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MAMMALIAN SPECIES No. 261, pp. 1-9, 3 figs.

Blarina brevicauda.

By Sarah B. George, Jerry R. Choate, and Hugh H. Genoways

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Blarina Gray, 1838

Blarina Gray, 1838:124. Type species *Corsira (Blarina) talpoides* Gray (=*Sorex talpoides* Gapper = *Sorex brevicaudus* Say), by original designation. Elevated to generic rank by Lesson, 1842:89.

Brachysorex Duvernoy, 1842:37–41. Type species *Brachysorex brevicaudus* Duvernoy (=*Sorex brevicaudus* Say), by original designation.

Talposorex Pomel, 1848:248. Type species *Talposorex platyurus* Pomel (=*Sorex brevicaudus* Say), by original designation.

Anotus Wagner, 1855:550–551. Type species *Sorex carolinensis* Bachman, by original designation.

CONTEXT AND CONTENT. Order Insectivora, Family Soricidae, Subfamily Soricinae, Tribe Blarinini (Repenning, 1967). The genus *Blarina* includes three species. Key characters used herein were adapted primarily from George et al. (1981, 1982) but with modification based on data presented by Braun and Kennedy (1983), Genoways and Choate (1972), Moncrief et al. (1982), and Tate et al. (1980).

1 Size large (total length usually greater than 110 mm; occipito-premaxillary length (Choate, 1972*a*) usually greater than 20.5 mm if east of Mississippi River, usually greater than 21.5 if west of Mississippi River); karyotype 2n = 48 to 50, FN = 48 .... *B. brevicauda*

Size smaller (total length usually less than 110 mm; occipito-premaxillary length usually less than 20.0 mm if east of Mississippi River, usually less than 21.5 if west of Mississippi River); karyotype other than indicated above 2

2 (1) Size smallest in genus (cranial breadth as small as 9.6 mm, usually less than 11.0); karyotype 2n = 50 to 52, FN = 52 (in the subspecies *B. c. peninsulae*) or 2n = 46, 39, 38, or 37, FN = 45 or 44 (in *B. c. carolinensis*) .... *B. carolinensis*

Size larger (cranial breadth as great as 12.2 mm, usually greater than 10.5); karyotype 2n = 52, FN = 60 to 62 .... *B. hylophaga*

Blarina brevicauda (Say, 1823)

Northern Short-tailed Shrew

Sorex brevicaudus Say, 1823:164. Type locality west bank of Missouri River, approximately 2 mi E Ft. Calhoun, formerly Engineer Cantonment, Washington Co., Nebraska (Jones, 1964: 68).

Blarina brevicauda: Baird, 1858:42; first use of current name combination.

Sorex talpoides Gapper, 1830:202. Type locality between York and Lake Simcoe, Ontario.

Sorex dekayi Bachman, 1837:377. Type locality New Jersey. The nomenclatorial history of this name and "*Sorex dekayi* De Kay" were reviewed by Handley and Choate (1970).

Galemys micrurus Pomel, 1848:249. A new name proposed for "*Sorex dekayi* De Kay" (Handley and Choate, 1970).

Blarina angusticeps Baird, 1858:34. Type locality Burlington, Chittenden Co., Vermont. Regarded by Merriam (1895) as based on a deformed skull (Bole and Moulthrop, 1942).

Blarina costaricensis J. A. Allen, 1891:205–206. Type locality supposedly La Carpintera, Costa Rica, but assumed by Merriam (1895) to have been somewhere in Upper Mississippi Valley, probably Iowa (Allen, 1897; Bole and Moulthrop, 1942).

Blarina telmalestes Merriam, 1895:15. Type locality Lake Drummond, Dismal Swamp, Norfolk Co., Virginia.

Blarina simplicidens Cope, 1899:219. Type locality Port Kennedy Cave (a pre-Wisconsinan local fauna), Montgomery Co., Pennsylvania.

Blarina brevicauda ozarkensis Brown, 1908:170. Type locality Conard Fissure (a pre-Wisconsinan local fauna), Newton Co., Arkansas. Elevated to specific rank by Graham and Semken, 1976:434.

Blarina fossilis Hibbard, 1943:238. Type locality Rezabek gravel pit (a pre-Wisconsinan local fauna), Lincoln Co., Kansas.

CONTEXT AND CONTENT. Context is given above in the generic account. Eleven Recent subspecies of *B. brevicauda* (exclusive of *B. carolinensis* and *B. hylophaga*), referable to two semispecies (Jones et al., 1984), currently are recognized (Hall, 1981; Handley, 1979):

B. b. aloga Bangs, 1902:76. Type locality West Tisbury, Martha's Vineyard, Dukes Co., Massachusetts.

B. b. angusta Anderson, 1943:52. Type locality Kelly's Camp, Berry Mountain Brook, near head of Grand Cascapedia River, Gaspe Co., Quebec, about 1,600 ft.

B. b. brevicauda (Say, *in* Long, 1823:164), see above.

B. b. churchi Bole and Moulthrop, 1942:109. Type locality Roan Mountain, Mitchell Co., North Carolina.

B. b. compacta Bangs, 1902:77. Type locality Nantucket, Nantucket Co., Massachusetts.

B. b. hooperi Bole and Moulthrop, 1942:110. Type locality Lyndon, Caledonia Co., Vermont.

B. b. kirtlandi Bole and Moulthrop, 1942:99. Type locality Holden Arboretum, Lake and Geauga counties (the county line bisects the type locality), Ohio.

B. b. manitobensis Anderson, 1947:23. Type locality Max Lake, Turtle Mountains, Manitoba, "latitude a little north of 49th parallel, longitude about 100 degrees west; altitude about 2,100 feet."

B. b. pallida R. W. Smith, 1940:223. Type locality Wolfville, Kings Co., Nova Scotia.

B. b. talpoides (Gapper, 1830:202), see above.

B. b. telmalestes Merriam, 1895:15, see above.

DIAGNOSIS. The Nearctic genus *Blarina* includes the nearly uniformly silver to black (often with brown tips on hairs), short-tailed shrews having five unicuspidate teeth in each upper jaw (Fig. 1). The dental formula is as in the genus *Sorex*: falciform incisor, five unicuspids, the fourth premolar, and three molars in each upper toothrow; procumbent incisor, one unicuspid, the fourth premolar, and three molars in each lower toothrow, total 32 (Choate, 1968, 1970, 1975). The genera *Blarina* and *Sorex* readily can be distinguished externally by the relatively much shorter tail of the former (20% of total length is typical for *Blarina*, whereas more than 40% is usual for *Sorex*). *Blarina* can be distinguished from *Cryptotis* in that the latter lacks one unicuspid (30 total teeth in *Cryptotis*, 32 in *Blarina*; Hall, 1981).

Blarina brevicauda is the largest species in the genus (Genoways and Choate, 1972; George et al., 1981; Graham and Semken, 1976; Moncrief et al., 1982). Its geographic range (Fig. 2) lies north of the ranges of *B. hylophaga* (in the west) and *B. carolinensis* (in the east), from which it usually can be distinguished by its greater size. In southern Iowa, northern Missouri, and northeastern Kansas, however, small individuals of *B. brevicauda* may fall within the range of measurements of *B. hylophaga* (Moncrief et al., 1982). Therefore, the most diagnostic character of *B. brevicauda* is its karyotype: FN = 48, 2n = 48 to 50 (George et al., 1982).

GENERAL CHARACTERS. *Blarina brevicauda* is a relatively large, robust shrew (Fig. 3). Its external ears are inconspicuous and concealed by pelage and its eyes are minute. The snout

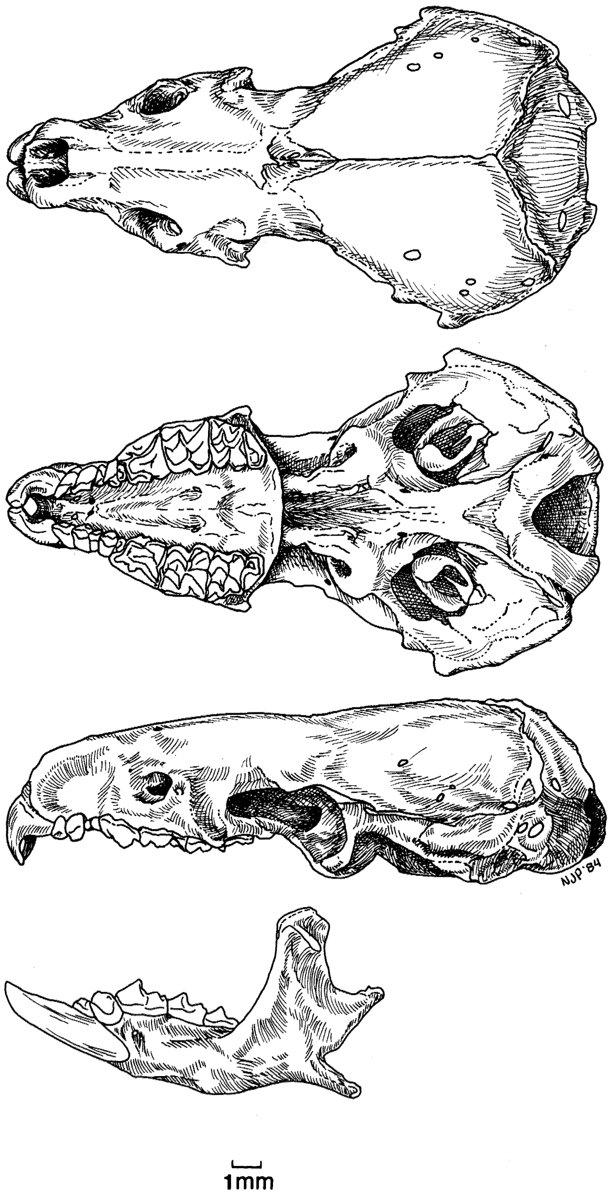

FIG. 1. Dorsal, ventral, and lateral views of cranium and lateral view of lower jaw of *Blarina brevicauda* (CM 50584, male, from Round Hill Regional Park, 13.7 mi S, 9.1 mi E Pittsburgh, Allegheny Co., Pennsylvania). Drawn by N. J. Perkins.

is pointed and somewhat proboscis-like but is comparatively shorter and heavier than in other shrews. The tail is noticeably hairy and in adults is faintly to indistinctly bicolored. Feet are pentadactylous and are relatively broader and stronger than those of all but the most fossorial of other American shrews (Choate, 1970). Dorsal pelage is short, soft, and mole-like in winter, when it often has a dark slate color; ventral pelage sometimes appears paler, at least in part because ventral fur is shorter and denser. Summer pelage is shorter and slightly paler than winter pelage and sometimes is nearly indistinguishable from the short, fuzzy, juvenal pelage. The skull is more massive and angular (Fig. 1) than those of other American shrews and is characterized (in adults) by prominent ridges and processes (Jackson, 1961:43). Teeth are pigmented (deep chestnut in color) and exhibit a relatively unspecialized soricid configuration: "first upper incisors incumbent with tips curved or hooked ventrad and . . . possessing a 2nd . . . unicuspidlike conule . . . ; all other incisors, canines, and all [but the fourth] premolars . . . unicuspid; crowns of upper molars W-shaped" (Hall, 1981:24). Other dental and mandibular characters of shrews were described and illustrated by Repenning (1967).

Nestling short-tailed shrews grow rapidly, and they attain es-

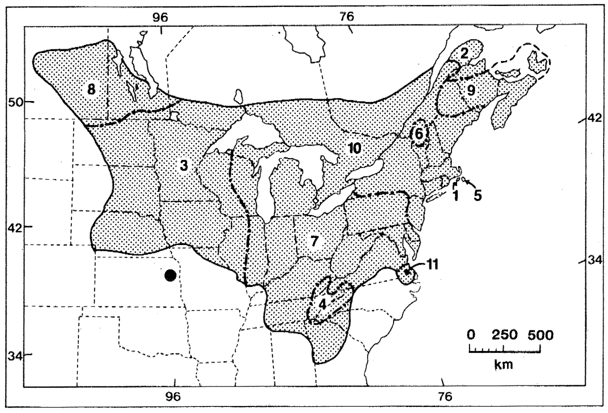

FIG. 2. Map showing the geographic range of *Blarina brevicauda*. Subspecies are: 1, *B. b. aloga*; 2, *B. b. angusta*; 3, *B. b. brevicauda*; 4, *B. b. churchi*; 5, *B. b. compacta*; 6, *B. b. hooperi*; 7, *B. b. kirtlandi*; 8, *B. b. manitobensis*; 9, *B. b. pallida*; 10, *B. b. talpoides*; 11, *B. b. telmalestes*. The dot in northeastern Kansas represents an apparently isolated population of *B. b. kirtlandi*.

sentially adult size (but not necessarily mass; Dapson, 1968) before they become susceptible to trapping (Guilday, 1957). Accordingly, most authors have opted to disregard variation with age in analyses of morphometric variation (Choate, 1972*a*). Certain authors (Baumgardner and McPherson, 1985; Guilday, 1957; Jackson, 1961) have asserted that males average slightly larger than females in external, cranial, and postcranial measurements, whereas others (Choate, 1972*a*) have found little or no secondary sexual variation in the species.

Ranges and means (in parentheses) of selected external and cranial measurements (in mm) of samples from Nebraska (Jones, 1964), Iowa (Bowles, 1975), Illinois (Ellis et al., 1978), Pennsylvania (males only, Guilday, 1957), and Connecticut (males only, Choate, 1972*a*) are as follows: total length, 125 to 141 (132.4), 120 to 138 (125.3), ———, 106 to 126 (117.2), ———; length of hindfoot, 16 to 18 (17.0), 14 to 17 (15.8), ———, 13 to 15 (14.0), ———; cranial breadth, 12.8 to 14.0 (13.5), 12.3 to 13.8 (13.1), 11.5 to 12.6 (12.1), 11.8 to 13.4 (12.5), 11.9 to 13.2 (12.6); maxillary breadth, 8.2 to 9.1 (8.7), 8.2 to 8.8 (8.5), 7.3 to 8.0 (7.6), 7.0 to 8.4 (7.8), 7.2 to 8.1 (7.7). Ranges and means of cranial measurements (in mm) of 25 specimens of *B. b. brevicauda* from Nebraska and 23 specimens of *B. b. kirtlandi* from Ohio (Moncrief et al., 1982) are as follows: occipito-premaxillary length, 23.1 to 25.2 (24.0), 20.8 to 23.0 (21.5); P4–M3 length, 6.3 to 6.8 (6.6), 5.6 to 6.0 (5.9); cranial breadth, 12.6 to 14.0 (13.5), 11.5 to 12.6 (12.0); breadth of zygomatic plate, 2.3 to 3.1 (2.7), 2.0 to 2.6 (2.3); maxillary breadth, 8.0 to 9.1 (8.7), 7.1 to 7.8 (7.6); interorbital breadth, 5.9 to 6.7 (6.2), 5.3 to 5.8 (5.5); length of mandible, 13.3 to 14.4 (13.8), 11.6 to 13.0 (12.1); height of mandible, 7.4 to 8.2 (7.9), 6.3 to 7.1 (6.6); articular breadth, 2.8 to 3.2 (3.0), 2.3 to 2.7 (2.4).

DISTRIBUTION. *Blarina brevicauda* occurs throughout much of the north-central and northeastern United States and southern regions of adjacent Canadian provinces (Fig. 2). Marginal records were identified by Hall (1981), but he regarded *B. carolinensis* as only subspecifically distinct from *B. brevicauda*, *B. hylophaga* as a synonym of *B. carolinensis*, and *B. b. telmalestes* as a distinct species. The distribution of *B. brevicauda* overlaps with that of *B. hylophaga* in southern Iowa, northern Missouri, northeastern Kansas, and possibly southeastern Nebraska (Moncrief et al., 1982), and with that of *B. carolinensis* in central Tennessee (Braun and Kennedy, 1983), southern Illinois (Ellis et al., 1978), eastern Virginia (Tate et al., 1980), western North Carolina and Georgia, and eastern Alabama (French, 1981).

FOSSIL RECORD. *Blarina brevicauda* or an ancestral species probably arose from the blarinine stem in the middle or late Pliocene. The earliest record of the genus is represented by specimens of the *talpoides* semispecies of *B. brevicauda* from late Blancan (early Pleistocene) faunas in Kansas. The *brevicauda* semi-

FIG. 3. Photograph of a feeding *Blarina brevicauda*. Photograph by Roger W. Barbour.

species of *B. brevicauda* appeared later in the early Pleistocene, perhaps during the Kansan glacial, but before the origin of the two other species of *Blarina* (*B. carolinensis* in the mid-Irvingtonian and *B. hylophaga* after the Wisconsinan glaciation). Continuity of gene flow between the two semispecies of *B. brevicauda* during the Pleistocene and Holocene and the absence of fixed chromosomal differences between the semispecies apparently prevented speciation of these phena (Jones et al., 1984).

FORM. Merriam (1895:11) described the pelage of *B. brevicauda* as "sooty-plumbeous above, becoming ashy-plumbeous below, varying with the light." Findley and Jones (1956) described three molts. The first, postjuvenal molt does not occur until the shrew is essentially of adult size. The fuzzy juvenal pelage sheds initially in the head region and proceeds caudad; the new pelage (whether long, silky winter fur or shorter summer fur) is determined by the time of year in which the shrew is born. Molt from summer to winter pelage proceeds in a tail-to-head direction in both first- and second-year animals and most often is seen in October and November. Spring molt can occur at any time between February and July; in females it is in a head-to-tail direction, whereas in males it is more irregular (Findley and Jones, 1956). Albinistic *Blarina* have been reported from Delaware, Indiana, New York, Pennsylvania, Vermont (Williams, 1962), and Ohio (Svendson and Svendson, 1975).

Blarina brevicauda possesses three dermal scent glands, one ventral and one on each flank. Sweat glands seem to be the principle component of the lateral glands, whereas sebaceous tissue is more pronounced in the ventral gland (Pearson, 1946). Scent glands are well developed in both males and females; they increase in size in males concomitant with testicular enlargement in spring and autumn (Eadie, 1938) and become smaller in females during estrus, pregnancy, and lactation (Pearson, 1946). Eadie (1938) suggested that scent glands might serve as a means of protection; the musky odor they produce is distasteful to many carnivores, and the abdominal skin is associated closely with the underlying muscles, possibly to facilitate secretion when a shrew becomes excited or upset. The glands also might be used for marking territories, thus serving to separate shrews at times other than during the breeding season (Pearson, 1946); however, the sense of smell is considered to be poorly developed (Schwartz and Schwartz, 1981).

The eye of *B. brevicauda* is degenerate (Gaughran, 1954; Ryder, 1890). It and the optic nerve are diminutive and, although slight motion is possible, the reduced ocular muscles do not arise directly from the skull. Vision probably is limited to perception of light (Schwartz and Schwartz, 1981). The lachrymal gland is much larger than the eyeball, and its duct opens into the conjunctival cavity. The gland has its own investment of striated voluntary muscles, suggesting that the shrew can compress the gland voluntarily, secrete over the eyeball, and wash away dirt that might accumulate there during burrowing activity.

There is controversy about the dental formula of short-tailed shrews. Merriam (1895) described it as i 4/2, c 1/0, p 2/1, m 3/3, total 32. Ärnbäch-Christie-Linde (1912) opined that the dental formula actually is I3, I4, I5, P1, P2, P3, P4, M1, M2, M3/i4, p1, p4, m1, m2, m3, and suggested that two additional rudimentary incisors are present early in embryonic development. Kindahl (1960) found no evidence for these rudimentary incisors and stated that the dental formula is I1, I2, I3, C, P2, P3, P4, M1, M2, M3/i1, i2, p4, m1, m2, m3. James (1963) reinterpreted Kindahl's results and suggested that the dental formula is, in fact, I1, I2, I3, C, P2, P3, P4, M1, M2, M3/i3, c, p4, m1, m2, m3. Choate (1968) described dental abnormalities in *B. brevicauda* and followed James' (1963) interpretation of the dental formula. Because of uncertainty regarding dental homologies, most authors employ the formula given in GENERAL CHARACTERS. Repenning (1967) described the anatomy of individual teeth.

Blarina brevicauda possesses "a pair of extrapulmonary bronchial diverticula emerging from the dorsal caudal margin of the right posterior lobe of the lung," which may be a morphological adaptation to the environment in which the shrews live (Parke, 1956:236). Dust collects in the diverticula, balls up, is ejected into the lungs by the muscular action of the diverticula, and is removed by peristalsis (Parke and Wetzel, 1968).

The ventral aspect of the brain of *B. brevicauda* was figured by Hyde (1959), and the lateral aspect by Le Gros Clark (1932). The secondary optic tracts of the brain are large relative to the primary visual elements (Gillilan, 1941); the optic, oculomotor, trochlear, and abducens nerves are small for mammals and are dwarfed by the trigeminal nerve (Hyde, 1959). With respect to the trigeminus, Hyde (1959:345) stated that *Blarina* "probably represents the greatest reduction in neuronal population that is consistent with adequate brain function." The olfactory tubercle and bulbs are large (Le Gros Clark, 1932). The relative size of the amygdaloid complex is similar to that of other mammals (Crosby and Humphrey, 1944).

The average hematocrit for *B. brevicauda* was 45% and the average hemoglobin was 16.5 g/100 ml, well within the range for other mammals. The average red blood cell count was 18 million/mm, very high for mammals, whereas the average white blood cell count of 2,730/mm was low (Doremus and Jaffe, 1964).

Allen (1894:270) commented on the skull and skeleton of *B. brevicauda* and concluded that the "posterior extremity is of low specialization, and one which supports the trunk imperfectly." Gaughran (1954) described and contrasted the osteology and myology of the cranial and cervical regions of *B. brevicauda* and the eastern mole, *Scalopus aquaticus*. He concluded that their crania have similar proportions and features, but that *Blarina* is specialized more for mastication and *Scalopus* more for burrowing.

Testes are situated inside the abdominal cavity; there is no scrotum (Pearson, 1944). Testes in winter vary in length from 2.5 to 3.5 mm, whereas in the breeding season they usually are longer than 9 mm. An erect penis in the breeding season measures about 30 mm, the terminal third to half of which is glans (Martin, 1967; Pearson, 1944). Male accessory reproductive glands include prostate and bulbo-urethral glands (Eadie, 1947). The vagina during estrus is bent in an S-shape (Pearson, 1944). The uterus is bicornuate; the distance from the base of the bladder to the junction of the uterine horns in winter was as little as 2 mm but in the breeding season increased to more than 12 mm (Pearson, 1944). Ovaries are completely enclosed in ovarian capsules and consist primarily of follicles, with relatively few interstitial cells (Pearson, 1944). The chorioallantoic placenta has been described as endotheliochorial in organization (Wimsatt et al., 1973). Females have three pairs of mammae in the groin region (Schwartz and Schwartz, 1981).

FUNCTION. The metabolic rate of *B. brevicauda* is characterized by short periods of activity with intervening periods of inactivity (Pearson, 1947). The pattern is nearly continuous, although there is a distinct tendency for short-tailed shrews to be more active in the early morning (Morrison, 1948). Periods of activity average about 4.5 min (Buckner, 1964). The shrews are active for only 16% of a 24-h period (Martinsen, 1969), the remainder being spent at a lower, resting metabolic rate (Randolph, 1973). Martinsen (1969) hypothesized that this, together with the proclivity of these shrews to eat nearly any source of energy, accounts for the ability of the species to survive in cold-temperature climates. Within the range of 0°C to 25°C, metabolism is inversely proportional to ambient temperature (Randolph, 1973).

Food consumption averages about 0.56 g g^{-1} day^{-1} in *B. brevicauda* (Morrison et al., 1957), whereas oxygen consumption averages about 5.2 cc g^{-1} h^{-1} (Pearson, 1947). Food consumption in winter is about 43% higher than in summer (Randolph, 1973). Calculated values for basal metabolic rate range from 2.18 to 3.4

cc O_2 g^{-1} h^{-1} (Martinsen, 1969; Neal and Lustick, 1973; Pearson, 1947). Because of its high evaporative water loss, *B. brevicauda* requires free water even though it derives free water from food and metabolic water from oxidation of food (Chew, 1951). Jackson (1961) illustrated and described shrew feces as being about 2.5 cm long, dark green in color, and twisted into a corkscrew shape.

Computed from oxygen consumption, the thermoneutral zone of *B. brevicauda* extends from 25°C to 33°C. Minimal oxygen consumption occurs at 30°C (Neal and Lustick, 1973). The upper lethal ambient temperature appears to be 35°C, at which no amount of evaporative water loss is effective in reversing hyperthermia. Mean body temperature ranges from 38°C to 38.5°C (Chew, 1951; Doremus, 1965), but body temperature elevates appreciably during periods of activity (Kendeigh, 1945).

The poisonous nature of the saliva of *B. brevicauda* was suspected as early as 1889, and several authors described the serious effects experienced after they were bitten by shrews (Krosch, 1973; Maynard, 1889). The poison is secreted from the submaxillary glands through a duct at the base of the lower incisors; when a short-tailed shrew bites another animal, the toxic saliva probably flows along the groove between the two teeth into the wound (Pearson, 1942). In small mammals, the toxin can lead to death from respiratory failure accompanied by severe peripheral vasodilation (Ellis and Krayer, 1955; Pearson, 1942); DeMeules (1954) also demonstrated a possible anti-adrenalin action of the venom. The toxin is a protein with several histimine-like features (Ellis and Krayer, 1955). The LD_{50} of crudely purified toxin is approximately 3.4 mg/kg in mice and cats and 0.6 to 1.2 mg/kg in rabbits (Ellis and Krayer, 1955). Lawrence (1945) compared shrew venom to snake venom and found that, in its neurotoxic and hemotoxic effects, it is most comparable to elapine venom. She suggested that, in addition to its role in predation, it may aid in the breakdown of protein during digestion. Tomasi (1978) opined that one function of the venom is to stun or paralyze its prey, thereby allowing short-tailed shrews to take advantage of prey even though it might not actually be eaten until later. Martin (1981*a*) described the immobilizing effect of the venom on insects and suggested that the venom facilitates food hoarding by *Blarina*.

Evidence that short-tailed shrews employ echolocation to explore their environment was first presented by Gould et al. (1964). Subsequently, Tomasi (1979) investigated the echolocating ability of *B. brevicauda* by testing the ability of individuals to discriminate between open-ended and closed tubes simulating burrows. Lacking other sensory input, ultrasonic "clicks" emitted by the shrews were used to distinguish between open and closed tubes up to 61 cm in length, and at 30.5 cm this distinction was possible for openings as small as 0.63 cm in diameter and around corners up to 90°. The shrews also could distinguish among different kinds of materials blocking the tubes. Echolocation "clicks" were recorded from 30 to 55 kHz (Gould et al., 1964; Tomasi, 1979).

ONTOGENY AND REPRODUCTION. The breeding season of *B. brevicauda* lasts from early February to September (Christian, 1969; Pearson, 1944). Females in estrus were caught in early January, when sexual maturation of males was only beginning (Christian, 1969); conversely, males in breeding condition were caught in mid-October (Pearson, 1944). Dapson (1968) recorded the capture in February of a short-tailed shrew that must have been born in January or December. Two peaks of breeding, in spring and late summer or early autumn, have been noted (Blair, 1940; Hamilton, 1929). Although Pearson (1944) assumed that there was no postpartum estrus in his captive females, Blus (1971) concluded that evidence from wild-caught shrews was too indirect to conclude that it never occurs. Both authors documented instances of estrus occurring after the death of a litter.

Copulation in *B. brevicauda* lasts as long as 25 min and averages 5 min. The shrews are locked together, probably by "the penis becoming rigid after it has passed around one or more sharp bends in the vagina" (Pearson, 1944:77). Erections were observed in sleeping shrews, and the rigid glans took on a flat, leaf-like appearance in an S-shape, caused partly by erectile tissues and partly by a pair of retractor penis muscles (Gibbs, 1955; Pearson, 1944). During copulation, the female usually is active and drags the inactive male behind her. No postcopulatory plug is formed in the vagina. After copulation, the male had to use his mouth to retract the penis. Twenty or more matings in 1 day were observed; at least six matings/day are required to induce ovulation, which usually occurs from 55 to 71 h after the first copulation and never occurs in the absence of copulation. Receptivity of the female decreases if ovulation has occurred but may last for as long as 1 month if it has not. During pregnancy, the corpora lutea regress (Pearson, 1944). Asdell (1965) suggested that the placenta produces enough progesterone to continue pregnancy.

Gestation lasts 21 or 22 days (Hamilton, 1929; Pearson, 1944). Average litter sizes of "six or seven" (Hamilton, 1929:134), 4.7 (Blus, 1971), and 4.5 (Pearson, 1944) have been reported. Hamilton (1929) described a litter of seven neonates as being naked (except for vibrissae, which averaged 1 mm in length), dark pink, and about "honeybee size," and as having closed eyes and ears. At 2 days, external measurements (in mm) were: total length, 31; length of tail, 4; and length of hindfoot, 4.5; weight averaged 1.34 g. At 4 days of age, they weighed an average of 3.8 g and were 48 mm in total length. At 8 days they weighed 6.2 g and had standard measurements of 61, 9.5, and 9. By that time, hair had appeared but teeth had not yet erupted; the shrews were noted to emit a sucking sound and were able to crawl. At 13 days, the young weighed 9 g and measured 73, 12, 16; sex was discernable by the appearance of mammae in females. At 19 days, the upper incisors had appeared through the gums, weight was 9.9 g, and total length was 91 mm. On day 22, when the last of the litter died, the eyes had not opened although the external ear was prominent. Weaning occurs by 25 days of age (Blus, 1971). Pearson (1944) mentioned a captive female that demonstrated receptivity at 47 days of age and noted that captive males had spermatozoa in their testes, which were nearly of adult size, at 50 days of age. The earliest successful breeding of a male recorded by Pearson (1944) was at 83 days of age; Blus (1971) observed a male to breed successfully at 65 days. *B. brevicauda* born in spring mature more rapidly than those born in autumn, and some breed in the same season in which they are born (Blus, 1971; Dapson, 1968; Pearson, 1944).

In mark and release experiments by Pearson (1945), 6% of the originally marked population was recaptured in the second summer. One wild-caught, captive female lived to at least 30 months of age, and one captive-born male lived 33 months. Blus (1971) studied mortality in a captive colony and found that 11.1% lived more than 1 year. The number of young that survived from birth to weaning was 72.6%. Average minimal survival for females and males was 4.4 and 4.6 months, respectively. Age may be determined from the degree of toothwear, with maximum wear indicating an age of about 18 months (Pearson, 1945).

ECOLOGY. Earthworms (Oligochaeta) (Mumford and Whitaker, 1982; Whitaker and Ferraro, 1963) or millipedes (Diplopoda) (Linzey and Linzey, 1973) make up a major portion of the diet of *B. brevicauda.* Hamilton (1941) analyzed 460 stomachs and found that the majority contained insects and annelids and that (in decreasing order of frequency) plant material, centipedes (Chilopoda), arachnids, molluscs, and vertebrates also were represented. He asserted that short-tailed shrews were not heavy predators on field mice, as they had the reputation of being (Merriam, 1884). Eadie (1944, 1948) analyzed *Blarina* feces during high and low population cycles of *Microtus pennsylvanicus* and found that, whereas insects predominated in the diet of *B. brevicauda* even when voles were most numerous, the diet included more voles during periods of high vole density than during low vole density. Eadie (1944, 1952) estimated that three shrews consumed 14 to 27 mice per 2.5 ha during the winter months, thereby acting as an effective control on microtine populations. Allen (1938) and Platt and Blakeley (1973) thought that mice might become important in the diet of *Blarina* when insects are relatively unavailable. In addition, *B. brevicauda* reportedly has preyed on *Sorex* (Eadie, 1949; Hamilton, 1940), a young *Lepus americanus* (Rongstad, 1965), a ribbon snake, *Thamnophis* sp. (O'Reilly, 1949), a 60-cm water snake, *Nerodia* sp. (Cope, 1873), and a slimy salamander, *Plethodon glutinosis* (Hamilton, 1930). *Endogone* and other fungi (Diehl, 1939; Whitaker, 1962) sometimes are included in their diet. Short-tailed shrews store food for future use (Hamilton, 1930; Robinson and Brodie, 1982), especially snails (Gastropoda) (Clench, 1925; Ingram, 1942). Martin (1984) found that food-hoarding by short-tailed shrews occurred primarily in autumn and winter although it could be induced in summer by a sudden abundance of prey.

Species predatory on *B. brevicauda* include: owls—*Aegolius acadicus, Asio otus, A. flammeus, Bubo virginianus, Otis asio,* and *Strix varia* (Choate, 1972*b*; Dexter, 1978; Getz, 1961*c*; Kirkpatrick and Conway, 1947; Mumford and Whitaker, 1982; Pearson and Pearson, 1947; Williams, 1936); hawks—*Buteo lagopus*, *Circus cyaneus*, and *Falco sparverius* (Mumford and Whitaker, 1982); shrikes—*Lanius* sp. (Jackson, 1961); snakes—*Nerodia* sp., *Agkistrodon contortrix*, *Pituophis melanoleucus*, and members of the Crotalinae (Jackson, 1961); felids—*Felis catus* and *F. rufus* (Errington, 1936; Story et al., 1982); canids—*Canis domesticus*, *C. latrans*, *Vulpes vulpes*, and *Urocyon cinereoargenteus* (Andrews and Boggess, 1978; Fowle and Edwards, 1955; Hamilton, 1935; Mumford and Whitaker, 1982); mustelids—*Mustela erminea*, *M. frenata*, *M. vison*, and *Mephitis mephitis* (Hamilton, 1928, 1959; Mumford and Whitaker, 1982); raccoon, *Procyon lotor* (Hamilton, 1936); opossum, *Didelphis virginianus* (Blumenthal and Kirkland, 1976). Shrews also have been discovered in the stomachs of lake trout, *Salvelinus namaycush* (Fowle and Edwards, 1955) and green sunfish, *Lepomis cyanellus* (Huish and Hoffmeister, 1947).

A literature search on parasites of *B. brevicauda* produced 127 citations, most of which were original descriptions of 144 ecto- and endoparasites. Wittrock and Hendrickson (1979) listed 18 helminths that occurred in *B. brevicauda* in Iowa, and Mumford and Whitaker (1982) listed 32 species of ectoparasites and three orders of endoparasites (Nematoda, Trematoda, and Cestoda) that occurred on and in short-tailed shrews in Indiana. Nixon Wilson (pers. comm.), after examining our bibliography, reported that the papers referred to the following ectoparasites: 2 species of Anoplura; 2 Coleoptera (both leptinids); 1 dipteran (a cuterebrid); 25 Siphonaptera; 34 Acari.

Miller and Getz (1977) calculated that short-tailed shrews have broad habitat requirements but were most common in areas with more than 50% herbaceous cover. Conversely, Dueser and Shugart (1979) iterated that short-tailed shrews in eastern Tennessee have a narrow, somewhat specialized niche. Getz (1961*a*) found that food was the limiting factor in wooded habitats; type of vegetation, cover, temperature, and moisture had little effect on local distribution, although shrews avoided areas with little cover and with extremes of temperature and moisture. Pruitt (1953, 1959) suggested that deep litter protected shrews in hardwood forest from temperature and moisture extremes. *B. brevicauda* was the most ubiquitous and abundant of five species of mammals studied in farmstead shelterbelts in southern Minnesota, based on captures in both wooded and unwooded habitats (Yahner, 1982, 1983). *B. brevicauda* moved between shelterbelts more often than other species studied. In Iowa, *B. brevicauda* was associated with big bluestem, *Andropogon gerardi* (Platt, 1975); in Quebec, they occurred primarily in mature deciduous-coniferous forest and secondarily in fields of tall grasses and sedges (Wrigley, 1969). Sinclair et al. (1967) found short-tailed shrews associated with stone walls in relatively dry situations in eastern deciduous forest; they suggested that humidity might be higher near the stone walls than in adjacent microhabitats, thereby enabling short-tailed shrews to inhabit otherwise dry areas. In eastern Tennessee, *Blarina* consistently occupied areas of high stump and log density, hard ground, few shrubs, and dense overstory, and they fed on larval insects found in the stumps and logs (Kitchings and Levy, 1981). The subspecies *B. b. telmalestes* occurs primarily in marshy habitats in and around the Dismal Swamp of Virginia and North Carolina (Handley, 1979).

Platt and Blakeley (1973) investigated the interspecific relationship between *B. brevicauda* and *Sorex cinereus*, and suggested that *Sorex* populations might be somewhat negatively correlated with density of *Blarina*. Hamilton (1940) thought *B. brevicauda* might have an adverse effect on *S. fumeus* populations, but Jameson (1949) found the opposite to be true. Lindeborg (1941) found a positive correlation between fluctuations in *Peromyscus leucopus* and *B. brevicauda*, and Calhoun (1963) found evidence that the presence of *P. leucopus* on the surface of the ground might force shrews to remain underground. Zegers and Ha (1981) postulated that *P. leucopus* used arboreal habitats to minimize competition with *Blarina*. In Iowa, Heideman et al. (1983) found that members of the genus *Peromyscus* reinvaded flooded areas much more quickly than *Blarina*.

Winter mortality of up to 90% of populations of *B. brevicauda* has been documented, probably related to stress from cold (Barbehenn, 1958; Gottschang, 1965; Jackson, 1961). Population density varies from year to year (Jackson, 1961; Platt, 1968), and populations of short-tailed shrews occasionally crash, requiring several years to recover (Ozoga and Verme, 1968). Christian (1963) found that mean adrenal weight was related directly to population size. Brenner et al. (1983) concluded that reproduction in *B. brevicauda* may not be affected adversely by behavioral interaction as it is in microtines. Estimates of population density range from 1.6/ha to nearly 121/ha (Jackson, 1961; Williams, 1936). Estimates of home-range size usually average about 2.5 ha (Blair, 1940, 1941; Buckner, 1966), and the range of each shrew usually overlaps with the range of one or more other shrews. Blair (1940) thought that *B. brevicauda* did not have territories defended from other shrews.

In abandoned strip-mines, *B. brevicauda* is found only in older areas with stable, moist environmental conditions (Jones, 1974; Kirkland, 1976; Wetzel, 1958). After a timbered area is clear-cut, populations of shrews decline abruptly (Kirkland, 1977). Powerline corridors seem to be a dispersal barrier for short-tailed shrews (Schreiber and Graves, 1977). Because shrews are predators, they concentrate DDT residues at levels 10 times those found in *Peromyscus* and *Clethrionomys* (Dimond and Sherburne, 1969). Stehn et al. (1976) found that shrews significantly increased their consumption of arthropods after an area was sprayed with orthene, thus increasing their intake of pesticide residues. Getz et al. (1977) documented concentrations of lead in *Blarina* adjacent to highways.

BEHAVIOR. Martin (1980) described 54 behavioral patterns in captive short-tailed shrews. *B. brevicauda* is a semifossorial mammal with runways usually in the top 10 cm of soil but with some as deep as 50 cm below the soil surface (Hamilton, 1931; Jameson, 1943). Runways usually parallel the surface but occasionally ascend vertically to it (Jameson, 1943). Shrews dig along and through old rotten logs and often use runways of microtines and moles (Hamilton, 1931). Although there is individual variation in digging behavior, shrews generally dig with their front feet and, when enough soil accumulates, kick it from the tunnel entrance with their hindfeet (Rood, 1958). If the distance to the entrance is great enough, shrews do a sideways somersault and push the dirt out with their noses. They dig at a rate of approximately 2.5 cm/min with frequent stops for short naps. Shull (1907) and Brooks (1908) found burrow systems of *B. brevicauda* literally to honeycomb an area. Shrews spend relatively little time on the surface of the ground (Rood, 1958) but have been reported to climb trees (Carter, 1936). Getz (1961*b*) found them to be more active on cloudy days than on sunny or rainy days.

Nests are underground and spherical in shape, and may be lined with vegetation and even fur of meadow voles, *Microtus pennsylvanicus* (Hamilton, 1929; Rapp and Rapp, 1945; Shull, 1907). However, leaves and grass provided by Rood (1958) for his captive shrews were ignored.

During lactation, female shrews constrict the openings of nests and reinforce the nesting materials (Martin, 1982). Activity of females increases during pregnancy and lactation, possibly as the result of increased nutritional needs. Female shrews retrieve their pups by dragging and by a behavior similar to caravanning. The latter, however, involves only the female and one young. All maternal behavior ceases when the young are weaned (Martin, 1982).

Feces rarely are found in the nest (Hamilton, 1929; Rood, 1958; Shull, 1907); they usually are deposited neatly on the side of a runway, outside the entrance to the nest, or, by captive shrews, in the corners of the cage. *B. brevicauda* twitches restlessly when sleeping. The most common position is with the nose and paws tucked under the belly (Rood, 1958). These shrews rarely stay in one position for more than a few minutes and often arouse to yawn, stretch, and clean themselves before going back to sleep. If several familiar individuals share a cage, they sleep together and constantly try to get to the bottom of the pile. Allison et al. (1977) quantified data on sleep in *B. brevicauda*.

Many authors consider *Blarina* to be solitary and unfriendly (Jackson, 1961; Martin, 1981*b*; Shull, 1907). Rood (1958), however, found that the sociability of short-tailed shrews depended greatly on individual dispositions with age and sex playing a lesser role; males and older animals tended to be less friendly than females and younger animals. Disposition also seems to have a bearing on predatory predilections. Some individuals seemed "terrified" of mice put into their cages, others attacked the mice half-heartedly, and some attacked without hesitation. Phillips (1956:543) noted that a shrew first "fastened its teeth just behind the left ear of the vole . . . and began to gnaw at the base of the skull. It required 11 minutes for the shrew to kill its prey, and during that time it was dragged roughly and rapidly about the cage, as the vole attempted to shake loose." Olsen (1969) analyzed the agonistic behavior of short-tailed shrews and recognized four action patterns and five postures. He suggested that the postures were used in species recognition, thus minimizing the amount of energy wasted in competition for food, space, and social position.

GENETICS. Standard karyotypes of *B. brevicauda* are characterized by a diploid number of 50, 49, or 48 and a fundamental number of 48 (George et al., 1982). Meylan (1967) concluded that variation in diploid numbers is the result of a fission–fusion event between a pair of large acrocentric autosomes and a pair of small acrocentric autosomes. The totally acrocentric diploid number of 50 is most common (Genoways et al., 1977; George et al., 1982), and a diploid number of 48 has been found in only one specimen from central Illinois (Lee and Zimmerman, 1969). The X-chromosome is a large metacentric (Genoways et al., 1977; Meylan, 1967). Genoways et al. (1977) reported the Y-chromosome to be a small acrocentric in *B. b. brevicauda* and *B. b. kirtlandi*, whereas Meylan (1967) reported it to be a small metacentric in *B. b. talpoides*. George et al. (1982) demonstrated that each speciation event in the genus *Blarina* has been accompanied by fixation of chromosomal differences.

Examination (using starch gel electrophoresis) of 18 presumptive loci in individuals of *B. brevicauda* from Massachusetts and Pennsylvania revealed that mean heterozygosity was nil and the percent of loci polymorphic was 11.1 (George, 1984). Brenner and Atno (1983) found seven distinct protein fractions, representing six autosomal genetic traits, in the lens of the eye of *B. brevicauda*.

REMARKS. Based on the revisionary studies of Merriam (1895) and Bole and Moulthrop (1942), the genus *Blarina* was thought to contain two species—*B. brevicauda* and *B. telmalestes*. The latter subsequently was shown by Handley (1979) to be a subspecies of *B. brevicauda*. However, a series of papers published since 1972 (Braun and Kennedy, 1983; French, 1981; Genoways and Choate, 1972; Genoways et al., 1977; George et al., 1981, 1982; Moncrief et al., 1982; Tate et al., 1980) has demonstrated that the genus consists of at least three species—*B. brevicauda*, *B. carolinensis*, and *B. hylophaga*. Moreover, the nominal subspecies *B. carolinensis peninsulae* may represent a fourth species. Finally, the taxon *B. carolinensis shermani* may prove to be an isolated subspecies of *B. brevicauda* or still another species of *Blarina* (Jones et al., 1984).

The generic name *Blarina* is a coined name that has no derivation. The specific epithet is a combination of two Latin words—*brevis* and *cauda*—meaning short tail.

There are literally hundreds of citations that pertain to *B. brevicauda*. We have not been able to include them all here, but have attempted to cite those that give the most complete information or that summarize other authors' work.

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