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Myotis sodalis.

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Myotis sodalis Miller and Allen, 1928

Indiana Bat

Myotis sodalis Miller and Allen, 1928:130. Type locality Wyandotte Cave, Crawford Co., Indiana.

CONTEXT AND CONTENT. Order Chiroptera, Suborder Microchiroptera, Family Vespertilionidae, Subfamily Vespertilioninae, Genus *Myotis*, and Subgenus *Selysius* (Findley, 1972). The genus *Myotis* includes approximately 80 species. *M. sodalis* belongs to the *sodalis* species group which includes *M. sodalis* and *M. nigricans* (Findley, 1972). At present, *M. sodalis* is considered monotypic (Hall, 1962; LaVal, 1970).

DIAGNOSIS. *Myotis sodalis* is often confused with *M. lucifugus*, from which it is distinguished by its short, inconspicuous toe hairs, small but definite keel usually present on the calcar, and smaller foot (9 instead of 10 mm). *M. sodalis* has a slightly more pronounced sagittal crest, a generally narrower braincase (6.4 to 7.2 versus 7.0 to 7.6 mm) and interorbital constriction (3.3 to 4.3 versus 3.6 to 4.4 mm), although overlap does occur in these measurements (Fig. 1). The fur is fine and fluffy in texture, may appear tricolored, and, in contrast to *M. lucifugus*, is not glossy. Bader and Hall (1960), Barbour and Davis (1969), Hall (1962), and Miller and Allen (1928) gave more detailed comparisons with *M. lucifugus*. Characteristics distinguishing *M. sodalis* from other closely related species were discussed by Barbour and Davis (1969) and Hall (1962). The sperm (Forman, 1968) and baculum (Rippy, 1965) of *M. sodalis* are morphologically distinct.

GENERAL CHARACTERS. General appearance is similar to other New World species of *Myotis*. The dorsal fur may range in color from black to light brown (Hall, 1962) but usually appears a dull chestnut gray (Lyon, 1936). The ventral fur is slaty at the base, and grayish-white at the tips with a cinnamon brown tinge, giving it a pinkish-white overall appearance (Miller and Allen, 1928). Ranges of measurements (mm) for selected characters are: forearm, 36.0 to 40.6; ear, 10.4 to 14.8; wingspread, 240 to 267; length of head and body, 41.4 to 49.0; greatest length of skull, 14.2 to 15.0; zygomatic breadth, 8.3 to 9.3; height of braincase, 4.6 to 5.1; length of maxillary toothrow, 5.2 to 5.6; maxillary breadth at M3, 5.3 to 5.8. Measurements of specimens from specific states are available in Glass and Ward (1959), Hall (1962), Layne (1958), and Muir and Polder (1960).

The short, blunt tragus measures slightly less than half the height of the ear. The tail ranges 80 to 81% of the length of the head and body, with the terminal vertebra and half of the penultimate vertebra projecting free of the interfemoral membrane. This membrane is furred on its upper surface as far down as a line joining the extended knees (Miller and Allen, 1928). The calcar is long (approximately 16.5 mm), and usually has a low keel. The foot measures slightly more than half the length of the tibia. Forearm measurements of females average slightly but significantly larger than males (Myers, 1978). This sexual dimorphism is also evident in winter weight measurements, with males averaging 7.1 g and females averaging 7.4 to 7.5 g (Sealander and Young, 1955). LaVal and LaVal (1980) reported a "squared-ear" anomaly in 3 male *M. sodalis* and 12 specimens of 3 other species of *Myotis* in Missouri.

DISTRIBUTION. The distribution of Indiana bats is associated with the major cavernous limestone areas and areas just north of cave regions in midwestern and eastern United States (Hall, 1962). They range from the western edge of the Ozark Plateau in Oklahoma, north to Iowa and southwestern Wisconsin, east to New Hampshire, and south to northern Alabama, with disjunct records from northwestern Florida (Fig. 2). In the winter, *M. sodalis* is apparently absent from Michigan, Ohio and northern Indiana where suitable hibernation sites are unknown (Barbour and Davis, 1969). Although summer distribution is poorly known, existing records show that *M. sodalis* ranges into these more northerly areas and apparently is absent south of Tennessee during this season (Barbour and Davis, 1969; Hall, 1962; Mohr, 1932). Maps of seasonal ranges may be found in Hall (1962). Fig. 2 includes summer records of pregnant or lactating females, and/or juveniles in northwestern Missouri (Easterla and Watkins, 1969; LaVal and LaVal, 1980), Iowa (J. Bowles, pers. comm.), Michigan (Kurta, 1980), and upstate New York (C. Downes, pers. comm.). The occurrence of *M. sodalis* in Wisconsin is documented by only a single specimen (Davis and Lidicker, 1955)—since no subsequent specimens have been found, it is thought now to be absent there (Long, 1976). There is no fossil record for this species.

FORM. Only scattered information is available on the structural or anatomical features of this species. In an osteometric analysis of skeletal elements of the appendages, Bader and Hall (1960) described a pronounced proximal to distal trend of increased variation for those digits of the wing that function in support of the flight membrane. The pattern of variation observed in other elements appeared to be associated with their relative function in locomotion. The authors found no evidence of sexual dimorphism in these trends or measurements. The dental formula is 2/3, 1/1, 3/3, 3/3, total 38.

Vision research included an investigation of the retinofugal fiber connections to the diencephalon and midbrain after unilateral eye enucleation (Crowle, 1974). Also, Suthers and Wallis (1970) provide optical data for *M. sodalis* including refractive errors, entrance pupil size, and various ocular dimensions. Indiana bats have an all-rod retina.

Quay (1970) described the histology of the pineal organ of an adult male *M. sodalis* while Forman (1968) and Rippy (1965) described the characteristic sperm and baculum, respectively, of this species. With the exception of the characteristics outlined in DIAGNOSIS, the general anatomy and morphology of *M. sodalis* is probably very similar to *M. lucifugus*, which has been studied extensively (Fenton and Barclay, 1980).

FUNCTION. *Myotis sodalis* has been the subject of several studies dealing with the physiology of hibernation and arousal. During arousal, the chest muscles warm slightly faster than rectal temperatures so that the mean rectal temperature required for flight is 21.0°C, while the chest muscle temperature at this point is 23.8°C (Studier, 1974). In contrast, Hall (1962) listed body temperatures (Celsius) associated with motor control as follows: end of flight, 39.6°; stopped flying at approximately 36°; flew with difficulty at 28 to 31°; and was unable to walk below 26°. The heart rate of dormant bats at 5°C was found to be 36 to 62 bpm, a high value compared to *M. lucifugus* (24 to 32) and *Lasiurus borealis* (10 to 16) (Davis and Reite, 1967). The heart rate of an active bat is approximately 600 bpm (Lyman, 1970). At any temperature during late hibernation, however, the heart rate is double what it would be at that temperature at any other time of the year (Henshaw, 1965). Also associated with hibernation is the storage of erythrocytes in the spleen, resulting in a 500% increase in spleen weight upon entering hibernation. This is accompanied by only a 41% decrease in the number of erythrocytes in the blood, which suggested to Lidicker and Davis (1965) that some plasma and cells other than erythrocytes may also be stored in the spleen, decreasing the circulating blood volume in hibernating bats. The rapid release of cells from the spleen (in 5 to 10 minutes) may be important in increasing the oxygen supply to the tissues necessary for rapid arousal (Lidicker and Davis, 1965). Reite and Davis (1970) found no differences in mast cell numbers or tissue histamine concentrations in the interfemoral membranes of hibernating and non-hibernating Indiana bats. An increase in number of mast cells would be expected if spontaneous thrombosis were to be prevented during hibernation, but high numbers were found throughout the year.

Basal metabolic rate, thermal conductance, and CO_2 production rate as functions of ambient temperature were discussed by Henshaw (1970). Indiana bats allow body temperature (T_b) to

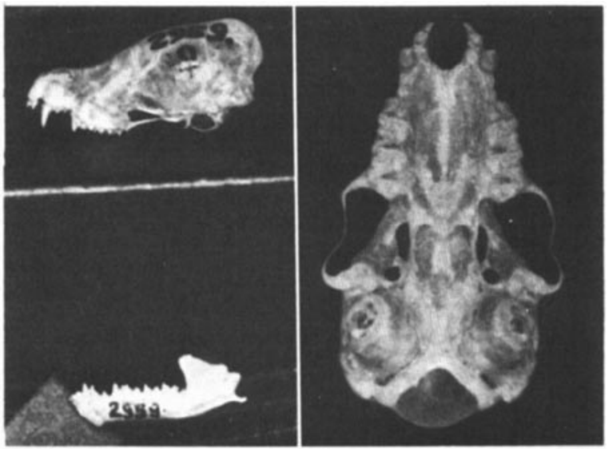

FIGURE 1. The skull of *Myotis sodalis* (Carleton University Museum no. 2959); length of skull, 14.5 mm.

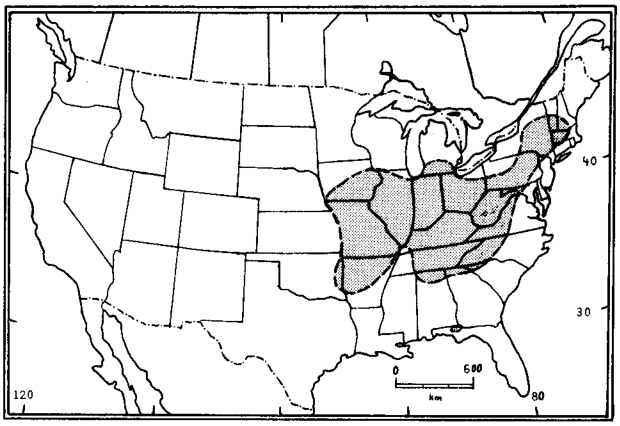

FIGURE 2. The distribution of *Myotis sodalis* (after Barbour and Davis, 1969).

vary directly with the ambient temperature (T_a) from 5°C to 35°C, with the body temperature 1.0 to 1.5°C above ambient. When T_a is 0 to −5°C, they remain torpid but maintain a T_b to T_a differential of up to +5°C and engage in muscular activity resembling shivering. Ambient temperatures over 35°C and the correspondingly high T_b are quite stressful and often fatal, especially during spring arousal (March to May) (Henshaw and Folk, 1966).

Rectal-interscapular temperature differentials during arousal suggest that brown adipose tissue in the subscapular region is important in thermogenesis (Brenner, 1974). Fat content and body weight increase by 50% in September and gradually decrease to a minimum in April, representing a 23 to 24% loss over prehibernation weights (Hall, 1962). *M. sodalis* consumes less water during late than early hibernation and less water overall than *M. lucifugus* during hibernation (Henshaw, 1965). This may be tied to Brenner's (1973) finding that *M. sodalis* loses less metabolic water during torpor than *M. lucifugus*.

Myotis sodalis has been the subject of several studies on the effects of respiratory gases, local pH, various drugs and anesthetics, and carotid artery occlusion on small veins and arteries in the wing (Harris et al., 1976; Hodoval et al., 1971*a*, 1971*b*; Hodoval, 1972; Longnecker et al., 1971; Miller et al., 1972; Miller and Harris, 1975). Investigations into central nervous system information processing revealed echo-ranging neurons in the inferior colliculus (Suga, 1970, 1971), and echo-detecting neurons in the lateral lemniscus (Suga and Schlegel, 1973). Suga (1971) also identified inferior colliculus neurons which responded to amplitude-modulated sounds with specific rise times. Some authors have suggested the use of vision by this species in long distance homing and navigation (see BEHAVIOR). Suthers and Wallis (1970) provided data that support the idea that vision may be important for sensing objects at greater distances at which echolocation is ineffective due to atmospheric attenuation and spreading losses. Quay (1976) described the annual cycle of pinealocyte activity in *M. sodalis*. Seasonal changes in pinealocyte nuclear and nucleolar diameter were found, with a peak in March (corresponding to arousal, ovulation, and dispersal from hibernacula), and the nadir in September prior to hibernation.

ONTOGENY AND REPRODUCTION. Little is known about reproductive and developmental patterns of *M. sodalis* as only a few nursery colonies (Cope et al., 1973; Humphrey et al., 1977) and pregnant or lactating females (J. Bowles, pers. comm.; C. Downes, pers. comm.; Easterla and Watkins, 1969; Kurta, 1980; LaVal and LaVal, 1980; Mumford and Calvert, 1960) have been found. The reproductive cycle is probably similar to that of *M. lucifugus*. Mating occurs at caves during a short interval in the fall, only occasionally during the winter, and to a limited extent in late April (Barbour and Davis, 1969; Guthrie, 1933*a*; Hall, 1962; LaVal and LaVal, 1980). Ovulation, fertilization, and implantation probably do not occur until females leave hibernation. Females segregate from males in the summer, forming small nursery colonies of up to 28 adult females (Humphrey et al., 1977). Maternity colonies have been found under the loose bark of a dead bitternut hickory tree, a living shagbark hickory, and in a dead elm (Cope et al., 1973; Humphrey et al., 1977). Parturition occurs in late June or early July in northwestern Missouri (Easterla and Watkins, 1969), and in eastern Indiana parturition dates of 25 June to 4 July were reported (Humphrey et al., 1977). Females give birth to one young. Pregnant females have been captured carrying embryos ranging from 6 to 39 mm crown-rump length (Easterla and Watkins, 1969; Mumford and Calvert, 1960). Humphrey et al. (1977) reported that juveniles in the Indiana colony were weaned after 25 to 37 days, the first young flying by 21 July, while LaVal and LaVal (1980) captured volant young as early as 12 July in Missouri. In 1974, 25 females in the Indiana colony reared 23 young to flying age and in 1975, 28 females weaned 23 young. Low ambient temperatures may have lengthened the total development time of juveniles at this nursery site (Humphrey et al., 1977). Nothing is known about gestation, prenatal development, prepubertal development, or age at maturity for this species.

ECOLOGY. Since *M. sodalis* was afforded endangered species status under the Endangered Species Act (U.S. Congress, 1973), much effort has been expended to complete our knowledge of its ecology and requirements for survival (e.g., Engel et al., 1976; Humphrey et al., 1977; Humphrey, 1978; Lera, 1978). Declining populations over the past two decades have resulted from natural hazards, human disturbance, and altered microclimate in caves where the bats hibernate. A decrease of 28% over the total range of the species in 15 years (1960 to 1975), with declines in individual states of 8 to 73%, have been reported (Engel et al., 1976; Humphrey, 1978; Myers, 1964). Only seven caves house 87% of the total known population of this species (IUCN, 1978). Such a situation of extreme aggregation increases the impact of local catastrophies such as flooding (DeBlase et al., 1965) on the survival of the species. Management aimed at increasing the population must include protection of existing roosts and habitat, and the restoration of recently destroyed habitat (Belwood, 1979; Engel et al., 1976; Humphrey, 1975, 1978; LaVal and LaVal, 1980; Lera, 1978). Steps toward such management goals have begun.

Winter habitat consists of suitable caves and mines with cool and stable temperatures (see BEHAVIOR) throughout the winter (Humphrey, 1978). Fourteen such sites were listed as critical habitat by Lera (1978). Little is known of the summer habitat requirements of *M. sodalis*. Although small groups of males remain near the hibernacula during summer, encountering diurnal temperatures of 11 to 15°C (Henshaw and Folk, 1966), it is not known where the majority of males go. Females and young are thought to roost in hollow trees and under loose bark of various species of trees (Humphrey et al., 1977), where roost microclimate is subject to the vagaries of weather. Humphrey et al. (1977) suggested that the optimal foraging habitat for *M. sodalis* is the foliage of riparian and floodplain trees, extending to the latter to reduce foraging density after the young of the year become volant. LaVal et al. (1977) described a Missouri population of adult males foraging under the forest canopy on ridges and hillsides and rarely over water. They attributed this difference to the presence of *M. grisescens*, which may have been competitively excluding *M. sodalis* from its optimal foraging habitat, and perhaps even forcing females to migrate northward out of the summer range of *M. grisescens*. Lactating females and juveniles were observed foraging in riparian habitats in northern Missouri (LaVal and LaVal, 1980).

Fecal analysis has revealed variation in prey selection related to reproductive condition by female *M. sodalis* in Indiana (Belwood, 1979). Almost 90% of the diet of pregnant females consisted of small, soft-bodied insects (41.5% Diptera, 30.8% Lepidoptera, and 17.0% Trichoptera). During lactation, a strong preference for moths was shown, constituting over 70% of the food items taken. A similar preference (60 to 95% by volume) was reported for both males and females during this period in Missouri (LaVal and LaVal, 1980), despite the low representation of moths in light trap samples taken in the forest canopy where the bats were feeding. During the post-lactation period, females and juveniles ate mostly moths (53.7%) and some beetles and harder-bodied dipterans (13.3% and 12.5%, respectively), even though dipteran insects were the most abundant numerically (Belwood, 1979). Belwood provided evidence to suggest that this shift to larger and harder-bodied insects by the end of the summer is facilitated by the versatile dentition and jaw characteristics of this species. Analysis of stomach contents revealed a diet consisting of 50% Hymenoptera (Ichneumonidae), 24% Coleoptera, and 19% Homoptera in 4 *M. sodalis* obtained during summer in Indiana (Whitaker, 1972).

Maximum reported longevity of *M. sodalis* was for one bat recovered 20 years after being banded as an adult of unknown age (LaVal and LaVal, 1980), and several individuals of at least 13 or 14 years of age have been recovered (Humphrey and Cope, 1977; LaVal and LaVal, 1980; Paradiso and Greenhall, 1967) Approximately 8% mortality is incurred between birth and weaning (Humphrey et al., 1977). Sex ratios during hibernation within a single cave may appear biased towards males (Griffin, 1940; Hall, 1962; Kirkpatrick and Conaway, 1948), biased towards females, or balanced (Hall, 1962). A balanced population sex ratio was obtained by Hall (1962) averaged over all caves, and by Myers (1964) for several Ozark winter colonies over a 9-year period. Although it has been suggested that winter populations of *M. sodalis* represent two major breeding units associated with major riverways in Kentucky and Missouri (Hall, 1962), restricting gene flow within the species (Hall, 1962; Humphrey, 1978), Hall (1962) found no morphological differences between these populations.

Studies of species diversity were carried out on bat communities of which *M. sodalis* was a part (Humphrey, 1975; Mills et al., 1977). Species with which *M. sodalis* has been associated in various roosting situations include *M. grisescens* (Sealander and Young, 1955), *M. lucifugus* (Cope et al., 1973; Griffin, 1940), *M. septentrionalis* (=*M. keenii septentrionalis*; van Zyll de Jong, 1979) and *M. austroriparius* (LaVal, 1967); and *Eptesicus fuscus*, *M. lucifugus*, and *Pipistrellus subflavus* (Fenton, 1966; Kunz and Schlitter, 1968).

During the winter, much movement between hibernation sites occurs (Fenton, 1966; Hall, 1962; Hardin and Hassell, 1970; Myers, 1964), although this may be related to disturbance (LaVal and LaVal, 1980). Individuals tend to return to the same cave each year to hibernate, but the number returning is usually less than 80% (Griffin, 1940; Hall, 1962; LaVal and LaVal, 1980).

Migration from hibernacula to summer colonies is usually northward to Indiana, Iowa, western Ohio and southern Michigan (Barbour and Davis, 1969; Hall, 1962; Kurta, 1980; LaVal and LaVal, 1980). Most migrations to summer habitat from caves in the Ozarks were less than 36 km north, although some were up to 483 km north (Myers, 1964). Most swarming individuals are migrants, so there is almost a complete turnover each day at swarming sites in the fall (Barbour and Davis, 1969; Cope and Humphrey, 1977).

Homing studies were summarized by Barbour and Davis (1969), Cockrum (1956), Davis (1968), and Griffin (1970). Although this species is purported to have remarkable homing abilities, more information about the home range of these bats is needed before precise interpretation can be made of experimental results reported in the literature. Hassell and Harvey (1965) demonstrated that the bats were able to home without waterways as a route of travel, a navigational aid proposed by Hall (1962).

Documented predators include mink, *Mustela vison* (Goodpaster and Hoffmeister, 1950), the pilot black snake, *Elaphe o. obsoleta* (Barr and Norton, 1965), and a screech owl, *Otus asio* (Humphrey et al., 1977). Ectoparasites include five species of mites, including *Macronyssus crosbyi*, which was reported by Whitaker (1973) as a new host record (Loomis and McDaniel, 1971; Sealander and Young, 1955; Whitaker, 1973). Williams (1962) reported five species of trematodes from the small intestine of *M. sodalis*, four of which were new host records. Adams and Morris (1971) found one trematode and one cestode in the viscera and Kusewitt et al. (1977) reported *Klossiella* sp. sporonts in the kidneys of two individual bats. Rabies has not been reported in *M. sodalis* (Constantine, 1979).

Myotis sodalis demonstrates a relatively high adaptability to captivity; however, the species is relatively difficult to tame and does not reproduce well (Gates, 1936). The survival record for an individual in captivity is 2 years (Orr, 1958). Successful diets were outlined by Orr (1958) and Ramage (1947).

BEHAVIOR. Swarming and parental care were described by Cope and Humphrey (1977) and Humphrey et al. (1977), respectively. Swarming occurs at hibernation sites from mid-August to late October with peaks in early September and mid-October. Most mating occurs at this time (Guthrie, 1933*a*; LaVal and LaVal, 1980). Parental behaviors include "checking," transport of young to more suitable portions of the roost tree, and mother-young foraging flights in tandem as the young become volant.

Cope et al. (1973) described crepuscular flight patterns of *M. sodalis* as direct and along hedgerows parallel to a nearby river. Monitoring of echolocation at this time revealed cruising as opposed to feeding pulses, indicating that these bats were in transit to or from a foraging site. LaVal et al. (1977) also attributed difficulties in trapping Indiana bats to their direct flight pattern. These bats were marked with chemiluminescent tags but were not monitored for feeding pulses. Flight speeds reported by Patterson and Hardin (1969) ranged from an average of 12.8 km/h in a closed hallway to an average of 20 km/h in an open field.

Davis and Barbour (1965) established the use of vision by this species during indoor flight experiments. Untreated bats repeatedly crashed into windows while blinded bats were reluctant to fly and crashed into other objects in the room as well. Barbour et al. (1966) suggested that Indiana bats use vision in long distance homing and navigation. They found that blinded bats did not home effectively over long distances (200 and 322 km north of capture point gave 1.7% returns), but were able to home over shorter distances (8, 24, 40, and 64 km north), although percent returns were lower than controls and those that did return took longer to do so (Barbour and Davis, 1969). Some problems involved in demonstrating the use of visual cues in distance orientation and homing were discussed by Mueller (1968).

Orientation or echolocation calls produced by *M. sodalis* under field conditions are of short duration (0.5 to 1.5 milliseconds), sweeping from approximately 96 kHz to 40 kHz (Fenton and Bell, in litt.).

Myotis sodalis has been called the "cluster bat" because of the large, dense aggregations or clusters they form during hibernation (Guthrie, 1933*a*; Fig. 3). The clusters, which are often irregular in shape and one tier deep, usually are formed on the flat surfaces of ceilings and walls of caves. Clusters form rapidly and recent arrivals do not necessarily remain at the edges. Although suitable clustering sites are well defined and used yearly, there appears to be little continuity in cluster composition both between years and within the same winter (Hall, 1962). Cluster size appears to vary inversely with ambient temperature; smaller transient or active clusters tend to be found in warmer regions of the caves (Hall, 1962; Henshaw, 1970). Clawson et al. (1980) presented a detailed analysis of clustering by Indiana bats in Missouri and concluded that, while some individuals formed small clusters in warmer sites, avoiding some of the risks of disturbance and disaster, others clustered in large numbers in cooler sites that offered metabolic advantages but higher risk of disturbance and disaster.

Bats enter the warm parts of the caves in early fall and forage each night to accumulate fat reserves for hibernation (Hassell, 1967). Females arriving at the hibernacula in October were reported to enter hibernation immediately, whereas males arriving at this time remained active, presumably so that they could copulate with females as they arrived (LaVal and LaVal, 1980). Bats move to cooler parts of the caves during the winter, tending to cluster in areas where temperatures range from 2 to 5°C (Hall, 1962; Henshaw, 1965; Henshaw and Folk, 1966). The water vapor saturation-deficit is usually low (<50 mm Hg), relative humidity ranges from 66 to 95% with an average of 87% (Hassell, 1967), and there is usually some air movement (Henshaw, 1965). *M. sodalis* is a more irritable species than *M. lucifugus*. Individuals awaken throughout the winter so that there are always a few active individuals within warmer areas of the hibernacula (Barbour and Davis, 1969; Henshaw, 1965; Henshaw and Folk, 1966). It is this behavior that led early workers to conclude that this species was not a true hibernator (Guthrie, 1933*b*). The frequency of arousal is unknown, although Hardin (1967) suggested that it occurred every 8 to 10 days. Bats leave the hibernacula from April to early June (Henshaw and Folk, 1966), the females leaving before the males (Cope and Humphrey, 1977; LaVal and LaVal, 1980).

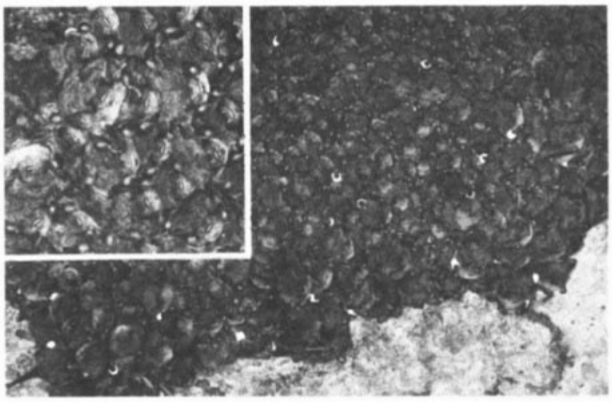

FIGURE 3. A hibernating cluster of *M. sodalis* in a cave near Watertown, New York. Note the dense packing of the bats in the cluster (inset). Some individuals bear reflective arm bands (banded by permission of the New York State Department of Environmental Conservation).

GENETICS. The karyotype of *M. sodalis* is the same as that described for all other North American species of this genus studied. The diploid number is 44, the fundamental number is 50, the X chromosome is submetacentric, 4 pairs of autosomes are metacentric and submetacentric, and 17 are acrocentric (Baker and Patton, 1967). The Y chromosome is undescribed but probably is submetacentric.

REMARKS. Before Miller and Allen described *M. sodalis* in 1928, several authors had identified specimens as *M. lucifugus* (summarized by Miller and Allen, 1928). Mumford and Cope (1964) listed other possible cases of misidentification before 1928.

The generic name *Myotis* means "mouse ear" and the specific name *sodalis* means "comrade or companion," referring to the highly gregarious nature of these animals.

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