). Calls issued by *M. lucifugus* arousing from torpor are loud and have frequency characteristics that may protect them from attacks by *Peromyscus* spp. (Martin and Fenton, 1978).

GENETICS. The karyotype of *M. lucifugus* is the same as that of other North American *Myotis*: 2n is 44; the fundamental number is 50. The X and Y chromosomes are submetacentric; four pairs of autosomes are metacentric or submetacentric, and 17 pairs are acrocentric (Baker and Patton, 1967). There has been some work on allozyme variation in this species (see also Behavior and Ecology; Carmody et al., 1971).

REMARKS. Much research has been done on *M. lucifugus*, making it one of the better known species of bats, but we still lack a great deal of information about this species. The status of different subspecies needs clarification, particularly in zones

of contact between different subspecies (see also Parkinson, 1979).

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