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Myotis grisescens.

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Myotis grisescens Howell, 1909
Gray Bat

Myotis grisescens Howell, 1909:46. Type locality "Nickajack Cave, near Shellmound, Marion Co., Tennessee."

CONTEXT AND CONTENT. Order Chiroptera, Suborder Microchiroptera, Family Vespertilionidae, Subfamily Vespertilioninae, Genus *Myotis*, Subgenus *Leuconoe*. The genus *Myotis* includes approximately 80 species. *Myotis grisescens* belongs to the *grisescens* species-group, which includes *M. grisescens*, *M. incautus*, *M. chiloensis*, *M. velifer*, and *M. occultus* (Findley, 1972). *Myotis grisescens* is a monotypic species.

DIAGNOSIS. *Myotis grisescens* is most likely to be confused with *M. lucifugus*, *M. sodalis*, *M. austroriparius*, and *M. septentrionalis*. It can be distinguished by its monochromic fur in which hair shafts are uniformly gray from base to tip; by the wing membrane, which attaches at the ankle of the foot instead of at the base of the toes; and by a notch in the claws of the hindfeet (see illustrations in Barbour and Davis, 1969:63 and Schwartz and Schwartz, 1981: 56). The darker color, taller skull, and attachment of the wing membranes also distinguish it from *M. velifer* (Howell, 1909). The calcar is not keeled. The skull has distinctive sagittal and lambdoidal crests (Fig. 1; Hall, 1981).

GENERAL CHARACTERS. *Myotis grisescens* is one of the largest species of the genus *Myotis* in North America (Figs. 1 and 2). Means of measurements (mm) for selected characters of males and females, respectively (*n* in parentheses) reported by Miller and Allen (1928) are: length of forearm, 43.3 (22) and 43.5 (17); length of head and body, 49.4 (21) and 50.3 (17); length of tail, 37.5 (21) and 40 (17); length of hind foot, 9.8 (22) and 9.9 (17); length of ear, 14.3 (21) and 14.0 (17); condylobasal length, 14.9 (25) and 14.9 (29); length of maxillary toothrow, 6.0 (25) and 6.0 (29); zygomatic breadth, 10 (17) and 9.9 (20); breadth of braincase, 7.7 (24) and 7.7 (29); interorbital constriction, 4.0 (24) and 4.0 (29); maxillary breadth at M^3, 6.3 (25) and 6.3 (29); and mandibular toothrow, 6.3 (25) and 6.3 (29). Sexual dimorphism of a data subset of 8 males and 7 females from Alabama (Miller and Allen, 1928) was not statistically significant (Myers, 1978). LaVal (1967) reported weights ranging from 7.9–9.1 g for males ($n = 11$) and from 8.0–13.5 g for females ($n = 6$). Ears extend to the nostrils or slightly beyond when folded forward and the tragus has a bluntly pointed tip, as in *M. velifer*.

Two color phases were described as "either Dark Mouse Gray above and whitish below, or Cinnamon Brown above and pale buff below" (Glass and Ward, 1959:198), also termed "dusky and russet" by Miller and Allen (1928:82). However, Tuttle (1979*b*) noted that the russet phase occurs when the slate-gray winter coat is faded by ammonia fumes in the summer colony.

DISTRIBUTION. The winter distribution of *Myotis grisescens* is restricted to relatively cold, humid caves in areas characterized by limestone karst at latitudes <39°N (Fig. 3; Tuttle, 1975). The easternmost record of the species is a female captured in Buncombe Co., North Carolina, after being banded in Rhea Co., Tennessee. This suggests that availability of suitable caves, and not mountain ranges, limits eastern dispersal (Tuttle and Robertson, 1969). Other eastern records are from Grainger Co., Tennessee and Scott Co., Virginia (Holsinger, 1964; Mohr, 1933). The first summer colony (4,000–9,000 individuals) from Georgia was reported recently from a small limestone cave in Chatooga Co. (Martin and Sneed, 1990). The most northern summer colony (400 gray bats) was found in an abandoned limestone quarry in Clark Co., southern Indiana (Brack et al., 1984). Summer colonies of *M. grisescens* range as far south as northern Florida, but are declining in that area (Lee, 1976; McNab, 1974; Rice, 1955; Tuttle, 1976*a*; Wenner, 1984). A southward range extension into Pope Co., Arkansas, was recently reported (Nelson et al., 1991). The most western occurrence of gray bats was a summer maternity colony found in a storm sewer in extreme southeastern Kansas (Choate and Decher, 1995; Grigsby, 1965; Hays and Bingman, 1964; Long, 1961). The only other use of a storm sewer by this species was reported from a maternity colony of an estimated 8,000 gray bats in Independence Co., Arkansas (Timmerman and McDaniel, 1992). *Myotis grisescens* reaches its western distributional limit in the Ozark biotic district of Oklahoma (Blair, 1939; Glass and Ward, 1959). In terms of faunal elements, *M. grisescens* is regarded as an "austral" species (Armstrong et al., 1986; Jones and Birney, 1988).

FOSSIL RECORD. The earliest record of *M. grisescens* stems from early middle Pleistocene (late Irvingtonian) of Cumberland Cave, Allegany Co., Maryland (Handley, 1956; Kurtén and Anderson, 1980). Late Pleistocene fossils "that resemble *M. grisescens* most closely" are reported in the Devil's Den Fauna from a limestone quarry at Ladds, Bartow Co., Georgia (Ray, 1967:120); in a cave system near Gainesville, in Levy Co., Florida (Martin and Webb, 1974); and from three caves in Greenbrier Co. and Monroe Co., West Virginia (Handley, 1956). It is possible that *M. grisescens* originated in a temperate climate because, being unable to adjust to a warm winter climate, most gray bats in northern Florida migrate every autumn to colder hibernation caves in Alabama (McNab, 1974; Tuttle, 1975).

FORM AND FUNCTION. Gross and microscopic anatomy of the male reproductive system in *M. grisescens* is similar to that in *M. lucifugus* (Miller, 1939). *Myotis grisescens* has two kinds of interstitial cells in the ovaries. One type is found throughout the ovary except at the periphery and serves to store lipids and steroid droplets in non-pregnant females. The other occurs in the form of small epithelial cells that have little cytoplasm, but include some granular mitochondria that contain phospholipids (Guraya, 1967*a*). Cell components such as yolk, nucleus, mitochondria, and lipid bodies change their location during oocyte growth. This may reflect genetically or environmentally driven "differences in metabolism at every stage of oocyte growth" (Guraya, 1967*b*:211).

The cytology of the ovaries has been thoroughly described and illustrated (Guthrie and Jeffers, 1938). The ovary of *M. grisescens* is rounder and larger (1.5 × 1.5 mm) than that of *M. lucifugus*.

The spermatozoon head of *Myotis grisescens* is larger than in all other species in the genus. Mean dimensions (in μm) of spermatozoa ($n = 10$, range in parentheses) were reported by Forman (1968): length of head, 5.81 (5.78–5.87); length of neck, 0.63 (0.60–0.65), length of midpiece, 17.97 (17.49–18.25), and length of tail 48.14 (47.92–48.92).

Myotis grisescens has been the subject of comparative studies of the fine structure of the tongue and cricothyroid muscle, which is used in echolocation (Reger, 1978). In both organs, fast twitch fibers (type A) are associated with the high speed feeding activity in flight. Tongue muscles were found to be similar to twitch and slow muscle fibers described in other vertebrate skeletal muscles (Reger and Holbrook, 1974).

The annual lipid cycle of *M. grisescens* shows low lipid levels during spring and summer. Fat accumulates gradually in late summer and rapidly in autumn. Increased lipogenesis begins in late July and early August and peaks in October. Total lipid level, measured in percentage of body weight, increased by a factor of 3.8 between May and October (Dodgen and Blood, 1956). The oxidation of protein during hibernation was suggested by high concentrations of blood urea nitrogen (Dodgen and Blood, 1956).

Krulin and Sealander (1972) distinguished three metabolic levels: 1) a level of minimal metabolism required for the conformation

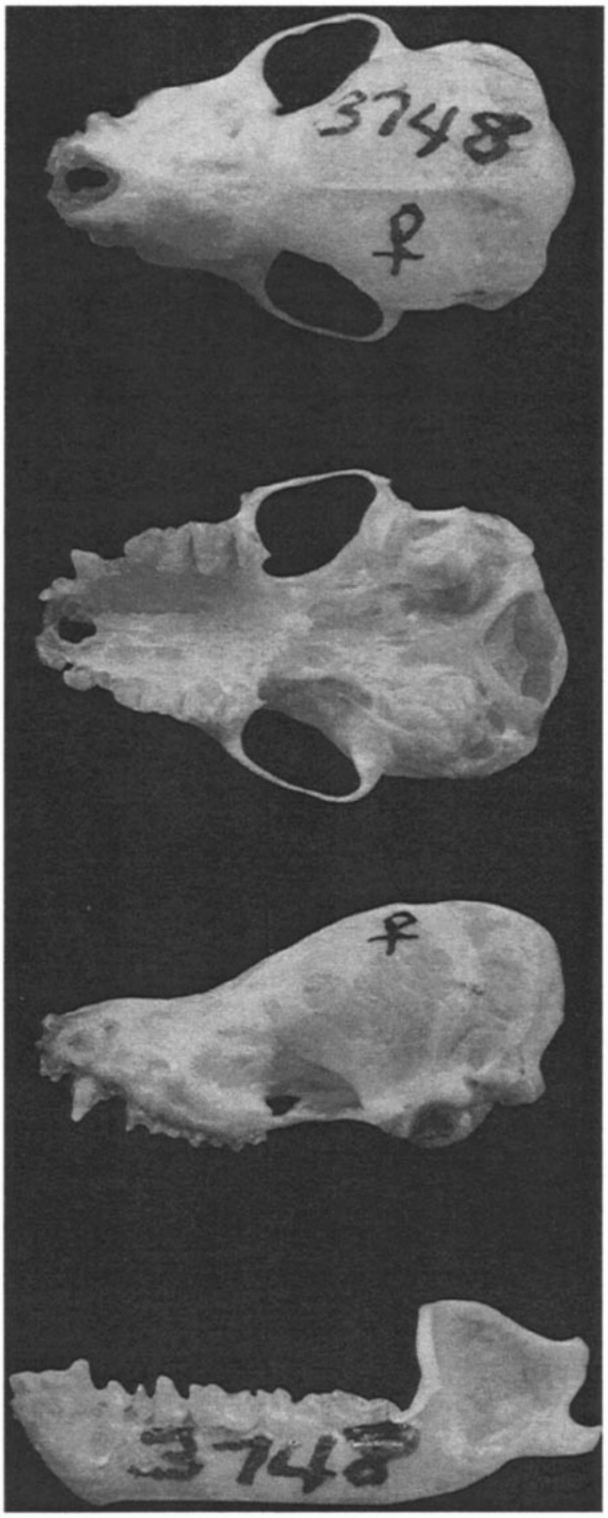

FIG. 1. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Myotis grisescens*, from Pulaski County, Missouri (male, Museum of the High Plains, Fort Hays State University, Kansas, 3748). Greatest length of cranium is 15.5 mm. Photographs by J. Decher.

of body and ambient temperature; 2) the sum of metabolic reactions needed for transient arousals; and 3) the sum of total metabolic reactions needed for full arousal. The minimum amount of fat needed for the gray bat to survive hibernation was calculated as 900 mg fat/g fat free dry weight (FFDW) for a 160-day hibernation period. The utilization rate was calculated to be 5.5 mg/g FFDW per day,

FIG. 2. *Myotis grisescens*, perched on a rock. Photograph taken in July 1978 at Oaks Cave, Tennessee. (Copyright, Merlin D. Tuttle, Bat Conservation International).

which allows enough surplus energy for three arousals. However, an additional 210 mg fat/g FFDW residual fat led to an estimate of 1,110 mg fat/g FFDW minimum pre-hibernation fat deposition level. The rate of fat utilization was found to be greater in females than in males in early and mid-March after final arousal. This rapid mobilization of fat in females may be associated with heat production and "may play a significant role in the activation and maturation of dormant Graafian follicles" (Krulin and Sealander, 1972:346). Whereas most temperate bat species show a decrease in seasonal fat deposition in lower latitudes that have higher mean January temperatures, both *M. grisescens* and *Pipistrellus subflavus* show large seasonal weight changes even in regions with warm climates such as Florida. Near Marianna, Florida, *M. grisescens* was found with maximally ¼ of its total weight as fat. Also in Florida, *M. grisescens* had doubled their weight up to 16.5 g in late summer (Tuttle, in litt.). Similar to *M. lucifugus*, *M. grisescens* is capable of drinking excessively on arousal, with constant urine flow in order to restore its water balance (Krulin and Sealander, 1972).

ONTOGENY AND REPRODUCTION. Male and female reproductive cycles are asynchronous (Saugey, 1978). Spermatogenesis begins in May of the second year of life and is completed by September, preceding ovulation by about 7 months. Seminiferous tubules are in an inactive stage throughout the winter months, after spermatogenesis and after the passage of spermatozoa into the epididymides (Miller, 1939). At Marianna, Florida, male *M. grisescens* had enlarged epididymides from October to February or mid-March, indicating that most copulations occur in fall or early winter and "thereafter the females store spermatozoa" (McNab, 1974:956). In Arkansas, however, copulation was observed in fall, winter, and spring (Saugey, 1978). The average number of growing follicles in *M. grisescens* during hibernation was 41% higher for young females and 91% higher for old females as compared to females of *M. lucifugus* (Guthrie et al., 1951). Follicles do not ripen until the second spring of life, but insemination occurs at the end of the first summer (Guthrie, 1933*b*; Tuttle, 1975). In northwestern Arkansas and southwestern Missouri, delayed fertilization of ova by stored spermatozoa occurs from mid- to late March or even early April (Krulin and Sealander, 1972). In one study, ovulation was first microscopically detected in females collected on 28 March (Saugey, 1978). Implantation of the single embryo almost always occurs in the right uterine horn, which is larger than the left horn (Guthrie et al., 1951). Fetal development takes place throughout April and May. Parturition coincides with the return to maternity caves at times ranging from early May (Florida—Rice, 1955) until late June (Kansas and Missouri—Barker, 1986; Guthrie, 1933*b*), probably depending on weather conditions during the year. Only a few gray bats are still lactating at the end of July (Guthrie, 1933*b*). During

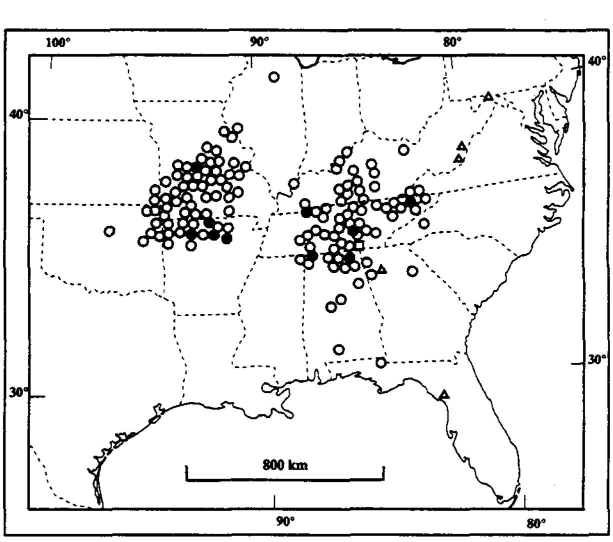

FIG. 3. Distribution of *Myotis grisescens* in the southeastern United States. Symbols correspond to county records. Open circles indicate summer caves. Solid circles indicate hibernation caves. Triangles symbolize fossil records from Allegany Co., Maryland; Greenbrier Co. and Monroe Co., West Virginia (Handley, 1956); Bartow Co., Georgia (Ray, 1967), and Levy Co., Florida (Martin and Webb, 1974). The open square indicates the type locality in Marion Co., Tennessee.

parturition and lactation, retrogressive follicles decrease steadily until the beginning of hibernation, when only "a single vesicular follicle is found in one ovary . . . This follicle persists with but little increase in size until just before its rupture, which normally occurs during April" (Guthrie and Jeffers, 1938:526).

Mean weight of neonates, which are born completely naked with their eyes closed, is 2.9 g (range 2.4–3.4 g—Saugey, 1978; Tuttle, 1975). Juveniles may be born with a full complement of deciduous teeth, which is replaced completely between the third and fourth week when young bats become volant. The sex ratio is 1:1. Juveniles continue to nurse until after they become volant (Saugey, 1978). Tuttle (1975) found that large colonies raise ambient roost temperature, which increases growth rates of juveniles. Thus, in a comparison of six colonies in Alabama and Tennessee, there was a linear increase in growth rate of juveniles in colonies varying from 1,000 to 28,400 adults. Young in a colony of 3,700 adults flew at 24 days of age, but young in the colony of 1,000 adults flew at 33 days of age. Mean individual weight gain in the six colonies ranged from 0.17 to 0.22 g per day. Equally important for growth rates are heat retention properties of caves, such as pockets, small chambers, and surface porosity of the cave ceiling, which enables young to cluster more densely and conserve heat (Tuttle, 1975). For newly volant young, growth rates and survival were found to be inversely proportional to the distance from their roost to the nearest over-water foraging habitat. Young bats weighing <7 g when newly volant have a lowered probability of survival. During the first 20 to 30 days of flight young demonstrate little movement between caves (Tuttle, 1976*b*).

ECOLOGY. Screech owls (*Otus asio*) have been observed preying on gray bats emerging from a roost (Tuttle, 1979*a*). A black rat snake, *Elaphe obsoleta obsoleta*, was found preying on a gray bat in total darkness 85 m inside a cave in Camden Co., Missouri (Easterla, 1967). Tuttle (1976*b*) reported scavenging by raccoons and opossums on juvenile bats that had dropped from a cave ceiling in Tennessee. Crayfish, *Cambarus laevis*, fed on 32 dead young gray bats in a summer colony in Jessamine Co., Kentucky (MacGregor and Westerman, 1982).

Tuttle (1979*b*) estimated that a maternity colony of ≥250,000 individuals may have consumed as much as a ton of insects each night. The gray bat's main prey consists of several genera and at least six species of mayflies (Ephemeroptera: Ephemeridae) and other aquatic insects (Tuttle, 1976*b*). Rabinowitz and Tuttle (1982) found differential digestibility of insects to be a problem in determining prey preferences from fecal pellets in gray bats. For example, in gray bats hand-fed predominantly with mayfly species (Ephemeroptera), these were rarely identifiable in feces relative to other orders of insects eaten. Thus, analysis of 100 fecal pellets from beneath a maternity roost revealed a diet consisting of 34.2% Diptera, 43.3% Coleoptera, 17.5% Lepidoptera, and 0.8% Homoptera and Trichoptera, and only 1.6% Hemiptera and Ephemeroptera. Diptera consisted mainly of the family Chironomidae and Coleoptera of the families Platypodidae, Carabidae, and Scarabaeidae. However, these results were not confirmed by nocturnal observations revealing that gray bats selected foraging areas where mayflies were exceptionally abundant (Rabinowitz and Tuttle, 1982).

Ectoparasites include the mite *Ichoronyssus jonesi* (Acarini: Dermanyssidae), for which *M. grisescens* is the only known host (White, 1966). Other mites found were *Spinturnix americanus* (=*S. iowae*), *S. banksi*, and *Paraspinturnix globosus* (all species of the family Spinturnicidae); one flea, *Myodopsylla collensi* (Siphonaptera: Ischnopsyllidae); the chigger *Trombicula myotis*; and the bat fly *Trichobius major* (Diptera: Streblidae). Internal parasites found were the trematodes *Plagiorchis micracanthum*, *Urotrema scabridum*, *Limatulum oklahomensis*, and *Allassogonoporus marginalis*; the cestode *Vampirolepis christensoni*; and the nematodes *Allintoshius travassosi* and *Trichuroides myoti* (Sealander and Young, 1955; Ubelaker, 1966; Ubelaker and Dailey, 1971).

The optimal foraging habitat of *M. grisescens* is riparian areas where gray bats often fly over bodies of water and in the protection of the forest canopy (Tuttle, 1976*b*). A study of bats over the Meramec River in eastern Missouri suggested that *M. grisescens* competitively excludes *M. sodalis* from the river area, forcing *M. sodalis* to forage away from water (LaVal et al., 1977).

Myotis grisescens is one of the few bats that roosts in caves in both winter and summer. Inside hibernacula in Arkansas, gray bats were associated with clusters of *M. sodalis* (Sealander and Young, 1955), as they were in a hibernaculum in Shannon Co., Missouri, ". . . where groups of *M. sodalis* were covered with *M. grisescens*" (Myers, 1964:80). In Florida, gray bats associated with *Pipistrellus subflavus* in the fall and with *M. austroriparius* in the summer (Lee, 1976; Tuttle 1976*a*).

For hibernation, *M. grisescens* selects the coldest caves of all *Myotis* species found in its range (Tuttle, 1975). Caves used must be capable of trapping cold (but not freezing) air, and <0.1% of caves in the gray bat's range are suitable (Tuttle, 1985). Cave temperatures in Florida are not cold enough for hibernation of this species (McNab, 1974). In Missouri, the two most important hibernacula are characterized by vertical entrance drops of more than 30 m (Myers, 1964). Mean temperatures in three hibernation caves in Tennessee and Alabama ranged from 6.7° to 10.0°C (Tuttle, 1976*a*).

As a summer habitat, this species chooses much warmer caves and mines that usually are located <1–2 km from rivers or other bodies of water (Tuttle, 1976*b*). Mean temperatures, measured 3 cm below the ceiling near maternity roosts, ranged from 13.9° to 26.3°C in six caves in Alabama and Tennessee. Mean relative humidity in the same caves ranged from 86% to 99% (Tuttle, 1976*a*). High temperatures in maternity roosts promote rapid growth of young (Tuttle, 1976*b*). Maternity roosts often are found in high places on nearly horizontal or domed ceilings with surfaces of porous limestone. Heat-trapping in domes is microclimatically advantageous to growth rates of juvenile bats. Ceilings used by clusters of gray bats appear darkly stained by urine and abraded by the claws of bats. In one cave in Alabama, clustered bats pulled out pieces resulting "in numerous pockets where juveniles aggregated in exceptionally dense clusters (Tuttle, 1975:4)." In Arkansas, females choose maternity sites in highly vaulted ceilings above the cave entrance (Saugey, 1978).

Seasonal movements of gray bats were first noted in Missouri (Guthrie, 1933*a*). Every year, gray bats disperse from a few hibernating caves to widely distributed summer caves (LaVal and LaVal, 1980). Gray bats from a hibernation cave in Kentucky moved seasonally to 10 caves in Kentucky, Illinois, and Tennessee, covering an area of 16,905 km² and involving a maximum movement of more than 164 km (Hall and Wilson, 1966). In another study, the average one-way migration distance was 200 km. Maximum migration distances measured were 640 km to an abandoned mine in La Salle Co., Illinois (Elder and Gunier, 1978), and 775 km between a hibernaculum in northern Tennessee and a summer roost in Florida (Tuttle, 1976*a*). The homing ability of 200 gray bats was tested experimentally by moving them in four groups of 50 bats 161 kilometers in all four compass directions from a hibernaculum in Tennessee. Seventeen individuals were recovered at the hibernaculum, most of these (8) having returned from the north (Harvey et al., 1976).

Using data from Tennessee, Alabama, Florida, and Virginia, Tuttle (1976*a*) divided the year into the following activity periods: spring migration (26 March–24 May); summer period (25 May–22 August), including a subunit, the maternity period (4 June–3 July); fall migration (23 August–20 November); and the hibernation or winter period (21 November–25 March). In Kentucky and Missouri, male and female gray bats arrive separately in summer caves from late March to late April (Guthrie, 1933*a*; Hall and Wilson, 1966). Females emerged before males at four hibernating sites in Alabama, Kentucky, and Tennessee. The maternity period in Tennessee and Alabama extends from 4 June to 3 July, with samples of gray bats taken in maternity roosts during that period yielding a mean of 91% females. Bachelor caves are used by adult males and yearlings and are 1–35 km away from the maternity caves. Females and juveniles join males in July and August, causing sex ratios to become more even (Tuttle, 1976*a*). The females were relatively sedentary at maternity caves, whereas males moved among caves as far as 30 km apart in the vicinity of maternity caves (Tuttle, 1976*a*). At Marvel Cave, southwestern Missouri, 311 bats returned from 14 nursery colonies spread over an area of 126,000 km² (Elder and Gunier, 1978). Aggregation of females with young and males prior to fall migration may serve to aid young bats in finding their way to the wintering cave. Females enter hibernation caves first during September or early October. Males remain active until about 10 November. Migration stress may be compensated by ideal conditions in the summer habitat. Gray bat populations are divided into discrete colonies which have developed a strong winter and summer philopatry–pronounced loyalty to a particular set of winter, summer, and transient caves year after year (LaVal and LaVal, 1980; Myers, 1964; Tuttle, 1976*a*).

The oldest recorded gray bat was 16.5 years of age when last captured in December 1976. At that time, it seemed in excellent condition with minimal teeth abrasion and an above-average weight of 12.0 g (Stevenson and Tuttle, 1981). Spring and autumn migrations seemed to be a major source of stress in a study of 71 public recoveries of individual banded bats (out of 40,182 banded bats). All 19 bats recovered during March and April and 17 out of 19 reported for September and October died before or during recovery, whereas only 7 out of 13 bats died that had been recovered in the summer period between May and August. Juvenile mortality was found to be significantly higher than adult mortality (Tuttle and Stevenson, 1977).

Rabies virus is known to occur in *M. grisescens* (Constantine, 1979). Dieldrin-induced mortality, resulting from routine insecticide usage, is believed to have led to the poisoning of *M. grisescens* beneath two maternity roosts in Missouri (Clark et al., 1978). The elimination of mayflies (Ephemeroptera) in areas of their former habitat through aquatic pollution may have a disastrous effect on predators like the gray bat (Tuttle, 1979*a*). Pesticide concentration during lactation led to a 30-fold increase of residue levels in gray bat milk, compared to residue levels in the insects. Gray bats were lethally poisoned by these chemicals at caves in Missouri and Alabama (Clark et al., 1981; 1983*a*; 1983*b*). Dieldrin was banned in 1974 and authorization for the use of heptachlor in Missouri expired in 1981. The short-lived organophosphate insecticides recommended as substitutes were hoped to be safer for bats (Clark et al., 1983*b*). Repeated sampling of dead gray bats, guano, and insects in three counties in Missouri in 1988 and 1989 revealed a lower but continued exposure to residues of chlorinated hydrocarbon pesticides still remaining in the food chain (Clawson, 1991). Metal pollution from a battery salvage plant in Jackson Co., Florida, was not harmful to the gray bat population (Clark et al., 1986), but cadmium in combination with DDD and DDE may have caused gray bat mortality at Cave Springs Cave, Alabama (Clark, 1988). Dead and dying juvenile gray bats collected during routine annual population censuses were found to be a sensitive indicator for monitoring the long-term dissipation of level and geographic extent of the organochlorine residue contamination from a former DDT plant near Huntsville, Alabama (Clark et al., 1988).

A study of 22 summer colonies in Alabama and Tennessee between 1970 and 1976 revealed a 54% decline in just 6 years. The population of these 22 colonies was estimated at 1,199,000 bats prior to 1968, but had declined by 76% to 293,600 bats in 1976. One of the largest maternity colonies declined by 95%. In 1981 (MacGregor and Westerman, 1982), one summer colony remained in Kentucky of six summer colonies and one winter colony reported in 1966 (Hall and Wilson, 1966). Based on estimates by M. D. Tuttle, the total population of the gray bat throughout its range in 1975 was 2,275,000 individuals (Harvey, 1975). During winter 1982, it was estimated that nine hibernacula in Alabama, Arkansas, Kentucky, Missouri and Tennessee contained roughly 95% (1,575,000 bats) of the estimated total gray bat population (Brady et al., 1982). Reasons for the decline are human disturbance and vandalism as well as large-scale habitat destruction and pollution (Clark et al., 1978; Tuttle, 1979*a*). For example, the deaths of several thousand gray bats, including 154 banded individuals, were caused by burning debris after construction work at Marvel Cave, Missouri, in 1971 (Mohr, 1972). Gray bats may move their colonies into less favorable caves if disturbed. Deforestation of areas near cave entrances and between caves and rivers or reservoirs where gray bats feed may have a negative effect (Tuttle, 1979*a*). Field research on this species must be carefully timed and limited (Elder and Gunier, 1978; Tuttle, 1979*a*, 1979*b*). To avoid serious disturbance from stress, it is very important that maternity colonies be left undisturbed between April and mid-July (Gunier, 1971; Tuttle, 1979*a*).

The gray bat was listed as endangered in the U.S. Federal Register on 28 April 1976. Development and implementation of a recovery plan for the gray bat (Brady et al., 1982) has led to cooperation of state agencies and conservation and caving organizations to protect roosting sites. Efforts by these groups resulted in gating of cave entrances, acquisition of caves, and public education in Missouri, Oklahoma, Arkansas, and Tennessee. Numerous smaller roosts, and especially nursery caves, remain threatened, but protective measures proved successful for many larger hibernacula. For example, the United States Fish and Wildlife Service acquired the important nursery caves Blowing Wind Cave and Cave Springs Cave, Alabama, and one of the three most important hibernacula, New Fern Cave, Alabama (Tuttle, 1986). With assistance from Bat Conservation International, The Nature Conservancy acquired Hubbards Cave, Tennessee and Judges Cave, Florida (Tuttle, 1985, 1986). The former is the second most important hibernaculum, which has been secured with the largest cave-entrance gate in the world (Tuttle, 1985), and the latter houses the most important remaining nursery colony in Florida (Tuttle, 1986). The third most important hibernaculum (James Cave, southwestern Kentucky), doubled in size over the last two decades from approximately 100,000 gray bats because of continued cave entrance protection (Bat Conservation International, 1993). Following human disturbance and vandalism, a large (≥250,000 bats) maternity colony at Hambrick Cave, Alabama, had disappeared by 1973 (identified as cave 50 in Stevenson and Tuttle, 1981), but has been reestablished through protective efforts since 1977 (Tuttle, 1986, and pers. comm.). As a result of recent conservation efforts, Blowing Wind Cave, Alabama, and Nickajack Cave, Tennessee, are accessible to visitors between May and September to watch the dusk emergence of 500,000 and 125,000 gray bats, respectively (Tuttle, 1986).

Few attempts to keep gray bats and hand-feed them in captivity have been made. In one case, each of two individuals were kept 21 hours to study prey preferences (Rabinowitz and Tuttle, 1982). In the other case, the length of captivity of a single female gray bat was not reported (Brack and Mumford, 1983). There have been no reports of gray bats breeding in captivity.

BEHAVIOR. Gray bats, like many other species of bats, display behavioral thermoregulation in maternity roosts during the lactation period (28 May–28 June) by their choice of roost sites, increase of colony size, clustering, and by remaining active as long as non-volant young are present (Tuttle, 1975). *M. grisescens* tends to cluster in summer caves (Fig. 4) with mean number found to be 1,828 individuals/m² (range 999 to 2575), depending on roughness of the cave surface and ambient temperature (Tuttle, 1976*a*). Unless they were in torpor, gray bats maintained their roost temperature at an average of 10°C above ambient temperature (Tuttle, 1975).

Several matings were observed in a cave in Jackson Co., Florida, on four occasions between 1230 h and 1400 h CST in October and November. "The males were mounted in the position of coitus *a posteriori* and, unlike the females, were active and usually departed when light was shone upon them" (Lee, 1976:71). In two pairs, the sex of the individuals was confirmed and fur at the neck and upper

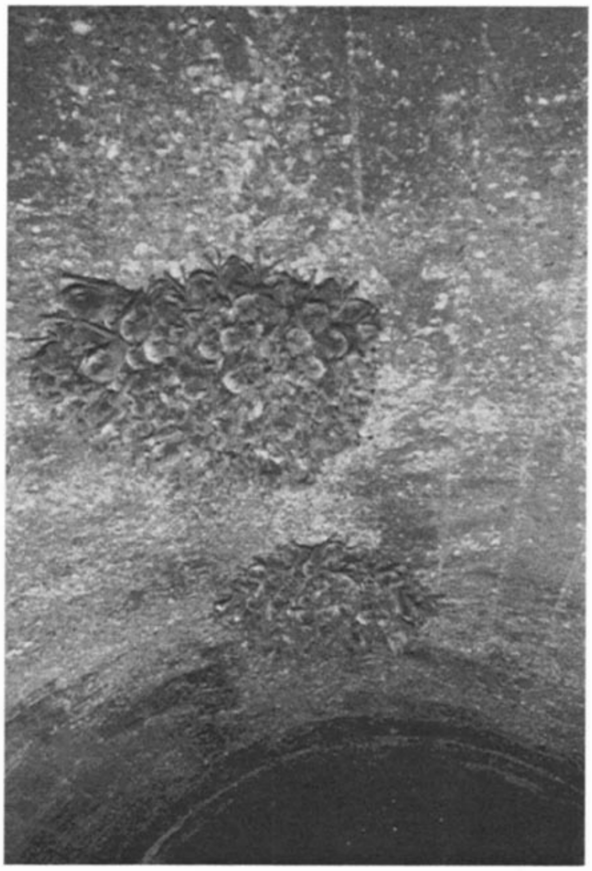

FIG. 4. Roosting bachelor colony of *Myotis grisescens* in a storm sewer in SE Kansas, showing propensity of this bat to cluster. Photograph by J. Decher, 11 August 1988.

back region and around the vaginal openings of females was found to be wet. Apparently, males had held onto them with their teeth. One pair had remained mounted for at least 15 minutes when last checked. In another pair, observed between 0800 h and 1015 h, "... the male's wings were flexed to form a canopy over both animals. Seconds later, the presumed male (sex not confirmed) flew away, leaving a wet-naped, sluggish female behind" (Lee, 1976:71).

When foraging, *M. grisescens* emits frequency-modulated (FM) sounds sweeping down from 100 to 45 kHz (Shimozawa et al., 1974). During the terminal phase and the latter part of the approach phase of searching, these bats emit FM sounds sweeping down about one octave from 50 to 15 kHz at a high repetition rate. The interaural distance for *M. grisescens* and *M. lucifugus* is 9 mm. Interaural time difference (ITD) and pressure difference (IPD) are assumed to be 5 msec and 0.5 dB, respectively. The sound field produced by *M. grisescens* between 55 and 95 kHz shows a main direction emitted 5–10° downward from the eye-nostril line and, at 95 kHz, two prominent side lobes. Directional sensitivity of the echolocation system (DSE) becomes sharper at high frequencies (Shimozawa et al., 1974).

Based on recaptures within a few days in different caves, gray bats traveled from 15.8–52 km per night (Tuttle, 1976*a*). The flight speed for three females, traveling from one cave to another in one night, averaged 20.3 km/h (Tuttle, 1976*a*). The latter value corresponds closely to the average of 21.26 km/h reported earlier for 6 males and 31 females (Kennedy and Best, 1972). In Missouri, LaVal et al. (1977) determined foraging routes by banding bats with light tags and following them by helicopter. Gray bats reached speeds of up to 39 km/h and flew mean distances of 12.5 km (2.5 to 35.4 km) from the site of banding. In southeastern Kansas (Choate and Decher, 1995), bats marked at the roost entrance (storm sewer) with reflective bands and spotlighted from the ground foraged as far away as 14.3 km.

Based on recoveries of banded bats, yearling males and females were found wandering considerably more during the summer than adult bats. But for one colony it could be shown that 91.4% of all summer recoveries of yearling males were within the summer home range of the colony. It was suggested that, through this behavior, young gray bats learned geographical routes and places and became acquainted with their home range (Tuttle, 1976*a*). Gray bats also learn to avoid traps at cave entrances and roosts that have been visited by researchers, a fact that may lead to underestimation of survival (Stevenson and Tuttle, 1981). Gray bats are easily disturbed, and mothers often drop their young in panic if disturbed by light; bats may drown if too many try to fly at once (Mohr, 1933). Female gray bats tolerated humans less than did male gray bats (Tuttle, 1974*a*).

In a study of prey manipulation, a captive female gray bat ate insects up to 2 cm in length and nearly always head first. In about 85% of cases, the elytra were clipped while the insects' thorax was masticated. This captive female preferred click beetles (Elateridae) and snout beetles (Circulionidae) and usually rejected Lepidoptera (Brack and Mumford, 1983). Gray bats observed by a night vision scope at feeding territories, on the other hand, routinely were observed catching moths, although they preferred mayflies (Tuttle, in litt.). In Missouri, gray bats usually foraged below tree top height, sometimes 2 m or lower over water or in adjacent riparian vegetation (LaVal et al., 1977). During exceptionally cold weather, gray bats sometimes limit their foraging activities to forested areas near their caves. After evening emergence, gray bats usually flew in the protection of forest canopy en route to rivers or reservoirs where they fed (Tuttle, 1979*a*). In Kansas and Missouri, males were observed flying directly cross-country without foraging, but never very far from bodies of water (Decher, 1989; LaVal et al., 1977). Bats migrating between Florida and a hibernating cave in northern Alabama were found flying directly between rivers but also deviating from the shortest possible pathway in order to stay near caves (Tuttle, 1976*a*).

Female gray bats are known to exhibit stress-induced abortion (Gunier, 1971). It is unlikely that females routinely carry young in flight, but some do when disturbed (Decher, 1989; Guthrie, 1933*a*; Mohr, 1933; Tuttle, 1975). A wounded, hand-held female emitted cries that attracted several dozen other individuals at a cave entrance (Guthrie, 1933*a*).

GENETICS. The karyotype of *M. grisescens*, which exhibits a diploid number of 44 and a fundamental number of 50, is the same as that described for all other North American species of *Myotis*. There are 4 submetacentric and 17 acrocentric chromosomes, and both the X and Y-chromosomes are submetacentric (Baker and Patton, 1967). *Myotis grisescens* is not known to hybridize with other species.

REMARKS. The name *Myotis* is derived from Greek roots meaning "mouse-ear." The species name *grisescens* refers to the Latin word "griseus" for the gray fur color (Schwartz and Schwartz, 1981). Gray bat guano was mined for the production of nitrates for gunpowder during the Civil War at Hubbards Cave, Tennessee (Tuttle, 1985). We thank E. C. Birney and R. S. Sikes for critically reviewing the manuscript.

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