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Eptesicus fuscus.

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Eptesicus fuscus (Palisot de Beauvois, 1796)

Big Brown Bat

Vespertilio fuscus Palisot de Beauvois, 1796:18. Type locality "Les environs de Philadelphia," Pennsylvania.

Vesp[ertilio]. carolinensis É. Geoffroy St.-Hilaire, 1806:193. Type locality "Carolina"; restricted by Temminck (1840:237) to Charleston, South Carolina.

Vespertilio phaiops Rafinesque, 1818:445. Type locality "the Western Region of the United States"; restricted by Miller (1897:96) to Kentucky.

Eptesicus melanops Rafinesque, 1820:2. Renaming of *V. phaiops* Rafinesque.

Vespertilio arquatus Say, 1823:167. Type locality near "Council Bluff[s]," Iowa; restricted by Hall and Kelson (1959:186) to about 12 mi SE Blair, Washington Co., Nebraska.

Scotophilus cubensis Gray, 1839:7. Type locality "Cuba."

Vespertilio ursinus Temminck, 1840:235. Type locality "sur le bords du Missouri."

Scotophilus carolinensis: H. Allen, 1864:28. Name combination.

Scotophilus fuscus: H. Allen, 1864:31. Name combination.

S[cotophilus]. miradorensis H. Allen, 1866:287. Type locality "Mirador [Veracruz], Mexico."

[*Vesperugo serotinus*] Var. β (*Vesperus fuscus*): Dobson, 1878: 192. Name combination.

Adelonycteris fuscus: H. Allen, 1894:112. Name combination.

[*Vesperugo* (*Vesperus*) *serotinus*] *fuscus*: Trouessart, 1897:108. Name combination.

[*Vesperugo* (*Vesperus*) *serotinus*] *cubensis*: Trouessart, 1897:108. Name combination.

Eptesicus fuscus: Méhelÿ, 1900:206. First use of current name combination.

[*Vespertilio*] (*Eptesicus*) *fuscus*: Trouessart, 1904:77. Name combination.

Eptesicus pallidus Young, 1908:408. Type locality "Boulder [Boulder Co.], Colorado."

Eptesicus wetmorei Jackson, 1916:37. Type locality "Maricao," Puerto Rico.

Eptesicus hispaniolae Miller, 1918:39. Type locality "Constanza, Santo Domingo" (=Dominican Republic).

CONTEXT AND CONTENT. Order Chiroptera, Suborder Microchiroptera, Family Vespertilionidae, Tribe Vespertilionini, Genus *Eptesicus*. The genus *Eptesicus* contains 32 species (Koopman, 1984). Eleven subspecies are recognized (Hall, 1981):

E. f. bahamensis (Miller, 1897:101). Type locality "Nassau, New Providence, Bahamas."

E. f. bernardinus Rhoads, 1902:619. Type locality "San Bernardino Valley (near San Bernardino) [San Bernardino Co.], Cal[ifornia]." (*E. f. melanopterus* Stone is a synonym, not *Vesperus melanopterus* Jentink [=*Eptesicus melanopterus*].)

E. f. dutertreus (Gervais, 1837:61). Type locality "Cuba." (*S. cubensis* Gray is a synonym.)

E. f. fuscus (Palisot de Beauvois, 1796:18), see above (*V. carolinensis* É. Geoffroy St.-Hilaire, *V. phaiops* Rafinesque, *E. melanops* Rafinesque, *V. arquatus* Say, and *V. ursinus* Temminck are synonyms).

E. f. hispaniolae Miller, 1918:39 see above.

E. f. miradorensis (H. Allen, 1866:287), see above (*pelliceus* Thomas is a synonym).

E. f. osceola Rhoads, 1902:618. Type locality "Tarpon Springs [Pinellas Co.], Fl[orid]a."

E. f. pallidus Young, 1908:408, see above.

E. f. peninsulae (Thomas, 1898:43). Type locality "Sierra Laguna, Lower [Baja] California," Mexico.

E. f. petersoni Silva Taboada, 1974:28. Type locality "Cueva los Lagos, Cerro de las Guanábanas, Isla de Pinos," Cuba.

E. f. wetmorei Jackson, 1916:37, see above.

DIAGNOSIS. *Eptesicus fuscus* (Fig. 1) is distinguished from most vespertilionids within its range by having a combination of large, broad head; husky body; short, rounded ears; short, broad wings; two incisors and one premolar in each of the upper jaws; and overall brown pelage. Throughout North America, *E. fuscus* is the only representative of the genus; however, in Central and South America and on the island of Jamaica, the geographic range of *E. fuscus* overlaps that of *E. brasiliensis*, *E. diminutus*, *E. furinalis*, and *E. lynni*. A key to these species, within the zone of overlap, follows (W. B. Davis, 1966; Hall, 1981):

1. Greatest length of skull of *Eptesicus* from tropical latitudes averaging >17.2 mm; length of maxillary tooth row >7 mm; length of forearm usually averaging >48 mm .... *E. fuscus*
   Greatest length of skull of *Eptesicus* from tropical latitudes averaging <17.2 mm; length of maxillary tooth row <7 mm; length of forearm usually averaging <48 mm 2
2. Length of forearm averaging approximately 47 mm; known only from Jamaica in the Greater Antilles .... *E. lynni*
   Length of forearm averaging <44.5 mm; known only from Central and South America; not reported from the Greater Antilles 3
3. Greatest length of skull averaging 16.8 mm; length of maxillary tooth row usually >6.0 mm; M2 averaging >1.8 by 1.6 mm; length of forearm averaging >41 mm .... *E. brasiliensis*
   Greatest length of skull usually ≤16.5 mm; length of maxillary toothrow usually <6.0 mm; M2 averaging <1.8 by 1.6 mm; length of forearm averaging <41 mm 4
4. Greatest length of skull 15.0–17.5 mm; length of maxillary toothrow 5.4–6.0 mm; zygomatic breadth 9.8–11.6 mm; length of forearm 37–43 mm .... *E. furinalis*
   Greatest length of skull 14.3–15.0 mm; length of maxillary toothrow 5.1–5.4; zygomatic breadth 9.4–9.7 mm; length of forearm 36.1–37.7 mm .... *E. diminutus*

GENERAL CHARACTERS. *Eptesicus fuscus* is medium-sized and heavy-bodied with a large head, broad nose, sparse vibrissae, and fleshy lips. Eyes are large and bright. Ears are thick, rounded, short, and when laid forward barely reach the nostrils. Tragus is broad; it narrows distally and bends forward slightly at the tip. Wings are short and broad; length of fifth metacarpal almost

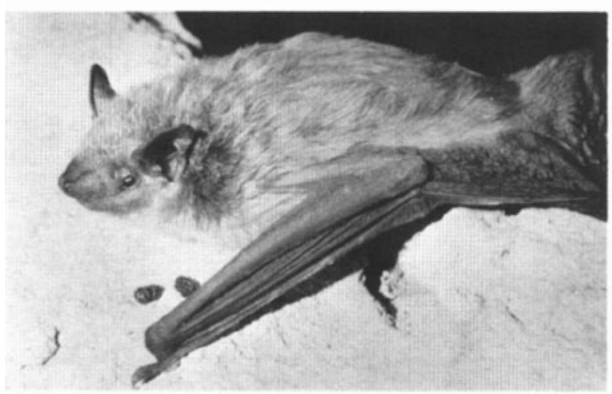

FIG. 1. Photograph of *Eptesicus fuscus pallidus* from Montana. Photograph by T. H. Kunz.

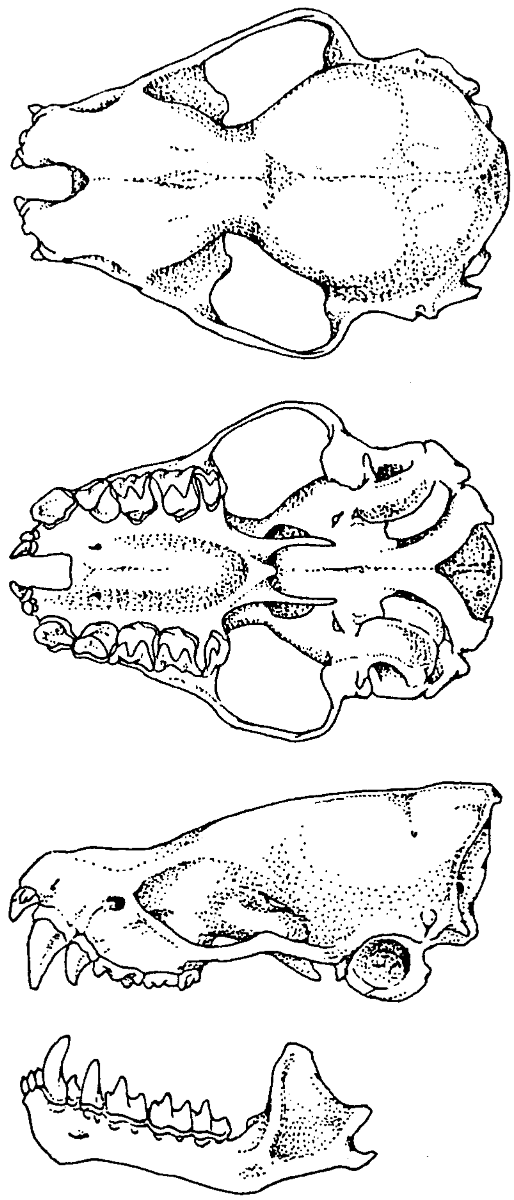

FIG. 2. Dorsal, ventral, and lateral views of the skull and lateral view of the mandible of an *Eptesicus fuscus fuscus* from Lexington, Massachusetts (Boston University 15, female). Greatest length of skull is 18.2 mm. Drawing by J. Love.

equals that of third. The calcar is keeled. Tip of the tail extends 3 mm beyond interfemoral membrane (Miller, 1907).

Pelage is soft, lax, somewhat oily in texture, and >10 mm long mid-dorsally. Ears are furred on medial side of base. The interfemoral membrane has a sprinkling of hairs on the basal one-fourth. Color depends on location and subspecies and ranges from pinkish tans to rich chocolates dorsally with longer hairs having shiny tips; ventral pelage is paler, from near pinkish to olive buff. Naked parts of face, ears, wings, and tail membrane are blackish (Miller, 1907).

Measurements (in mm) are: total length, 87–138; length of tail vertebrae, 34–57; length of hind foot, 8–14; length of ear from notch, 10–20; length of tragus, 6–10; length of forearm, 39–54; length of third metacarpal, 43–50; length of tibia, 17–21; greatest length of skull, 15.1–23.0; zygomatic breadth, 11.1–14.2; breadth of braincase, 7.5–9.6; length of maxillary toothrow, 7.0–9.8; weight of adults, 11–23 g (W. B. Davis, 1966; Hall, 1981). Females are slightly larger than males (Burnett, 1983*a*). Wing and skull size is positively correlated with environmental moisture (Burnett, 1983*b*).

Skull is large and heavily constructed (Fig. 2); rostrum is rounded and somewhat flattened. Palatal emargination is at least as deep as wide. Dental formula is i 2/3, c 1/1, p 1/2, m 3/3. Canine is separated from outer incisor by a space equal to the greatest diameter of incisor. Upper incisors are large with inner one heavier and usually with distinctive secondary cusp. Lower incisors are trifid, subequal in size, closely crowded, and distinctly imbricated; they present a strongly convex row of teeth between canines. Crown of the third lower incisor is wider than crowns on either first or second incisor; crowns on M1 and M2 are narrower than on M3. Hypocones on M1 and M2 are obvious; apex of second triangle of M3 is $<50\%$ the height of the anterior side of first triangle (Hall, 1981).

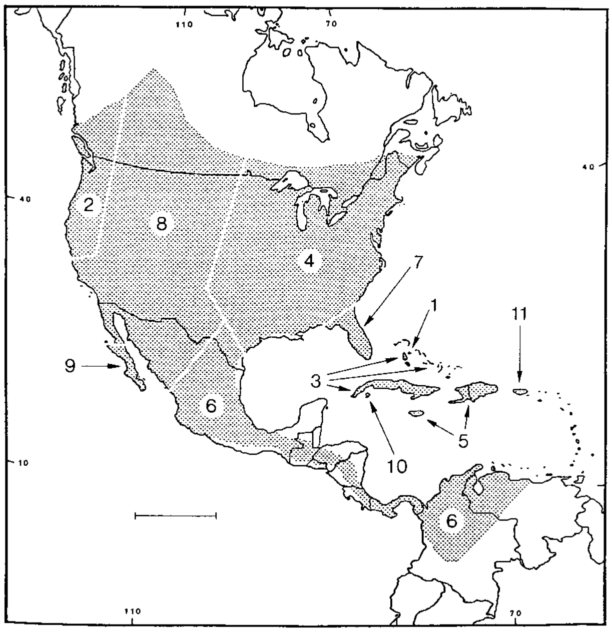

FIG. 3. Geographic distribution of *Eptesicus fuscus* (Hall, 1981; Koopman, 1982; van Zyll de Jong, 1985). Extralimital records from Alaska (Manville and Young, 1965), Brazil (Piccinini, 1974), and Dominica (Hill and Evans, 1985) are not indicated. Subspecies (Buden, 1985; Burnett, 1983*a*) are as follows: 1, *E. f. bahamensis*; 2, *E. f. bernardinus*; 3, *E. f. dutertreus*; 4, *E. f. fuscus*; 5, *E. f. hispaniolae*; 6, *E. f. miradorensis*; 7, *E. f. osceolae*; 8, *E. f. pallidus*; 9, *E. f. peninsulae*; 10, *E. f. petersoni*; 11, *E. f. wetmorei*. Distance bar represents 1,000 km.

DISTRIBUTION. *Eptesicus fuscus* occurs throughout most of North America and Central America and reaches its southern limit in northwestern South America (Fig. 3). The species is resident on some of the Bahama Islands (Buden, 1985) and the Greater Antilles, including Cuba, Hispaniola, Jamaica, and Puerto Rico (Hall, 1981). The only record from the Lesser Antilles is from Dominica (Hill and Evans, 1985). Specimens are known from all Canadian provinces bordering the USA (van Zyll de Jong, 1985), from all the United States except Hawaii (Hall, 1981; Manville and Young, 1965), and from all the states of Mexico except those of the Yucatan Peninsula (Villa-R., 1966). In arid western and southwestern North America, *E. fuscus* generally is restricted to forested highlands. In northern Mexico, it is most prevalent in the eastern and western Sierra Madres bordering the arid midlands of the Mexican Plateau. In Central America, it is found in and along the central mountain chain that dominates the region. South American records are from northern Colombia, northwestern Venezuela, and northern Brazil (W. B. Davis, 1966; Koopman, 1982; Piccinini, 1974).

FOSSIL RECORD. *Eptesicus fuscus* is the most widespread Pleistocene bat in North America. Fossils are known from more than 30 sites in the United States, including Arizona, Arkansas, Florida, Georgia, Kentucky, Missouri, Montana, New Mexico, Pennsylvania, Tennessee, Texas, Virginia, West Virginia, and Wyoming. In addition, Pleistocene fossils are reported from Mexico, the Bahamas, and Puerto Rico. Most fossils are Rancholabrean in age, but some are from 600,000-year-old Irvingtonian faunas in Arkansas, Maryland, Texas, and West Virginia (Dalquest and Carpenter, 1988; Harris, 1985; Kurtén and Anderson, 1980; Morgan, 1985).

FORM AND FUNCTION. The annual molt occurs during late June in Kansas (Phillips, 1966). Pelt insulation is 0.208°C $kcal^{-1}$ h^{-1} m^{-2} in summer and 0.280°C $kcal^{-1}$ h^{-1} m^{-2} in winter (Shump and Shump, 1980). Albinos and individuals with spotted wings are known (Jackson, 1961; Trapido and Crowe, 1942). There are two pectoral mammae; milk consists of 2.5% lactose, 6.2% protein, and 16.4% fat; dominant fatty acids are oleic and palmitic (Kunz et al., 1983). Pararhinal glands are prominent and consist of many small apocrine (sudoriferous) tubules over large sebaceous units (Dapson et al., 1977).

Red blood cell count is 11.96 × 10^6/ml, mean corpuscular volume is 38 μm^3, and hematocrit is 46% (Dunaway and Lewis, 1965). Hemoglobin is not specialized for flight; the Bohr effect is −0.8 for *E. fuscus* compared to −0.7 for *Myotis lucifugus* (Manwell and Kerst, 1966). Serum potassium is 6.06 mg%, and magnesium is 7.13 mg% (Riedesel, 1977). The heart is large, representing 0.9% of fat-free body mass (Rauch, 1973). Lactate dehydrogenase from heart and skeletal muscle have identical isoenzyme profiles (Manwell and Kerst, 1966). Heart mitochondrial structure and enzyme activity does not differ between hibernating and aroused *E. fuscus* (Fonda et al., 1983). Stroke volume is 24 to 30 μl (Rauch, 1973). Heart rate in torpor at an ambient temperature of 5°C is 4 to 62 beats/min (Davis and Riete, 1966; Rauch, 1973). Heart rate when resting at an ambient temperature of 37°C is 450 beats/min. The heart is equally efficient at normothermic or hibernating body temperatures (Harris and Hilton, 1977). Heart rate increases to 1,022 beats/min in flight (Studier and Howell, 1969).

In general, the inferior colliculus is responsible for sound localization and signal analysis, while the superior colliculus is responsible for orienting the bat toward a sound source. The spatial response area of inferior colliculus and superior colliculus neurons to free-field acoustic stimuli increases with increasing sound intensity. The inferior colliculus, but not superior colliculus, neurons are tonotopically arranged. The superior colliculus units are more sensitive to frequency modulated stimuli than to pure tones, but the inferior colliculus units respond equally well to either stimulus (Jen et al., 1987). The response center of auditory neurons in the inferior colliculus changes with pinna orientation, thus aiding in sound localization (Jen and Sun, 1984). Some pathways between the lateral lemniscus and the inferior colliculus are organized as sheets that are precisely related to the tonotopic organization of the inferior colliculus (Covey and Casseday, 1986). The superior colliculus receives auditory projections from the inferior colliculus bilaterally (Zhang et al., 1987). The midbrain controls ultrasound emission, and part of the vocalization control system is located in regions adjacent to the inferior colliculus (Suga et al., 1973). The response center of cerebellar neurons is located in the central portion of the frontal auditory space and may aid in orienting this bat toward a sound source within its frontal gaze (Sun et al., 1987).

Nervous projections from the eye to the brain are similarly arranged in *E. fuscus* and the fruit-eating *Artibeus jamaicensis*, but the projections are better developed in the latter (Cotter, 1985). There are two photopigments—rhodopsin and an unidentified molecule that absorbs at 560 to 580 nm (Hope and Bhatnagar, 1979*a*). Compared to *A. jamaicensis*, *Carollia perspicillata*, and *Desmodus rotundus*, the retina of *E. fuscus* is the least tolerant of light (Hope and Bhatnagar, 1979*b*). Ocular anomalies, such as an unpigmented choroid, undifferentiated retina, and underdeveloped lens are known (Kunz and Chase, 1983). The ocular axis is 45°; the monocular field covers 110°, and the binocular field is 19° (Bell and Fenton, 1986).

The vomeronasal organ is absent (Bhatnagar, 1980). The hyoid skeleton consists of a body and anterior and posterior cornu; the ceratohyal has been lost (Griffiths, 1983). There is no difference in mass of skeletal elements from the right or left appendages indicating that *E. fuscus* is, in effect, ambidextrous (Dawson, 1975). Skeletal abnormalities include polydactyly, deformed vertebrae, and underdeveloped radii (Kunz and Chase, 1983).

Pectoralis mass and protein content increase prior to hibernation and decrease throughout the hibernating period (Yacoe, 1983*a*). Most protein degradation takes place during periodic arousals, and most of the protein goes to support gluconeogenesis (Yacoe, 1983*b*). There are seasonal biochemical adjustments in muscle tissue that favor glucose conservation during hibernation (Yacoe, 1983*c*).

The cricothyroid muscle is greatly hypertrophied and is a powerful glottal constrictor (Griffiths, 1983). Contraction time of the cricothyroid (6.5 milliseconds) is comparable to the fastest contraction times reported for vertebrate muscle (Suthers and Fattu, 1973). An unusual arrangement of tubulofilamentous fasiculi may facilitate the fast action of this muscle (Cho et al., 1972). The cricothyroid creates maximum tension on the vocal cords just before each ultrasonic pulse and relaxes during the pulse; this results in the downward frequency-modulated sweep of the echolocation call. The glottis acts to gate phonation (Suthers and Fattu, 1982).

Mean mucosal surface area of the small intestine is 6.42 cm^2/g; the small intestine represents 98.7% of the surface area and 91.5% of the length of the hind gut (Barry, 1976, 1977). On average, the small intestine contains 34.8 lymph nodules situated in 3.4 Peyer's patches; about 90% of the nodules are located in the distal 40% of the small intestine. There is no lymphoid tissue in the colon-rectum (Barry, 1986). Germinal centers within the lymph nodules of the insectivorous *E. fuscus* are small compared to those of frugivorous and carnivorous bats (Forman, 1974). Defecation begins 90 to 130 min after ingestion, and a meal is completely passed within 24 h (Luckens et al., 1971). Digestive efficiency may be greater at higher ambient temperatures (Pagels and Blem, 1973).

Mean urinary osmotic pressure of wild-caught *E. fuscus* is 1,232 milliosmoles/kg. Mean urea concentration is 343 mg%, but it decreases throughout the dayroosting period; mean potassium and sodium ion concentrations are 62 and 100 milliequivalents/l, respectively (Studier and Rimle, 1980). Maximal urine concentration is 3,130 milliosmoles/kg; the ratio of renal medulla to cortex thickness is 7.0 (Geluso, 1978). This bat can maintain weight, without drinking water, on artificial diets of 19% protein, but not 28% (Carpenter, 1969).

Spermatozoan heads are 6.47 μ in length, oval-shaped, and slightly concave basally. The ratio of length of midpiece to length of head (1.42) is low compared to other Nearctic bats (Forman, 1968). The penis has well-developed accessory erectile bodies (Smith and Madkour, 1980). The baculum is small (0.8 mm in length) and arrow-shaped (Hamilton, 1949).

Neurons that secrete luteinizing releasing hormone have been identified in the forebrain (Anthony, 1987). A specific sex-steroid binding protein exists in the circulation of male *E. fuscus*; the protein has high affinity for androgens and for estradiol (Kwiecinski et al., 1987).

At ambient temperatures <30°C, solitary *E. fuscus* in the laboratory are either torpid with body temperature close to ambient or active with body temperature between 32 and 36°C (Herreid and Schmidt-Nielsen, 1966). For active bats, a thermoneutral point exists at 35°C where oxygen consumption is 0.8 ml g^{-1} h^{-1}. Dilation of blood vessels leading to the wings can significantly lower core temperature (Kluger and Heath, 1970). Some *E. fuscus* resort to panting and saliva-spreading when ambient temperature exceeds 40°C (Holt, 1969). Body temperature in flight is positively correlated with ambient temperature (O'Farrell and Bradley, 1977). In the field, body-surface temperature at rest is dependent on ambient temperature and on reproductive condition (Audet and Fenton, 1988). Unlike other mammals, control of body temperature is independent of the preoptic anterior hypothalamus (Kluger and Heath, 1971).

Brown adipose tissue is widely distributed between the muscles of the dorsal thoracic region, around the neck, and around major vessels of the heart (Hayward and Ball, 1966). During arousal from torpor, there is a marked anterior–posterior thermal gradient with a maximum difference of 18°C between the interscapular region and the colon (Rauch, 1973). Concentrations of ATP in brown adipose tissue and liver decrease during arousal (Dryer and Paulsrud, 1966), while pyruvate and lactate increase in various tissues (Cuddihee and Fonda, 1981). Heart rate increases from 12 to 800 beats/min during arousal (Rauch, 1973). Complete evacuation of the spleen occurs within 6 min after the initiation of arousal (Lidicker and Davis, 1955). In the laboratory, arousal is induced by lowering ambient temperature below 5°C (Davis and Riete, 1966), but *E. fuscus* in the field frequently hibernate at cooler temperatures (Fenton, 1972). Arousal occurs at a faster rate during winter compared to summer (Rauch and Beatty, 1975).

ONTOGENY AND REPRODUCTION. In Maryland, spermatogenic activity peaks in August and declines in September; interstitial cell development is maximal in June (Christian, 1956). Copulation occurs between September and March (Mumford, 1958; Phillips, 1966). In temperate regions, ovulation and fertilization is delayed until after arousal from hibernation (Wimsatt, 1944). Gestation is about 60 days. Litter size is usually one in western North America, but two in the East and in Cuba (Barbour and Davis, 1969;

Silva Taboada, 1979). Females release two to five eggs/ovary, but generally only one full-term fetus is found in either uterine horn indicating uterine control of litter size (Birney and Baird, 1985). There is no specific mention of triplets, but Gates (1937) states that 10 captive females gave birth to 23 offspring. Siamese twinning occurs (Peterson and Fenton, 1969). In Alberta, 74% of the singletons are found in the right uterine horn (Schowalter and Gunson, 1979). Births occur from May to July with a slight trend toward earlier parturition in lower latitudes (Barbour and Davis, 1969).

Females deposit fat early in pregnancy and withdraw some to support accelerated fetal growth late in pregnancy. During lactation, the amount of fat, ash, and ash-free lean dry tissue declines, but postpartum levels are regained by the end of lactation (Stack, 1985). In the wild, females require an average of 48.9 kilojoules of assimilated energy/day during pregnancy and 105.1 kilojoules/day during lactation; water flux is 8.5 and 17.1 ml/day for pregnant and lactating bats, respectively (Kurta et al., in press). Lactation lasts 32 to 40 days (Kunz, 1974).

Newborn *E. fuscus* are naked and almost immobile; eyes and ears open within a few hours of birth (Gould, 1971). Litter mass is 1.6 times greater than predicted for a bat the size of *E. fuscus* (Kurta and Kunz, 1987). In New England, neonates weigh 3.3 g or 20% of the mother's postpartum mass; length of forearm at birth (16.8 mm) is 37% of the adult's. At fledging, body mass reaches 75% of the adult's, and length of forearm, 99%. Juveniles begin to fly at 18 to 35 days of age. Postnatal growth is slower in *E. fuscus* than in *M. lucifugus* (Burnett and Kunz, 1982). Males become sexually mature in their first autumn (Christian, 1956), but not all females reproduce at the end of their first year (Schowalter and Gunson, 1979). Juvenile pelage is duller, darker, and shorter than that of the adults, and juveniles show less differentiation in color between dorsal and ventral hairs (Phillips, 1966).

ECOLOGY. This species greatly decreases in abundance as one moves from the Deciduous Forest Biome to the Coniferous Forest Biome (Kurta et al., 1989). After hibernation, adult females form maternity colonies. Adult males are most often solitary in summer, but they may roost with the females or in all-male colonies (Davis et al., 1968; Barbour and Davis, 1969). In mountainous regions, males occur at higher elevations than females (Fenton et al., 1980). In eastern North America, maternity colonies usually are located in manmade structures such as barns, houses, and churches (Barbour and Davis, 1969); however, colonies in hollow oak (*Quercus*) and beech (*Fagus grandifolia*) trees are known (Christian, 1956; Kurta, 1980). In western Canada, maternity colonies often are found in rock crevices and dead ponderosa pines (*Pinus ponderosa*; Brigham, 1988). *E. fuscus* moves from its roosting location, perhaps abandoning the colony site, when ambient temperature exceeds 33 to 35°C (Davis et al., 1968). Size of maternity colonies varies from 5 to 700 animals, but most colonies in the East contain 25–75 adults (Davis et al., 1968; Kurta, 1980; Mills et al., 1975). Pregnancy rates generally exceed 90%. Reproductive success may be negatively correlated with colony size (Mills et al., 1975). About 10–30% of volant, immature females return to the natal roost the following spring; up to 72% of adult females return (Brenner, 1968; Davis, 1967; Mills et al., 1975).

Foraging occurs throughout the night with most activity within the second hour after sunset (Kunz, 1973). Foraging begins 18 min after sundown in Michigan (Kurta, 1980) but 49 min after sundown in Kansas (Phillips, 1966). Distance from roost to foraging ground averages 1–2 km. Total flight time averages 100 min/night. These bats generally use night roosts other than the main colony site (Brigham, 1988). In terms of foraging habitat, *E. fuscus* is a generalist; it shows no preference for over-water versus over-land sites, edge versus nonedge habitats, areas with versus without canopy enclosures, and urban versus rural environments (Furlonger et al., 1987; Geggie and Fenton, 1985). In forested areas, it begins foraging at 50 m and later descends to 10–15 m (Whitaker et al., 1977). Over a canopy-enclosed stream, median foraging height for *E. fuscus* is 4.9 m compared to 1.5 m for *M. lucifugus*; median height of juvenile *E. fuscus* (3.7 m) is significantly lower than that of adults (5.2 m; Kurta, 1982). Small Coleoptera are the most common prey (Freeman, 1981; Silva Taboada, 1979); elytra and wings may be culled before ingestion (Coutts et al., 1973). Vegetation and nonflying prey make up 4% of stomach contents (Whitaker, 1972). Juveniles feed at a rate of 1.2 g insects/h, while adults capture 2.7 g/h (Gould, 1955).

Lasionycteris noctivagans forages later in areas where *E. fuscus* is common, suggesting competition (Reith, 1980). At a localized food source, a bat, purported to be *E. fuscus*, aggressively forced the larger nighthawk (*Chordeiles minor*) to forage in less desirable areas (Shields and Bildstein, 1979). Aggressive intraspecific actions occur at foraging grounds, but their significance is not known (Fenton, 1980).

Although summer colonies begin to disperse as early as August, many *E. fuscus* do not appear at hibernacula until November (Barbour and Davis, 1969). Females deposit fat, in anticipation of hibernation, one month earlier than do males (Pistole, 1989). Males, however, enter hibernation before females (Phillips, 1966). Bats may enter and leave hibernacula throughout the winter (Mumford, 1958). They rarely move more than 80 km between summer and winter roosts (Mills et al., 1975). Hibernation sites are cooler, drier, and more exposed to air currents than those of *M. lucifugus* (Goehring, 1972; Raesly and Gates, 1987). *E. fuscus* frequently hibernates at ambient temperatures below freezing and is often found within cracks or crevices or beneath rocks in the hibernaculum floor (Barbour and Davis, 1969; Fenton, 1972). It often hibernates in buildings as well as mines and caves (Mills et al., 1975).

Many hibernate singly, but small clusters are common (Mumford, 1958; Nagorsen, 1980). Mean cluster size in Kansas is 3.7 (range, 2–21); males cluster more than females (Phillips, 1966). *E. fuscus* enters hibernation weighing about 21 g and loses 24% of its body mass by April; females lose 0.03 g/day and males, 0.04 g/day (Fenton, 1972). Males make up about 70% of hibernating populations although there is considerable variation among hibernacula (Goehring, 1972). *E. fuscus* in Cuba apparently do not hibernate, but may enter torpor on cool winter nights and may lose >30% of their body mass between October and March (Silva Taboada, 1979).

This bat survives up to 19 years in the wild (Paradiso and Greenhall, 1967). Survivorship is lower than in *M. lucifugus* but similar to *M. leibii* (Hitchcock et al., 1984). Male *E. fuscus* live longer than females (Hitchcock et al., 1984; Kurta and Matson, 1980). Postnatal mortality before weaning is 7–10% (Kunz, 1974). After weaning, mortality factors include failure to store sufficient fat for hibernation (Brigham, 1987), accidents (Walley et al., 1969), inclement weather (Rysgaard, 1942), and predation. Opportunistic predators include common grackles (*Quiscalus quiscula*; Long, 1971), American kestrels (*Falco sparverius*; Black, 1976), various owls (Strigidae; Beer, 1953; Kunz, 1974; Rysgaard, 1942; Silva Taboada, 1979), long-tailed weasels (*Mustela frenata*; Mumford, 1969), house cats, rats (Rysgaard, 1942), and bullfrogs (*Rana catesbiana*; Kirkpatrick, 1982). Man-made chemicals (DDT, DDE, PCB, dieldrin, methyl parathion) are concentrated in milk, embryos, and adult tissues and may cause death (Clark, 1981, 1986; Henny et al., 1982).

Ectoparasitic insects include species of *Basilia* (Guimarães, 1966), *Cimex*, *Myodopsylla* (Lewis, 1978; Whitaker, 1973), and *Nycteridopsylla* (Mitchell and Hitchcock, 1965). The following acarine genera are ectoparasitic on *E. fuscus*: *Acanthopthirius*, *Cheletonella*, *Euschoengastia*, *Leptotrombidium*, *Neotrombicula*, *Ornithodoros*, *Spinturnix* (Whitaker, 1973), *Macronyssus*, *Parasecia* (Dood and Kurta, 1988), *Perissopalla* (Goff and Brennan, 1982), *Neospeleognathopsis* (Mitchell and Hitchcock, 1965), and *Olabidocarpus* (Silva Taboada, 1979; Whitaker, 1973). Density of the macronyssid mite *Steatonyssus occidentalis* increases from 4.6 mites/bat in April to 59.6 mites/bat in July (Miller et al., 1973). The rosensteiniid mite *Nycteriglyphus fuscus* lives in the guano of *E. fuscus* and may be parasitic as well (Dood and Rockett, 1985).

Endoparasitic nematodes include species of *Allintoshius*, *Capillaria*, *Rictularia* (Pistole, 1988), *Cyrnea*, *Litomosoides*, *Physocephalus* (Rutkowska, 1980), and *Seuratum* (Specian and Ubelaker, 1976). *E. fuscus* is the type host for *Maseria vespertilionis*, a nematode found only in subcutaneous tissue near the plantar surface of the rear feet. Infective larvae move from the roost surface into the bats' feet; hence, colonial females are more frequently parasitized than solitary males (Rausch and Rausch, 1983). Cestodes include *Hymenolepis* (Pistole, 1988) and *Vampirolepis* (Zdzitowiecki and Rutkowska, 1980). Parasitic trematodes are species of *Acanthatrium*, *Dicrocoelium*, *Plagiorchis*, *Prosthodendrium* (Blankespoor and Ulmer, 1970, 1972), *Anenterotrema*, *Ochoterenatrema*, *Postorchigenes* (Zdzitowiecki and Rutkowska, 1980), *Allassogonoporus*, *Glyptoporus*, *Limatulum*, *Ochoterenatrema*, *Paralecithodendrium*, and *Urotrema* (Lotz and Font, 1985). Over 20 species of helminths parasitize this bat in Wisconsin alone (Lotz and Font, 1985). Of 464 *E. fuscus* from Indiana, 37% harbored nematodes, 68% had trematodes, and 8% carried cestodes (Pistole, 1988). The protozoan parasite *Trypanosoma hedricki* is found in the blood of *E. fuscus* (Bower and Woo, 1981).

Rabies in *E. fuscus* occurs throughout the United States (Baer and Adams, 1970; Kurta, 1979; Trimarchi and Debbie, 1977; Whitaker et al., 1969), Canada (Rosatte, 1987), and Cuba (Silva Taboada and Herrada Llibre, 1974). Rabies is enzootic at low prevalence in most areas; local epizootics are rare and generally short-lived (Kurta, 1979; Pybus, 1986). The virus infects brown fat, brain tissue, and salivary glands (Bell and Moore, 1960), but the virus is not transmitted across the placenta (Constantine, 1986). Incubation lasts up to 209 days (Moore and Raymond, 1970). *E. fuscus* also may be a vector for St. Louis encephalitis virus (Herbold et al., 1983). The fungus *Histoplasma capsulatum* occasionally is found in the tissues or guano of *E. fuscus* (Bartlett et al., 1982; Hoff and Bigler, 1981).

Many humans object to sharing their homes with *E. fuscus*; consequently, this bat is often the subject of control measures. Introducing lights into the roost area may decrease populations by 41 to 96% (Laidlaw and Fenton, 1971). Application of DDT is ineffective, expensive, and potentially dangerous to the human occupants (Barclay et al., 1980). The most effective measure is sealing roost entrances after bats leave to forage. One-way valves, which allow bats to leave but not re-enter, are effective temporary measures (Frantz, 1986). After eviction, the bats generally move to alternate roosts nearby (Brigham and Fenton, 1986).

Eptesicus fuscus takes well to captivity. Most artificial diets contain mealworms, banana, cottage or cream cheese, and a vitamin supplement (Rasweiler, 1977). Juveniles as young as 6 days may be hand-reared using a stomach catheter (Taylor et al., 1974). The canine teeth undergo severe wear if *E. fuscus* is housed in hardware-cloth cages (Clark, 1976).

BEHAVIOR. *Eptesicus fuscus* has maximum hearing sensitivity over a broad range of 10 to 45 kHz (Dalland et al., 1967). This bat utilizes echolocation for obstacle avoidance and to capture flying insect prey. During the search phase, emitted ultrasounds consist of multiple-harmonic frequency-modulated sweeps that include both broadband and narrowband components. The short narrowband component is lost as the calls progress to the approach and terminal stages (Simmons et al., 1979). In the laboratory, pulse duration is 3–4.2 milliseconds during the search phase and decreases to 0.25–0.60 milliseconds in the late terminal stage; pulse durations are longer in the field (Novick, 1971). Typical echolocation pulses sweep from 48 down to 27 kHz, but call structure varies among individuals and populations (Brigham et al., 1989; Thomas et al., 1987). Volant juveniles (25–29 days old) have longer inter-pulse intervals than adults; immature bats presumably need the longer silent period to process incoming echos (Gould et al., 1981). Some arctiid moths produce clicking sounds that may interfere with information processing by *E. fuscus* in the terminal stages of pursuit (Fullard and Fenton, 1979).

Eptesicus fuscus has been the subject of numerous behavioral discrimination experiments in connection with its echolocating ability. Stationary bats detect 4.8 mm spheres at a distance of about 3 m. Targets that vary in distance by only 1 to 2 cm are differentiated. This bat distinguishes angular differences between vertical bars $\geq 1.5°$ of arc and differences between horizontal bars $\geq 3°$. Deflection of the tragus impairs vertical angle discrimination. When following a moving target, the head is kept aimed at the target's position; *E. fuscus* does not "predict" the target's trajectory, but follows it by pointing the head at the target's last known position. Differences in target surface structure of <1 mm are detected (Suthers and Wenstrup, 1987).

Although *E. fuscus* is less sensitive to low-frequency sounds, it detects and responds to frequencies of 0.5 to 5.0 kHz (Poussin and Simmons, 1982) and may identify prey by their low-frequency flight sounds (Hamr and Bailey, 1985). When leaving a roost in Maryland, *E. fuscus* orients and flies toward sounds of 3 to 12 kHz produced by chorusing cricket frogs (*Acris crepitans*) and stridulating katydids (*Pterophylla camellifolia*); this behavior may be important in locating concentrations of potential prey (Buchler and Childs, 1981).

The most prominent infant vocalization is the isolation call. Initially the call is emitted whenever the young bat is separated from its mother; as the bat develops, the call is emitted less frequently. Mothers respond to the call with an ultrasonic "chirp" (Gould, 1971; Gould et al., 1981). Although the specific cues are not known, mothers recognize their own young and retrieve fallen infants (Davis et al., 1968).

Eptesicus fuscus has a well-documented homing ability. In general, return rate is inversely proportional to distance from the home roost; however, other factors are important. For example, 85% of the *E. fuscus* released 400 km north of their roost returned, but only 6% of those released 400 km to the south found their way home. Returning bats covered the 400 km in 4 to 6 days (R. Davis, 1966).

Vision may be used in long-distance homing. Blinded and control bats return with equal frequency when released 51 km from the roost, but only controls return from 88 km (R. Davis, 1966). Single-point visual acuity is 1° of arc, which is inferior to the few gleaning, frugivorous, and nectarivorous species that have been examined (Bell and Fenton, 1986). This bat detects starlight of moderate intensity (Childs and Buchler, 1981), although its use in long-distance navigation has not been demonstrated. The post-sunset glow in the western sky can be used to determine the correct direction to foraging grounds (Buchler and Childs, 1982). When flying in familiar areas, it may rely on spatial memory (Mueller and Mueller, 1979).

Flight speed is 13–18 km/h in an enclosed space, but 33 km/h in the open (Craft et al., 1958; Patterson and Hardin, 1969). Wingbeat frequency at a speed of 13 km/h is 9.1/s. When swimming, *E. fuscus* travels 0.98 body lengths/stroke (Craft et al., 1958).

When kept in the dark for 6 months, active *E. fuscus* display an endogenous activity rhythm with a period slightly shorter than 24 h (Rawson, 1960). Most arousals from hibernation occur between 1400 and 2000 h indicating a persistent but inexact 24-h rhythm; this rhythm is independent of ambient temperature and the length of the preceding hibernating period (Twente and Twente, 1987).

In the laboratory, *E. fuscus* quickly acquires novel behaviors by observing conditioned animals (Gaudet and Fenton, 1984). In the field, mother and offspring spend considerable time roosting and feeding together; this may facilitate learning by the young (Brigham and Brigham, 1989).

GENETICS. The diploid number of chromosomes is 50, and the fundamental number is 48. Autosomes and the Y chromosome are acrocentric; the X chromosome is submetacentric (Baker and Patton, 1967). Karyotypes do not differ among populations in Puerto Rico, Mexico, and mainland United States (Baker and Lopez, 1970). The DNA content of postkinetic nuclei is greater than in *Rhinolophus*, *Myotis*, and *Miniopterus*, and approximately the same as in *Barbastellus* and *Pipistrellus* (Manfredi Romanini et al., 1975).

REMARKS. The specific epithet *fuscus* means dusky or somber. The generic name *Eptesicus* means "house flyer" (Rafinesque, 1820).

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