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Abstract

The southern short-tailed shrew, *Blarina carolinensis*, inhabits a broad range of ecological situations in the southeastern United States and, in many areas, is among the two or three most abundant species of small mammals. Nevertheless, its natural history is poorly known and much of what researchers assumed was fairly well understood about this species actually resulted from work on another species (*Blarina brevicauda*) and may not be correct in all instances. This problem resulted when modern systematic methods revealed that the wide-ranging and well-studied species known at that time as *Blarina brevicauda* actually consisted of three species (*B. brevicauda*, *B. carolinensis*, and *B. hylophaga*). The purposes of this investigation were: 1) to review published literature on the natural history of short-tailed shrews and determine which information actually pertains to the southern short-tailed shrew, and 2) to summarize current knowledge about this shrew.

In the sections that follow, the existing body of knowledge concerning the southern short-tailed shrew is reviewed in the categories of taxonomy, morphology, fossil record, distribution, genetics, habitats, populations, reproduction, movements and home range, nests and runways, diet, physiology, predators, and parasites and disease. Throughout the paper, suggestions are provided for future research on *B. carolinensis*.

INTRODUCTION

The southern short-tailed shrew, *Blarina carolinensis*, is a common inhabitant of a broad range of habitats in the Gulf and Atlantic Coastal Plain and Mississippi Alluvial Plain of the eastern and southern United States. In most of these areas, it is among the two or three most abundant species in the small mammal fauna. In overall size, it is the smallest of the three species currently recognized in the genus.

B. carolinensis was considered a subspecies of *B. brevicauda* from the time of Merriam's revision of the genus *Blarina* in 1895 until publications by Handley in 1971 and Genoways and Choate in 1972. Most recent authors have recognized *Blarina carolinensis* as a distinct species. The work of Braun and Kennedy (1983), Bryan (1991), Ellis et al. (1978), George et al. (1981, 1982), Moncrief et al. (1982), Schmidly (1983), Tate et al. (1980), and Webster (1996) gave better definition to the systematic and geographic relations among the three species of *Blarina* currently recognized.

In recent years, we became aware that many monographs regarding the mammalian fauna of states and regional areas have followed this new taxonomic arrangement but have continued to cite some of the classical works on short-tailed shrews when discussing natural history phenomena. Most notable of these classic works are the studies by W.J. Hamilton, Jr. (1929, 1930, 1931, 1941), O.P. Pearson (1942, 1944, 1945, 1946, 1950), W.F. Blair (1940, 1941), and A.F. Shull (1907). Much of this work was conducted in New York state and Michigan and was performed on *Blarina brevicauda* (*sensu stricto*); thus, it does not apply to *Blarina carolinensis.* Initially we assumed that little or nothing was known about the natural history of the southern short-tailed shrew, but a preliminary review of the literature revealed this assumption to be incorrect.

We have undertaken an exhausting, if not exhaustive, literature review concerning short-tailed shrews. A problem faced by researchers is that the natural history information for *Blarina carolinensis* is scattered in many publications, most of which do not have the shrew as a focus. Also, taxonomic changes that subdivided *Blarina brevicauda* into three species made it difficult for anyone not thoroughly familiar with these changes to survey the literature. Most of the natural history information for the southern short-tailed shrew, for example, has been published under the scientific name *Blarina brevicauda.*

Because we are familiar with this literature and have been partly responsible for the changing taxonomy of these shrews, we have taken this opportunity to pull together as much of the natural history data for *Blarina carolinensis* as possible. It is our hope that, by summarizing this information here, we will be able to stimulate research by other investigators in areas of the natural history of the southern short-tailed shrew that are poorly understood, including such topics as population density and fluctuations, diet, reproduction, physiology, molt, anatomy, and pharmacology of the submaxillary glands. It is also our hope that summarizing what is known about the southern short-tailed shrew will stimulate comparative studies of the natural history of the species of *Blarina.* Elsewhere (George et al. 1986), we have summarized the natural history information for the northern short-tailed shrew, *Blarina brevicauda*, and we are preparing a similar summary for Elliot's short-tailed shrew, *Blarina hylophaga.* In a separate study, we will review the taxonomy and natural history of populations of short-tailed shrews in southern Florida.

Members of the genus *Blarina* present a unique opportunity to study comparative aspects of mammalian biology. The species of the genus exhibit little morphological variation and maintain nearly parapatric distributions across half of the United States. These shrews are common members of a broad range of habitats from southern Canada to the Everglades of Florida and from the Atlantic coastal marshes westward to the grasslands of western Nebraska and eastern Colorado. How and why the parapatric distributions are maintained (except in eastern North Carolina) is not understood. The role of this diminutive predator in small mammal populations is still poorly studied. How are the species similar or dissimilar in various aspects of their natural history such as diet, reproduction, non-shivering thermogenesis, molt, temperature regulation, genetics, and population dynamics? How have the species maintained a parapatric distribution throughout the late Pleistocene when climatic conditions moved this zone to the north or south? We hope that our summary of the natural history of the southern short-tailed shrews will serve as a starting point for these and many other studies of this interesting group of small mammals.

TAXONOMY

The southern short-tailed shrew, *Blarina carolinensis* (Fig. 1), is one of three species currently recognized in the genus, together with *B. brevicauda* (including *B. telmalestes*) and *B. hylophaga.* The species initially was named *Sorex carolinensis* by Bachman (1837) based on material from "South Carolina." Merriam (1895) treated this taxon as a subspecies under the name *Blarina brevicauda carolinensis* and restricted the type locality to "Eastern South Carolina"; however, on a subsequent page he described a new subspecies of shrew under the name *Blarina carolinensis peninsulae.* Despite this ambivalent treatment by Merriam (1895), the name *Blarina brevicauda carolinensis* was used in the

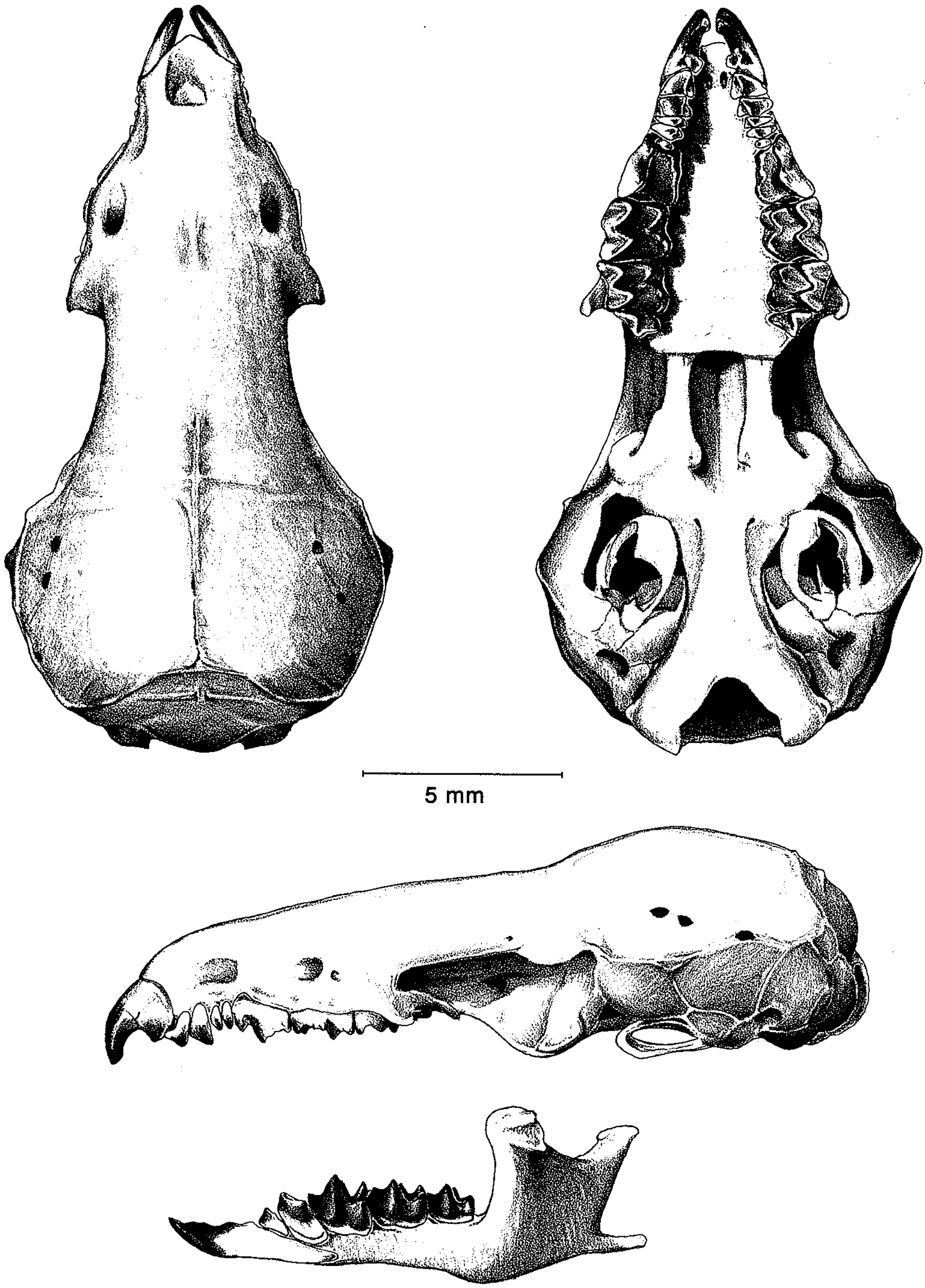

Fig. 1. Dorsal, ventral, and lateral views of the cranium and lateral view of the lower jaw of a female *Blarina carolinensis* from 2 mi north and 1½ mi west of Jackson, Aiken County, South Carolina (Collection of Mammals, Sternberg Museum of Natural History, Fort Hays State University, no. 15253).

mammalogical literature for the next 75 years (for example, Miller 1912, Bole and Moulthrop 1942, Miller and Kellogg 1955, Hall and Kelson 1959). It is important to note that Rhoads and Young (1897) concluded that *B. carolinensis* was a distinct species, but their work was either overlooked or ignored by other mammalogists until Handley (1979) noted the oversight. During most of this time, two species of *Blarina* were recognized—*brevicauda* widespread throughout the eastern United States and southern Canada and *telmalestes* confined to the Dismal Swamp of southeastern Virginia and northeastern North Carolina (Hall and Kelson 1959, Hall 1981). Not until the work of Handley (1971) and Genoways and Choate (1972) did the name *Blarina carolinensis* come back into widespread use. The current geographic range of the species was broadly defined in papers by Tate et al. (1980), French (1981), George et al. (1981, 1982), Braun and Kennedy (1983), Schmidly (1983), Webster et al. (1985), Hoffmeister (1989), and Bryan (1991).

Merriam (1895) described and named *Blarina carolinensis peninsulae*, with its type locality at Miami River, Dade County, Florida. Some recent authors (Hamilton and Whitaker 1979, George et al. 1982, Jones et al. 1984, Layne 1992) have treated this taxon as a subspecies of *B. carolinensis*. We have chosen not to follow this course of action in the current paper primarily because George et al. (1982) found appreciable karyotypic differences between *carolinensis* (2N = 37–46, FN = 44, 45) and *peninsulae* (2N = 50–52, FN = 52). The taxonomic status of *peninsulae* remains uncertain.

Hamilton (1955) described and named *Blarina brevicauda shermani*, with its type locality 2 mi north of Fort Myers, Lee County, Florida. The taxonomic status of this taxon also is uncertain. Because of its larger size (Layne 1992), *shermani* resembles *B. brevicauda* more than *B. carolinensis*. Given the geographic distribution of these species, it might seem implausible for *shermani* to be a subspecies of *B. brevicauda*. However, French (1981) documented other disjunct populations of *B. brevicauda* (in Georgia). Moreover, the recent discovery of a Pleistocene relict population of a Boreal living species (*Microtus pennsylvanicus dukecampbelli*) near Cedar Key, Florida (Woods et al. 1982, Woods 1992), shows the feasibility of the geographic disjunction that would exist if *shermani* were aligned with *brevicauda*. One of the problems in determining the taxonomic status of *shermani* is that, in spite of ongoing efforts, no recent specimens have been obtained at or near the type locality (Layne 1992). Karyotypic data for this population will be key to understanding its taxonomic relationship. Thus, we have deferred making a taxonomic assignment of *shermani* at this time and await the results of our ongoing study of the relationships of Floridian populations of *Blarina*.

Lowery (1943) described and named *Blarina brevicauda minima*, with its type locality at Comite River, 13 mi northeast of Baton Rouge, East Baton Rouge Parish, Louisiana. Lowery distinguished this taxon as the smallest of the named subspecies in the genus *Blarina* and described (p. 218) its distribution as "extreme lower Mississippi River Valley and central Gulf Coast." He assigned material from Louisiana and Mississippi to the new taxon. Hall and Kelson (1952) referred previously reported shrews from East Texas to *minima*. Many recent authors (Lowery 1974, Sealander 1979, Schmidly and Brown 1979, Schmidly 1983, Jones et al. 1984, Hoffmeister 1989, Jones and Carter 1989) have referred specimens to this taxon under the name *Blarina carolinensis minima*. This is a taxonomic arrangement with which we agree.

Unfortunately, at this time we are not able to precisely delineate the geographic range of *B. c. minima*. Hall (1981) showed *B. c. minima* occurring in southeastern Texas, all of Louisiana, western Mississippi, and in the Mississippi River Valley of eastern Arkansas, western Tennessee, and into southeastern Missouri. The work of Schmidly (1983) confirms the distribution in Texas, as do the works of Lowery (1974) in Louisiana and Jones and Carter (1989) in Mississippi. Easterla (1968) reported specimens of this subspecies from extreme northeastern Arkansas and southeastern Missouri. The measurements that he presented indicate that these specimens indeed are quite small, like those of *B. c. minima*. Schmidly (1983) showed northeastern Texas and adjacent Arkansas occupied by the taxon *B. c. carolinensis*. Garland and Heidt (1989) pointed out taxonomic problems with populations of

Blarina in Arkansas but did not resolve the issues involved. Hall (1981) showed western populations of the taxon he termed *B. b. carolinensis* in Texas, Oklahoma, Kansas, Nebraska, Arkansas, and Missouri connecting to eastern populations by means of a narrow corridor across southeastern Missouri and southern Illinois. We know now that most of these western populations of *Blarina* should be assigned to *Blarina hylophaga* (George et al. 1981). George et al. (1981), however, assigned specimens from northeastern Texas, central and eastern Arkansas, and extreme southeastern Missouri to *Blarina carolinensis*. The subspecific status of these populations needs to be reassessed.

Hoffmeister (1989) found that specimens from southern Illinois averaged larger in many measurements than other populations of the species, and therefore he assigned the southern Illinois population to *B. c. carolinensis*. Braun and Kennedy (1983:421) found "The general pattern of character variation for *B. carolinensis* was an increase in size from western Tennessee to southern Illinois." This would appear to confirm Hoffmeister's (1989) conclusions. Handley and Varn (1994) reported that populations of *B. carolinensis* from coastal South and North Carolina had a slightly longer rostrum than shrews from the Piedmont of South Carolina and Virginia. Our conclusion, based on these confusing and sometimes contradictory reports, is that geographic variation, and its impact upon subspecific taxonomy of *B. carolinensis*, is badly in need of review.

Handley and Varn (1994) reviewed the taxonomic status of three species of shrews described by Bachman in 1837. They concluded that the name *Sorex carolinensis* Bachman currently is applied appropriately to the taxon *Blarina carolinensis* (Bachman 1837) as used in the current study. Because none of Bachman's original type material of *B. carolinensis* is known to exist, Handley and Varn (1994:396) restricted the type locality to "Charleston County, South Carolina" and designated a neotype as follows: USNM 574157, adult male, skin and skull, taken on 27 July 1989 by Charles O. Handley, Jr., and Merrill Varn, along Awendaw Creek, 3.2 km E Awendaw Post Office, Charleston County, South Carolina, original no. COH 15236. Measurements of the neotype are given in Table 1.

MORPHOLOGY

Much of the morphological work that has been published on short-tailed shrews has dealt with *Blarina brevicauda*. Below, we review the literature relating to description, measurements, morphometrics, and pelage of *Blarina carolinensis*. Initially, we included in this section a paper by Nauman (1966) with the descriptions of anatomy and histology of *Blarina*, but, based on the latest information, it appears that his specimens from Forsyth County, North Carolina, are best assigned to *Blarina brevicauda*.

Description

This is the smallest of the three species of *Blarina* currently recognized. It is a stout-bodied, short-legged shrew with a tail that is less than half the length of the head and body. These shrews have a long, pointed snout that protrudes well beyond the mouth. The external ears are short and hidden by the pelage, as are the minute eyes. The pelage of the upper parts and underparts is nearly uniformly dark slate-gray with the underparts only slightly, if at all, paler than the upper parts. The velvety soft fur is nearly the same length throughout. The vibrissae are whitish and extend beyond the eye when laid back. The tail is darker above than below. The forefeet are buffy, whereas the hind feet are more of a pale fuscous.

The southern short-tailed shrew has 32 teeth, as do other members of the genus, with a dental formula of I 1/1, U 5/1, P 1/1, M 3/3 (George et al. 1986). The first and second upper unicuspid teeth are large and subequal, the third and fourth upper unicuspids are also subequal in size, but are much smaller than the first two unicuspids, and the fifth upper unicuspid often is tiny and may or may not be visible in lateral view. The maxillary process extends behind M2 (Fig. 1). The teeth are tipped with a dark chestnut-brown coloration. Carraway (1995) described differences in the dentaries of the three species of *Blarina*. *Blarina brevicauda* was distinguished from the other two species by the height (in mm) of the coronoid usually being ≥ 6.0 as opposed to ≤ 6.0, length of c1-m3 usually being ≥ 6.5 as opposed to ≤ 6.5, length of coronoid–condyloid processes usually being ≥ 5.2 as opposed to usually being < 5.0, mental foramen positioned be-

Table 1. Selected external and cranial measurement of *Blarina carolinensis* from eight geographic areas.

	Total length	Tail length	Body length	Length of hind foot	Greatest length of skull	Condylobasal length	Occipito–pre-maxillary length	Breadth of braincase	Maxillary breadth	Interorbital breadth	Maxillary toothrow	Length P4–M3
Alexander and Union counties, Illinois (after Hoffmeister 1989) (n = 35)												
mean	88	18.4	69.8	11.7	19.9		19	10.4	6.7	5.1		5.4
range	77–98	12–25	59–84	10–15	19.1–20.7		18.2–19.8	10.0–10.8	6.5–7.0	4.8–5.4		5.2–5.7
1 SD	5.61	2.85	5.92	1.18	0.47		0.47	0.24	0.18	0.18		0.18
Lake, Lauderdale, and Obion counties, Tennessee (after Ellis et al. 1978) (n = 30)												
mean			74.8	11.3	19.6		18.8	10.5	6.6	5.1		5.4
range			67.0–91.0	8.0–13.0	18.1–20.6		17.4–19.9	10.0–11.1	6.2–7.1	4.9–5.5		4.9–5.6
1 SE			1.17	0.16	0.08		0.09	0.05	0.03	0.02		0.03
Hardin, Tyler, Newton, and Walker counties, Texas (after Schmidly 1983) (n = 49)												
mean							18.6	10.2	6.5			5.2
range							17.9–19.4	9.6–10.6	6.2–7.0			4.9–5.5
Holotype of *B. c. minima* from Comite River, 13 mi NE Baton Rouge, East Baton Rouge Parish, Louisiana (after Lowery 1943) (n = 1)												
LSU 2196	82	17.5	64.5	11	19.3			10.1		5.4		
Louisiana (after Lowery 1974)												
n	73	73	73	73	75			75	75	75		
mean	85	17.8	67.2	12	18.4			9.7	6.4	5.1		
range	72.0–95.0	13.0–22.6	59.0–72.5	10.0–14.0	16.9–19.2			9.1–10.6	5.5–6.9	4.7–5.8		
Alachua and Putnam counties, Florida (after Hamilton 1955) (n = 17)												
mean	92.2	21		12.5		19.3		10.3	6.6	5.2	7	
range	84–102	18–26		11.5–14		18.1–20.1		9.7–10.8	6.2–7.0	5.0–5.5	6.4–7.3	
Neotype of *B. c. carolinensis* from Awendaw Creek, 3.2 km E Awendaw Post Office, Charleston County, South Carolina (after Handley and Varn 1994) (n = 1)												
USNM 57415	105	21	84	12		19.4		10.7	6.8	5.2	7.3	

Table 1 continued

	Total length	Tail length	Body length	Length of hind foot	Greatest length of skull	Condylobasal length	Occipito–pre-maxillary length	Breadth of braincase	Maxillary breadth	Interorbital breadth	Maxillary toothrow	Length P4–M3
Charleston County, South Carolina (Handley and Varn 1994)												
n	2	8		8		7		7	6	7	8	
mean	102	20		12.4		19		10.4	6.6	5.1	7.3	
range	99–105	15–23		12–13		18.5–19.4		10.1–10.7	6.4–6.8	5.0–5.2	7.0–7.6	
2 SE	6	1.73		0.37		0.2		0.16	0.13	0.07	0.14	
Amelia County, Virginia (after Handley and Varn 1994)												
n	17	15		13		17		14	18	19	17	
mean	93.2	19.5		12.2		18.6		10.3	6.6	5.1	7.1	
range	86–102	18–22		11–14		18.1–19.3		10.0–10.5	6.3–7.0	4.8–5.7	6.6–7.5	2
SE	1.76	0.64		0.5		0.15		0.09	0.1	0.9	0.11	

neath hypoconid of m1 as opposed to being positioned beneath midpoint between protoconid and hypoconid of m1, and basin present in lingual side of interarticular area as opposed to the basin being absent. She distinguished *Blarina carolinensis*, having the first lower incisor set at an angle ≤ 17° from the horizontal ramus of the dentary, from *Blarina hylophaga* in which this angle is ≥ 18°.

Measurements

Representative measurements for eight localities of *Blarina carolinensis* are presented in Table 1. Additional sources for external and cranial measurements for populations of the southern short-tailed shrew are as follows: Arkansas (George et al. 1981; measurements given by Ramsey 1977, Sealander 1979, and Sealander and Heidt 1990, may represent mixed species samples); Florida (Hamilton 1955, Layne 1992); Georgia (measurements given by Golley 1962, represented a mixed species sample); Illinois (Ellis et al. 1978, Hoffmeister 1989); Kentucky (Rippy 1967, Ellis et al. 1978); Louisiana (Lowery 1943, 1974, George et al. 1981); Mississippi (Rippy 1967); North Carolina (Tate et al. 1980, Handley and Varn 1994); Oklahoma (George et al. 1981); South Carolina (Rippy 1967, Handley and Varn 1994; measurements given by Golley 1966, represented mixed species samples); Tennessee (Rippy 1967, Ellis et al. 1978); Texas (Schmidly and Brown 1979, George et al. 1981, Schmidly 1983); Virginia (Tate et al. 1980, Handley and Varn 1994). Carraway (1995) gave length, height, and angular measurements of the dentary of one specimen.

Morphometrics

A number of investigators have used multivariate morphometric analyses to study relationship among members of the genus *Blarina*. Ellis et al. (1978) studied the relationships among populations of *Blarina* in Illinois using cluster analysis. They concluded that there were two morphologically distinct populations in the state and that the one in the southern part of the state was *Blarina carolinensis*. Schmidly and Brown (1979) studied populations of *Blarina* in Texas using a canonical analysis. They associated all populations with *Blarina carolinensis*, although subsequently *plumbea* was reassigned as a subspecies of *B. hylophaga.* Tate et al. (1980) used discriminant analyses to distinguish between *B. carolinensis* and *B. brevicauda* in Virginia. These species were found occurring sympatrically at two localities, but only one of the 74 test specimens suggested possible hybridization. French (1981) also used discriminant analyses to review the *Blarina* populations in the southeastern United States. Some of his most important findings included redefining the boundary between *B. brevicauda* and *B. carolinensis* in Georgia and finding disjunct populations of *B. brevicauda* in Georgia and Alabama. George et al. (1981) used discriminant and canonical analyses to study southern populations of *Blarina.* They concluded that populations in the southwestern portion of the range of the genus were a distinct species to which the name *Blarina hylophaga* should apply, and that the name *B. carolinensis* should be reserved for populations in the Southeast. Braun and Kennedy (1983), employing several multivariate techniques, studied populations of *Blarina* in Tennessee and adjacent areas. They found two taxa in the region whose ranges abutted along a line just east of the Tennessee River. The two taxa were *Blarina brevicauda* east of the line and *B. carolinensis* to the west.

Thomas (1977) studied the coefficient of variation in eight external and cranial measurements of seven species of small mammals in Louisiana. He found the following coefficients of variation for 18 specimens of *Blarina carolinensis*: body length, 11.31; maxillary breadth, 2.70; cranial breadth, 2.20; basilar length, 2.75; palatilar length, 3.26; P4–M3 length, 3.00. *Blarina carolinensis* exhibited the least amount of variation in all cranial measurements among the seven species he examined except for the P4–M3 length in *Reithrodontomys fulvescens.* Coefficients of variation in *B. carolinensis* more closely resembled those of *Cryptotis parva* than those of the five species of rodents examined, although they were always slightly less than those in *C. parva.*

Pelage

Findley and Jones (1956) described the pattern of molt in *Blarina.* Unfortunately, the geographic origins of the specimens were not recorded and it is impossible to assess how their information relates to *B. carolinensis.* It is apparent, therefore, that the molt patterns of species of *Blarina* should be re-examined and compared. Comparing the timing of molt among the species may prove to be of particular interest.

Dew (1992) studied seasonal pelage changes in populations of *B. carolinensis* in eastern Virginia. There were no seasonal differences in hair density in this population, with the number of hairs per square mm being: winter, 132.5; spring, 135.8; summer, 168.3; autumn, 155.4. Dew, however, found that the two types of guard hairs were significantly shorter in summer pelage (June to August) than at other times of the year. The length of guard hairs in winter (December to February) was 1.3 times that in other seasons. Although the woolly underhair was not significantly shorter in summer than in winter, it averaged 1.2 times longer in winter.

The only record of aberrant pelage in a southern short-tailed shrew was an albinistic male taken in Gibson County, Tennessee (Smith 1976).

FOSSIL RECORD

The fossil record of *Blarina* suggests that the species became segregated as the result of the increasing continentality of the climatic regime (Graham and Semken 1976). Jones et al. (1984) proposed that *B. brevicauda*, or an ancestral species similar to *B. brevicauda,* arose from the blarinine stem in the middle or late Pliocene. The earliest remains of *B. brevicauda* are from the late Blancan of Kansas. Subsequently, during the early Pleistocene, *B. brevicauda* became isolated into two populations, possibly as the result of a glaciation event 2.5 to 2.3 Ma (Boellstorff 1978), with differentiation and chromosomal rearrangements resulting in a smaller southern species, *B. carolinensis.*

The earliest known specimens of *B. carolinensis* are from the Inglis IA fauna of western Florida. This site is believed to be of earliest Irvingtonian age (2.0–1.7 Ma; Morgan and Hulbert 1995). The fauna at Inglis IA suggested that it was associated with a coastal savanna habitat. As indicated in Table 2, *Blarina carolinensis* specimens are known from 26 Pleistocene and Holocene sites in nine states. *B. carolinensis*

Table 2. Fossil record of *Blarina carolinensis* (based on Jones et al. 1984)[†].

State	County	Site	Land Mammal Age	Age
Florida	Indian River	Vero 2 and 3	Rancholabrean	Late Wisconsinan
Florida	Levy	Waccasassa River IIB and III	Rancholabrean	Wisconsinan
Florida	Alachua	Arredondo IB and IIA	Rancholabrean	Late Sangamonian
Florida	Manatee	Bradenton 51st St	Rancholabrean	Sangamonian
Florida	Alachua	Haile XIB and XIIA	Rancholabrean	Sangamonian
Florida	Marion	Reddick IA	Rancholabrean	Sangamonian
Florida	Levy	Williston IIIA	Rancholabrean	Sangamonian
Florida	Sumter	Coleman IIA	Irvingtonian	Late Kansan to early Illinoian
Florida	Citrus	Inglis IA	Irvingtonian	Early Pleistocene (2.0–1.7 Ma)
Georgia	Bartow	Ladds Quarry	Rancholabrean	Late Wisconsinan
Illinois	Monroe	Meyer Cave	Rancholabrean	Early Holocene
Kansas	Meade	Jinglebob	Rancholabrean	Early Wisconsinan
Kansas	Meade	Mt. Scott	Rancholabrean	Late Illinoian
Kansas	Doniphan	Wathena	Irvingtonian	Aftonian or Kansan
Maryland	Allegany	Cumberland Cave	Irvingtonian	Possibly late Kansan or early Illinoian
Mississippi	Lowndes	Catalpa Creek	Rancholabrean	Pleistocene to Holocene
Pennsylvania	Adams	Hanover Quarry Fissure	Irvingtonian	Yarmouthian
South Dakota	Walworth	Java	Irvingtonian	Kansan
Texas	Travis	Barton Springs Road	Rancholabrean	Holocene (1,015 + 105)
Texas	Kerr	Hall's Cave	Rancholabrean	Holocene
Texas	Burnet	Longhorn Cavern	Rancholabrean	Holocene
Texas	Llano	Miller's Cave	Rancholabrean	Holocene (7,200 + 300)
Texas	Kerr	Klein Cave	Rancholabrean	Holocene (7,683 + 643)
Texas	Sutton	Felton Cave	Rancholabrean	Holocene (7,770 + 130)
Texas	Kendall	Cave Without a Name	Rancholabrean	Wisconsinan (10,900 + 190)

(Table continues on the next page)

Table 2 continued

State	County	Site	Land Mammal Age	Age
Texas	Bexar	Friesenhahn Cave	Rancholabrean	Wisconsinan (19,000–17,000)

†*Blarina* in numerous late Holocene sites were mentioned by Graham et al. (1987). We have not seen any of those specimens, but we assume, based on geographic locations and geological times, that most, if not all, of them represented species other than *B. carolinensis*.

evidently became divided into eastern and western populations shortly after the Wisconsinan glaciation, with subsequent morphological and chromosomal changes resulting in the species *B. hylophaga* in the southwestern portion of the geographic range of the species.

All three of the modern species possibly were sympatric during the past. Specimens of *B. brevicauda* and *B. carolinensis* have been identified in three faunas: Cumberland Cave, Maryland (late Kansan or early Illinoian age); Ladds Quarry, Georgia (late Wisconsinan age); Meyer Cave, Illinois (early Holocene age). Specimens of *B. hylophaga* and *B. carolinensis* have been identified in two faunas: Miller's Cave, Texas (Holocene 7,200 ± 300); Klein Cave, Texas (Holocene 7,683 ± 643). Identification of specimens from Wathena (Kansas) and Java (South Dakota) as *B. carolinensis* were considered to be tentative because only three specimens were available for study from each site (Jones et al. 1984).

DISTRIBUTION

Blarina carolinensis is an Austral species whose distribution corresponds approximately to the Gulf and Atlantic Coastal Plain and Mississippi Alluvial Plain (Choate et al. 1994). Its distribution thus includes all or part of Alabama, Arkansas, Florida, Georgia, Illinois, Kentucky, Louisiana, Mississippi, Missouri, North Carolina, Oklahoma, South Carolina, Tennessee, Texas, and Virginia.

Alabama

French (1981) reported that *B. carolinensis* occurred below the Fall Line in Alabama, whereas *B. brevicauda* occurred on the Piedmont above the Fall Line and to the northeast along the southern edge of the Great Valley (between the Piedmont and Ridge and Valley physiographic provinces). French (1981) also reported an isolated population of *B. brevicauda* below the Fall Line in Barbour County and two adjacent counties in Georgia. In the Piedmont area, French (1981) reported specimens of *B. brevicauda* from four counties, including Chambers, Elmore, Lee, and Tallapoosa. Although we have no reason to question the exciting results of French's (1981) study, we would like to see these results confirmed by karyological studies and additional distributional studies to test French's conclusion concerning the rather extensive geographic range proposed for *B. brevicauda* without actual specimens. French (1981) believed that Howell (1921) failed to report *B. brevicauda* from Alabama because he did not have specimens of *Blarina* from the Piedmont. Linzey (1970) has shown that *B. carolinensis* is relatively abundant in the two coastal counties (Baldwin and Mobile) in extreme southwestern Alabama.

Arkansas

The southern short-tailed shrew occurs throughout Arkansas except for the northwestern corner (George et al. 1981, Garland and Heidt 1989, Sealander and Heidt 1990, Tumlison et al. 1992), which is occupied by *B. hylophaga* (George et al. 1981). Earlier reports of a broad zone of intergradation in central Arkansas (Ramsey 1977, Sealander 1979) were not supported by these later studies.

Florida

The exact distribution of *B. carolinensis* in Florida and its relationship with the taxa *peninsulae* and *shermani* are poorly understood. The relationship between *carolinensis* and *peninsulae,* which are known to differ in chromosome number (George et al. 1982), will be more extensively explored in a future publication in this series. For now, we consider populations as far south as Alachua County assignable to *carolinensis* (Sherman 1937, French 1981) and those from south of 28° latitude (such as specimens from Micco and Oak Lodge in Brevard County) assignable to *peninsulae* (Bangs 1898, Sherman 1937). It will be more difficult to determine the exact relationship between *carolinensis* and *shermani* because no extant populations of *shermani* have been found. Because of the overall large size of specimens of *shermani* (Hamilton 1955), there is speculation that *shermani* may represent an isolated southern population of *B. brevicauda.* This will not be known for certain, however, until a karotype is available for examination from this taxon (Layne 1992).

Georgia

Recent studies of the southern short-tailed shrew in Georgia have shown that it occurs throughout the Coastal Plain (below the Fall Line) and in the extreme northwestern part of the state (French 1981, Laerm et al. 1981, Choate et al. 1994, see also Bangs 1898, Harper 1927, Neuhauser and Baker 1974). The Piedmont and Appalachian Mountains (above the Fall Line), except for the extreme northwestern corner of the state, are occupied by *B. brevicauda* (French 1981, Laerm et al. 1981). French (1981) assigned specimens from Quitman and Stewart counties, together with specimens from an adjacent county in Alabama, to an isolated population of *B. brevicauda* that occurred below the Fall Line. Golley (1962) recognized only one species of short-tailed shrew in Georgia, and, in fact, he assigned all specimens from the state to *B. brevicauda carolinensis.* Because he recognized only one taxon in the state, he mixed all biological information for the two species. Therefore, his data cannot be used with certainty.

Illinois

Southern short-tailed shrews are confined to the area of Illinois south of a line running through Macoupin and Wayne counties (Ellis et al. 1978, Hoffmeister 1989). The northernmost record from this western portion of the geographic range of the species is from 4½ mi south and 3½ mi east of Wilsonville in Macoupin County.

Kentucky

In Kentucky, *B. carolinensis* appears to occur only west of the Tennessee River (and Kentucky Lake) with no currently known areas of sympatry with *B. brevicauda* (Bryan 1991, Choate et al. 1994). Rippy (1967) recognized the differences between populations of *Blarina* in Kentucky and speculated on the taxonomic status of *B. carolinensis,* but he treated the taxa as a single species. His studies found *B. carolinensis* confined to areas west of the Tennessee River and populations of *B. b. kirtlandi* to areas east of the Cumberland River. Rippy (1967) found no evidence of intergradation between these taxa in Kentucky. Barbour and Davis (1974) recognized the differences between the taxa, but treated them as a single species and did not comment on the exact geographic ranges of the taxa.

Louisiana

B. carolinensis occurs throughout the state of Louisiana (Lowery 1943, 1974, George et al. 1981, Choate et al. 1994) although, as Lowery (1974) pointed out, the species may be absent from the coastal tier of parishes. George et al. (1981) reported *B. hylophaga* from two localities in Caddo Parish in northwestern Louisiana.

Mississippi

The southern short-tailed shrew occurs throughout Mississippi (Crain and Cliburn 1965, Wolfe 1971, Kennedy et al. 1974, French 1981, Jones and Carter 1989, Choate et al. 1994).

Missouri

This species is known from only seven localities in six counties in the extreme eastern part of the state. The counties from which the species has been reported include Mississippi and Wayne (Easterla 1968), as well as Butler, Dunklin, St. Louis, and Stoddard (George et al. 1981). The remainder of the state is occupied by *B. hylophaga* and *B. brevicauda* (Moncrief et al. 1982), but the exact geographic relationship of *B. hylophaga* and *B. carolinensis* on the Mississippi floodplain is still not understood (George et al. 1981).

North Carolina

The distribution of the two species of short-tailed shrews in North Carolina is extremely complex and probably still not fully understood. *B. carolinensis* appears to occur in the Piedmont and Coastal Plain areas of the state (Webster et al. 1985, Webster 1996). *B. brevicauda churchi* occupies the mountains of western North Carolina. Two other subspecies of *B. brevicauda* have been reported from the Dismal Swamp, Coastal Plain, and Sandhill regions of eastern North Carolina. *B. b. telmalestes* has long been known from the Dismal Swamp and Albermarle–Pamlico Peninsula (Rhoads and Young 1897, Paul 1965, Handley 1979), but recent work has shown that this taxon also occurs to the south in North Carolina into the Upper Coastal Plain and Sandhill regions as far as Hoke, Robeson, and Bladen counties (Handley 1979, French 1981, Webster et al. 1984, Clark et al. 1985, Webster et al. 1985, Webster 1996). The Lower Coastal Plain, between the Pamlico and Cape Fear rivers in east-central and southeastern North Carolina, is occupied by the newly described subspecies *B. b. knoxjonesi* (Webster 1996). In eastern North Carolina, where the two species both occur, Webster (1996) believed that there is habitat separation of the species, with *B. carolinensis* occupying the relatively dry, well-drained uplands and *B. brevicauda* occurring in moist-to-swampy situations. Lee et al. (1983) showed that *B. b. kirtlandi* occupied the foothills of the Appalachian Mountains and Upper Piedmont of North Carolina, whereas *B. carolinensis* occurred on the Coastal Plain and Lower Piedmont. As was shown in the preceding discussion, this distributional pattern is not supported by work of other recent investigators. All other investigators do not list *B. b. kirtlandi* as occurring in North Carolina, and *B. carolinensis* is shown as occurring throughout most of the Piedmont and Coastal Plain. In an interesting paper that has often been overlooked (Handley 1979), Rhoads and Young (1897) examined specimens of *Blarina* from northeastern North Carolina. They were confused when both large and small *Blarina* were taken together at Chapanoke in Perquimans County. At first they assigned the large specimens to *Blarina telmalestes* (then considered a distinct species) and assigned the small specimen to *Blarina brevicauda carolinensis* (*carolinensis* was then and for many subsequent years considered to be a subspecies of *brevicauda*); however, they (Rhoads and Young 1897:311, see footnote) made the following statement: "A specimen of typical *brevicauda*, recently taken in eastern Gloucester County, Virginia, indicates not only that *telmalestes* is connected with the northern form [*brevicauda*] but that *carolinensis* is a distinct species whose habitat overlaps *brevicauda* in these regions." Thus, Rhoads and Young solved the puzzle of these eastern *Blarina* that would take other investigators more than a half century to redefine (Handley 1979).

Recently, as we have been trying to make decisions on publications to be included in this paper, we have received additional information on the distribution of *Blarina* in North Carolina from Wm. David Webster (*in litt.*, to H.H.

Genoways on 28 October 1996), who is actively working on this problem. "Based on what is currently available, *B. carolinensis* appears to be distributed throughout eastern and central North Carolina as far west as the Central Piedmont (< 800 ft in elevation). Its distribution does not appear to overlap that of *B. brevicauda* anywhere in the north–central Piedmont Mountain regions of the state. In the Central Plain, however, both species are broadly sympatric, but apparently not syntopic except at Corapeake (Rhoads and Young 1897)." "*B. brevicauda* appears to be distributed throughout the Upper Piedmont and Mountain provinces in western North Carolina as well as the Coastal Plain. In my opinion, specimens . . . from Forsyth County must be referable to *B. brevicauda*." For this reason, we have not included information from studies by Christenbury (1966) and Nauman (1966) based upon specimens from Forsyth County.

Oklahoma

B. carolinensis is known in Oklahoma from only three specimens taken at two localities in the vicinity of Eagleton, McCurtain County, in the extreme southeastern corner of the state (George et al. 1981, Caire et al. 1989). Much of the remainder of the state is inhabited by *B. hylophaga* (George et al. 1981).

South Carolina

The southern short-tailed shrew occurs throughout South Carolina except in all or part of five counties in the Appalachian Mountains of the extreme western portion of the state—Abbeville, Anderson, Greenville, Oconee, and Pickens (French 1981, Webster et al. 1985, Mengak et al. 1987). Golley (1966) recognized two taxa of short-tailed shrews as occurring in South Carolina, but because he treated them as subspecies of *B. brevicauda*, he mixed their biological data, and, therefore, his information cannot be used with certainty.

Tennessee

Braun and Kennedy (1983) found the contact zone between *B. carolinensis* and *B. brevicauda* to be slightly east of the Tennessee River; therefore, *B. carolinensis* occupies approximately the western third of the state (Choate et al. 1994, Kellogg 1939, Kennedy 1991, Rhoads 1896). French (1981) questioned the status of some populations of *Blarina* from south–central Tennessee based on morphometric analyses. It is clear that a karyotypic analysis will be needed before the status of these populations from south–central Tennessee is fully understood.

Texas

The distribution of the southern short-tailed shrew recently has been well documented by Schmidly and colleagues, as well as earlier workers (Bailey 1905, Baumgardner et al. 1992, Davis and Schmidly 1994, George et al. 1981, McCarley 1959, McCarley and Bradshaw 1953, Schmidly 1983, Schmidly and Brown 1979). The species occupies approximately the eastern quarter of the state with a recently discovered, disjunct population in Bastrop State Park, Bastrop County (Baumgardner et al. 1992, Davis and Schmidly 1994). At the latter locality, *B. carolinensis* was found occurring in close proximity to a disjunct population of *B. hylophaga.*

Virginia

The southern short-tailed shrew occurs in south–central and eastern Virginia (Handley and Patton 1947, Tate et al. 1980, Webster et al. 1985). The northern limit of the contiguous populations was found along the Appomattox River to the north and west of Chesterfield Court House, Chesterfield County (Tate et al. 1980). There are at least four isolated populations to the north and east of the contiguous populations on islands and peninsulas along the western shore of Chesapeake Bay—North Neck Peninsula, Gwynn's Island, Old Port Comfort, and Virginia Beach (Tate et al. 1980). Handley (1971) believed that these isolated populations were the result of the northward spread as far as the Potomac River and subsequent retreat of populations of *B. carolinensis*, with *B. brevicauda kirlandi* reoccupying most of the areas in central and eastern Virginia. The Dismal Swamp region of southeastern Virginia and northeastern North Carolina remained as the stronghold for *B. brevicauda telmalestes*. Tate et al. (1980) found two localities where *B. carolinensis* and *B. b. kirtlandi* were sympatric in central Virginia—south bank of Appomattox River, 9.8 mi north and 0.7 mi east of Amelia Court House, Amelia County, and 14 mi southwest of Richmond, Chesterfield County.

GENETICS

Much of what is known about taxonomic relationships of shrews of the genus *Blarina* is based, in part, on genetic studies. Nevertheless, additional genetic investigations are badly needed; only a few populations have been studied, and in most cases sample sizes were small. Below, we review the literature on cytogenetic and genic variation in *Blarina carolinensis*.

Chromosomal Variation

George et al. (1982) described karyotypes of *B. carolinensis* from several areas throughout the range of the species. Specimens from Polk Co., Texas, Lincoln Parish, Louisiana, Leon Co., Florida, and Aiken Co., South Carolina, were found to have a 2N = 46 and FN = 44. Specimens from Shelby Co., Tennessee, however, were found to have a variable karyotype, with 2N = 37, 38, 39 and FN = 44, 45. After studying the karyology of all species of *Blarina*, George et al. (1982) decided that the material from Tennessee was best grouped with material from the Gulf and Atlantic coastal lowland because the groups shared a common fundamental number.

The population in Shelby Co., Tennessee, subsequently was studied by Beck et al. (1991), Elrod (1992), and Elrod et al. (1996). Beck et al. (1991) confirmed the variation found in the earlier study and documented additional diploid numbers of 36 and 40, plus a new fundamental number of 43. The X chromosome was a metacentric and the Y chromosome was a small acrocentric (Beck et al. 1991). Elrod (1992) and Elrod et al. (1996) confirmed the diploid numbers found by George et al. (1982) and Beck et al. (1991), and documented new diploid numbers of 35 (one specimen) and 41 (two specimens). Elrod et al. (1996) reported new fundamental numbers of 41 and 42. Elrod (1992) and Elrod et al. (1996) trapped at four sites and reported that no karyotype was unique to a particular site; they also were the first to prepare G-banded chromosomes from these *Blarina*, reporting both Robertsonian polymorphisms and inversions. Qumsiyeh et al. (1997), in a G-banding study of 30 individuals, reported that all differences in karyotypes among specimens from western Tennessee could be accounted for by five variable Robertsonian translocations. They also found for the first time the diploid number 34 in this population.

Genic Heterozygosity

Tolliver et al. (1985), studying variation in levels of genic heterozygosity in Insectivora using electrophoresis, found *B. carolinensis* (30 specimens) from Aiken County, South Carolina, to be monomorphic for the 12 loci analyzed. The 12 genetic loci analyzed for the southern short-tailed shrew included the following: albumin; glucose-6-phosphate dehydrogenase; superoxide dismutase; isocitrate dehydrogenase-1; lactate dehydrogenase-1 and -2; malate dehydrogenase-1 and -2; phosphoglucomutase-1 and -2; phosphogluconate dehydrogenase; sorbital dehydrogenase. Tolliver et al. (1985) concluded that the mean heterozygosity per population of insectivores (2.3%) was lower than for other mammalian groups such as rodents (5.5%).

Tolliver and Robbins (1987), following up on the study by Tolliver et al. (1985), tested another 51 specimens of southern short-tailed shrews from Aiken and Barnwell counties, South Carolina, for genetic variability at 28 loci. The 12 genetic loci tested earlier by Tolliver et al. (1985) were re-examined and again found to be monomorphic, except for one specimen that was heterozygous for phosphogluconate dehydrogenase. This new study revealed that *B. carolinensis* was polymorphic at the following 11 loci: adenosine deaminase; asparate aminotransferase-1 and -2; creatine kinase; glucose phosphate isomerase; glutamate dehydrogenase-2; isocitrate dehydrogenase-2; malic enzyme; nucleoside phosphorylase; peptidase-2; phosphoglucomutase-3. The mean heterozygosity per population of *B. carolinensis* was 5.03%. Mean heterozygosity was higher for males (5.50%) than for females (3.90%). All males were heterozygous for at least one locus, whereas about 25% of the females were monomorphic.

George (1986) analyzed 18 loci for nine species of soricine and three species of crocidurine shrews, including *B. carolinensis* (n = 9) and *B. brevicauda* (n = 10). She found no fixed differences between the two species of *Blarina*, although unique alleles were found in

Table 3. Habitat notes concerning *Blarina carolinensis*.

Geographic Locality	Habitat Notes	References
General	"Woodlands and open fields, living in tunnels and runways just beneath the surface."	Merriam,1895: 13
Pope Co., IL	"variety of habitats from grassy fields to open woods to dense thickets with a heavy cover of briars and honeysuckle" . . . caught with *Sorex longirostris* "in debris adjacent to a drainage ditch. Blackberries, wild rose, and various grasses together with river birch were present."	Hoffmeister 1989: 73
Union Co., IL	"greatest number (76% of the catch) was taken in the drier woodland and open, grassy field communities of the lowlands."	Klimstra 1969: 3
southern Illinois	"Specimens were trapped in surface runways in a variety of grassy situations and in subsurface burrows in mature oak–hickory woodlands."	Layne 1958: 222
Massac and Pulaski counties, IL; Ballard and McCracken counties, KY	50% of southern short-tailed shrews taken in oldfield habitats and 50% in forested habitats.	Rose and Seegert 1982
Kentucky west of Tennessee River	"occur in every habitat investigated" . . . "often abundant on highway fill slopes under a cover of crown vetch (*Coronilla varia*) and fescue (*Festuca* sp.)."	Bryan 1991: 189
Wayne Co., MO	"found in rotten log."	Easterla 1968: 448
Lake and Obion counties, TN	"common in all areas trapped around Reelfoot Lake" . . . traps in "either wooded places or in fields procured specimens. In drier parts of the swampy woodlands around the lake shore, *Blarina* were often found under fallen logs or heavy pieces of bark. After heavy spring rains, it was not unusual to take by hand four or five shrews from under or inside rotten logs in a short search in the woods."	Goodpaster and Hoffmeister 1952: 365
Lake and Obion counties, TN	Specimens taken in these situations: "woodlot . . . trees mainly sweet gum, with a few hackberry and sycamore. Heavy ground cover of blackberry briars, grasses, etc." . . . "pile of old cypress logs overgrown with jewel weed." "Flat, dry bottom land . . . Trees consist of hackberry, sweet gum, hickory, sycamore, and elm" . . . "weedy and eroded gully" . . . "hickory-cane bottom at the base of bluff."	Calhoun 1941: 179-182
Obion and Shelby counties, TN	"bottom lands of West Tennessee both in the open and in deep, swampy woods."	Rhoads 1896: 202
Fayette, Lincoln, and Wayne counties, TN	"in runways under matted leaves on tussocks on cypress knees in the swamp as well as in the canebrake" . . . "under matted leaves along side rotten logs in deciduous woods" . . . "on a dry hillside in deciduous woods."	Kellogg 1939: 253
Tennessee	"locally abundant and may occur in a variety of habitats that includes woodland, grasslands, marshy areas, and relatively dry uplands."	Kennedy 1991: 183
Clay Co., AR	"area of capture was a low, flat, poorly drained woodland dominated by *Quercus* sp. and *Liquidambar styraciflua*."	Easterla 1968: 448

(Table continues on the next page)

Table 3 continued

Geographic Locality	Habitat Notes	References
Arkansas	"most often found in moist deciduous woods or brushy areas; it is less common in meadows, old fields or swampland."	Sealander 1979: 42; Sealander and Heidt 1990: 51
Arkansas	"captured in every county and habitat trapped; most common in moist hardwoods or brushy areas" . . . "In several old fields, this species was captured together with the least shrew (*Cryptotis parva*), and in a honeysuckle (*Lonicera japonica*) thicket it was captured together with a southeastern shrew (*Sorex longirostris*)."	Garland and Heidt 1989: 36
Shelby Co., TX	"in a runway under old grass on low ground at the edge of a cotton field."	Bailey 1905: 207-208
Hardin Co., TX	"by old logs in the woods."	Bailey 1905: 208
Nacogdoches Co., TX	"taken in considerable numbers in a grassy pasture."	McCarley and Bradshaw 1953: 516
Harrison and Sabine counties, TX	"collected in pine oak uplands."	McCarley and Bradshaw 1953: 516
Cherokee and Shelby counties, TX	"found living on densely wooded floodplains."	McCarley and Bradshaw 1953: 516
Texas	"occur throughout the pine-oak forest and pine forest regions of eastern Texas but probably do not occur extensively in the oak–hickory belt. These shrews have been collected in both upland and lowland wooded environments and also in open pastures."	McCarley 1959: 392
Texas	"occur in the pine-oak forest and pine forest regions of the pineywoods" . . . "in Big Thicket National Preserve in mixed hardwood-pine forests in traps placed adjacent to or under old logs and in the leafy cover and humus of the forest floor in lower slope hardwood-pine, upper-slope pine-oak, and flatland hardwood-pine habitats which, during the winter months, are often damp or wet."	Schmidly 1983: 47
San Augustine Co., TX	In Angelina National Forest short-tailed shrews were taken in all plots located in four growth stages (seedling, sapling, pole, and sawtimber) of loblolly-shortleaf pine stands. The most shrews were captured in stands of saplings.	Whiting and Fleet 1987
Bastrop Co., TX	"obtained from a habitat comprised primarily of oak (*Quercus stellata* and *Quercus marilandica*) with some pine (*Pinus taeda*) and juniper (*Juniperus virginiana*). The terrain was hilly with hard-packed soil of clay and sand interspersed around numerous rocks. This area had light to moderately heavy leaf litter and numerous fallen logs." Specimens of *Blarina hylophaga* were taken in the same area, but from a more grassy habitat.	Baumgardner et al. 1992: 327
LaSalle, Lincoln, and Rapides parishes, LA	"Shrews were caught most frequently on well-drained sites dominated by hardwoods; such areas are favorable for burrowing, and hardwood litter supports abundant arthropods and earthworms. Pine stands were apparently a moderately good habitat. Grass and herbaceous roughs had fewer shrews. Captures were more frequent during rainy periods, when burrows became filled with water. Shrews avoided poorly drained sites that usually have saturated soils during winter."	Hatchell 1964: 9-10

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Table 3 continued

Geographic Locality	Habitat Notes	References
Louisiana	"Although it is most common in wooded areas, it is also occasionally found in brushy thickets adjacent to forests."	Lowery 1974: 76
Kisatchie National Forest, LA	"Shrews were ubiquitous, high numbers were captured in each stand-age class" (sawtimber, poles, saplings, and regeneration) of longleaf pine (*Pinus palustris*) and/or slash pine (*Pinus elliottii*) forests.	Mullin and Williams 1987: 123
Kisatchie National Forest, LA	"Short-tailed shrew was ubiquitous in the forest." They were found in a variety of habitats (unforested, pine, pine-upland hardwoods, and streambottom hardwoods) within the loblolly-shortleaf pine type forest.	Hamilton et al. 1987: 90
Mississippi	"Sizable populations occur in old fields and forests throughout the state."	Wolfe 1971: 2
Mississippi	"collected near forest edges, in brushy areas, and around honeysuckle vines, often in the same trapline with *Mus, Microtus, Peromyscus,* and *Sigmodon.*"	Kennedy et al. 1974: 3
Claiborne Co., MS	Short-tailed shrews captured in all habitats sampled including loessial bluff forest, bottomland forest and related field habitats along the lower Mississippi River.	Hayden and MacCallum 1976
Harrison and Stone counties, MS 175;	"*Blarina* was ubiquitous" in habitats associated with longleaf-slash pine forest. Specimens	Wolfe and Lohoefener 1983: 44, 1987:
	captured in saplings, poletimber, sawtimber, and bayheads ("areas of mesic-hydric hardwoods along small streams where sweetbay, *Magnolia virginiana*, is often dominant").	Johnson 1987: 169
Kemper Co., MS	Short-tailed shrews were captured on all young loblolly pine plantations of one to four years in age.	Perkins et al. 1989
Alabama	"is wholly nocturnal. It lives chiefly in hollow logs and stumps and in underground burrows, usually in moist or peaty soil. It makes shallow runways under the surface vegetation and uses the burrows and runways of other animals."	Howell 1921: 21
Autauga Co., AL	"a number of specimens were trapped around rotten logs" in Bear Swamp.	Howell 1921: 21
Baldwin and Mobile counties, AL	"majority were taken from moist woodland bordering swamps or streams."	Linzey 1970: 68
Blount Co., AL	"two were caught in the same spot beside a log in a wooded ravine" in Bucks Pocket on Sand Mountain.	Howell 1921: 21
Clarke, Hale, and Russell counties, AL	"individuals have been taken in fields of broom sedge."	Howell 1921: 21
Cullman Co., AL	"animals plentiful in pine woods."	Howell 1921: 21
Sumter Co., AL	"a number were secured at rotten logs in weedy fields."	Howell 1921: 21
Alachua Co., FL	"confined to the grassy swamp border and blackberry briers." . . . "patches of dead grass beaten down by rain and water along the swamp have numerous small runways beneath them which are probably used by both *Blarina* and *Cryptotis*."	Blair 1935: 274
Alachua Co., FL	"at the base of a waxmyrtle in the marshy swamp area." . . . "in unburned thicket on the south side of Tiger Bay swamp."	Pournelle 1950: 313

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Table 3 continued

Geographic Locality	Habitat Notes	References
Liberty Co., FL	Single specimen of southern short-tailed shrew trapped in a planted stand of slash pine (*Pinus elliottii*) during a study of habitats in the Apalachicola National Forest.	Labisky and Hovis 1987
Putnam Co., FL	Specimens taken along pond border and in bayhead.	Moore 1943
Putnam Co., FL	"Six specimens were taken, all in moist situations: one in a flatwoods-pond border (natural ponds bordered by a narrow band of shrubs), four in bayheads (stands of hydrophytic trees dominated by broad-leaved evergreens), and one in the flatwoods (nearly level, sandy land with thinly scattered, tall pines standing solitary above a low growth of shrubs and herbs, among which gallberry, palmetto, fetterbush and wiregrass are prominent)."	Moore 1946: 53
Okefenokee Swamp, GA	"specimen trapped at the base of an old stump in a canebreak in the hammock on Floyd's Island."	Harper 1927: 271
Georgia	"common inhabitant of mesic habitats in the Coastal Plain, south of the Fall Line."	Laerm et al. 1981: 122-123
Carolinas and Virginia	"habitats such as forests are preferred. Individuals, however, have been observed in grassy fields, bogs, meadows, and tidal marshes."	Webster et al. 1985: 55
western South Carolina	Of three habitats sampled, *B. carolinensis* was taken only in "loblolly pine (*Pinus taeda*) stands (0 to 25 years old)."	Mengak et al. 1987: 63
Savannah River Site, SC	Greatest abundance appears to be in lespedeza (*Lespedeza cuneata*) oldfields.	Golley et al. 1965; Cothran et al. 1991
Savannah River Site, SC	Specimens of short-tailed shrews taken in upland hardwoods dominated by oak (*Quercus* sp.) and hickory (*Carya* sp.) and lowland hardwood–swamp forest dominated by sweetgum (*Liquidamber styraciflua*), black gum (*Nyssa sylvatica*), yellow poplar (*Liriodendron tulipifera*) and lowland oaks (*Quercus* sp.), but were not taken in an oldfield dominated by broomsedge (*Andropogon* sp.) with scattered second growth pines (*Pinus* sp.).	Gentry et al. 1968, 1971a, Whitaker et al. 1994
Savannah River Site, SC	Short-tailed shrews were taken on two 5.8-ha grids laid out in hardwood cove forest.	Smith et al. 1970
Savannah River Site, SC	Short-tailed shrews were taken throughout a 14.1-ha grid constructed in a lowland mesic–hardwood forest.	Gentry et al. 1971b, 1971c
Savannah River Site, SC	Captures of *Blarina* were uniformly distributed around the periphery of a 3.6-ha oldfield where the habitats included "grassy road shoulder," . . . "an ecotone between a grassy field and pine plantation," . . . "a pine plantation," . . . "a mixed mesophytic forest."	Briese and Smith 1974: 616
Charleston Co., SC	"in a thicket at the edge of a salt marsh."	Handley and Varn 1994: 396
Bladen Co., NC	"upland areas."	Clark et al. 1985: 17
Perquimans Co., NC	Taken together with *Blarina brevicauda* in "moss in pine woods."	Rhoads and Young 1897: 310
eastern North Carolina	"occupies relatively dry well-drained uplands, ranging from early successional herbaceous habitats to disclimax fire-maintained pine forests."	Webster 1996: 53

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Table 3 continued

Geographic Locality	Habitat Notes	References
Great Dismal Swamp, NC and VA	"occurs near southern and eastern margins of the Swamp, but probably not actually within it." Taken together with *B. brevicauda* "in the Northern Neck of Virginia."	Handley 1979: 311
Great Dismal Swamp, NC and VA	"The smaller shrews are more or less restricted to grasslands and other openings of early successional habitat, and the larger shrews [*B. brevicauda*] tend to be found in shrubby or forested locations, suggesting an ecological separation of *Blarina* species ".	Rose 1992: 191
Virginia	"Forests, thickets, and fallow fields."	Handley and Patton 1947: 111
Amelia Co., VA	*B. carolinensis* and *B. brevicauda* "collected in the same habitat (grass–shrub vegetation along a highway right-of-way)."	Tate et al. 1980: 53

malic enzyme in *B. carolinensis* populations (28% occurrence) and in glutamate-oxaloacetate transaminase-1 in *B. brevicauda* populations (12% occurrence). Overall, nine specimens of *B. carolinensis* from Leon County, Florida, were found to have a mean heterozygosity of 1%. In a cladistic analysis, the two species of *Blarina* clustered together with *Cryptotis parva* as the sister taxon (George 1986).

In a study to determine the relationship of *Blarina* from the Land Between The Lakes in Kentucky and Tennessee (n = 78), Driskell (1992) conducted electrophoretic analyses of 29 genetic loci. Specimens of *Blarina brevicauda* from Montgomery County, Tennessee (n = 5), and *Blarina carolinensis* from Jackson and Union counties, Illinois (n = 58), were used as reference samples for comparative purposes. All *Blarina* samples were monomorphic at 23 loci, but more than one allele was found at six loci: aspartate aminotransferase-1; esterase; L-iditol dehydrogenase; isocitrate dehydrogenase-2; mannose-6-phosphate isomerase; proline dipeptidase. Driskell (1992) found a fixed difference between the sample of *B. carolinensis* and all other samples of *Blarina* at the mannose-6-phosphate isomerase locus. This was the first reported fixed allele difference between species of *Blarina,* but none of the earlier studies examined this locus. The *Blarina carolinensis* sample was variable at two loci—esterase (three alleles occurring at 67.8%, 25.4%, and 6.8% frequencies) and proline dipeptidase (two alleles occurring at 62.7% and 37.3 % frequencies). This gave populations of the southern short-tailed shrew a mean heterozygosity of 3.3%, whereas samples of the northern short-tailed shrews had a mean heterozygosity of 4.7% (Driskell 1992).

HABITAT

According to the published literature (Table 3), the southern short-tailed shrew is a habitat generalist. The species has been captured in a broad range of habitats, including various types of hardwood and pine forests, bayheads, thickets, and brushy areas (including blackberry, honeysuckle, and wild rose), canebrakes, grassy, weedy, or broom sedge fields, swamps and bogs, tidal marshes, and oldfields. With a few exceptions, the species does not appear to have any local habitat preferences; authors used such terms as "variety of habitats" (Hoffmeister 1989:73, Kennedy 1991:183), "in every habitat investigated" (Bryan 1991:189, Garland and Heidt 1989:36, Hayden and MacCallum 1976:85), "common in all areas trapped" (Goodpaster and Hoffmeister 1952:365), "ubiquitous" (Mullin and Williams 1987:123, Hamilton et al. 1987:90, Wolfe and Lohoefener 1983:44, 1987:175, Johnson 1987:169), and "uniformly distributed" (Briese and Smith 1974:620) to describe the habitat distribution of these shrews. In southern pine forests, specimens of the southern short-tailed shrew were captured in all growth stages of pine plantations from seedlings through saplings, poletimber, and sawtimber to regeneration (Whiting and Fleet 1987, Mullin and Williams 1987, Wolfe and Lohoefener 1983, 1987, Johnson 1987, Perkins et al. 1989).

Several investigators (see Table 3) have indicated that *B. carolinensis* may prefer the most mesic habitats that are available. For example, Gentry et al. (1971a) found these shrews in about a 3:1 ratio in mesic lowland hardwood forest as compared with upland hardwood forest in South Carolina. However, in Louisiana, Hatchell (1964) observed that these shrews appear to avoid poorly drained sites that usually have saturated soils during winter. Handley's (1979) work in the Great Dismal Swamp would support this conclusion; *B. carolinensis* was taken along the margins of the swamp, but not actually in it. There also do not seem to be records of these shrews from the driest habitats available, such as sand dune areas with scattered vegetation and dry areas with only short grass or other vegetation.

Another indication that southern short-tailed shrews are habitat generalists is the ability of this species to invade and become established in highly disturbed habitats. Verts (1960) took this species in a 17-year-old strip-mined area in Perry County, Illinois, which had been converted to a black locust plantation. He (p. 137) included *B. carolinensis* in a group of mammal "species becoming established in older strip-mined areas." Urbanek and Klimstra (1986) examined vertebrate populations in seven habitat types (reed marsh, fescue grassland, oldfield, woodland edge, pine woodland, black locust woodland, and other deciduous woodland) at sites in Williamson and Saline counties, Illinois, that had been surfaced mined five to 34 years earlier. Of 12 species of small mammals captured during this study, only *Peromyscus leucopus* and *Blarina carolinensis* were taken in all seven habitats. Population levels of *P. leucopus* always exceeded those of *B. carolinensis*. Relative population levels were highest for short-tailed shrews in the pine woodland habitat, where it was the second most common small mammal, and the reed marsh habitat, where it was the third most abundant species behind *P. leucopus* and *Synaptomys cooperi*. In Claiborne County, Mississippi, Hayden and MacCallum (1976) studied small mammal populations in grassy fields and bottomland forests that were inundated by the Mississippi River for approximately eight months. *Mus musculus* was the most successful species in re-invading these disturbed habitats, but a specimen of *B. carolinensis* was taken in the bottomland forest within a month after trapping could be resumed.

There are few, if any, reports of *B. carolinensis* occurring in areas where there is a lack of ground cover under which they may construct runways and burrows. The vegetation type seems to be immaterial so long as it can produce ground cover to afford protection from avian predators, which are the primary predators of these shrews (see section on Predators). We believe that short-tailed shrews seek more mesic areas to inhabit, with the higher populations of invertebrate prey species in these areas possibly being the critical factor. Also, as noted above, short-tailed shrews tend to avoid areas that are too wet, probably because they are unsuited for making burrows and runways.

Authors have suggested that *B. carolinensis* may be limited in its habitat distribution in two areas of its geographic range. Both of these areas are places where *B. carolinensis* is sympatric, but not syntopic, with other species of *Blarina*. In eastern North Carolina, Webster (1996) found that *B. carolinensis* occupied coastal communities consisting of relatively well-drained uplands, ranging from early successional herbaceous habitats to disclimax, fire-maintained pine forest, whereas *B. brevicauda telmelestes* occupied habitats at the other end of the moisture gradient and usually were associated with swamp forest, river floodplain, bay forest, and

Carolina Bay habitats. A newly described subspecies of *Blarina brevicauda* from the central and southeastern coast of North Carolina was found to occupy alluvial swamp forest and pocosin-bay habitats. Soils in these areas were usually sandy and well drained with moisture content ranging from mesic to wet. In the Dismal Swamp region of northeastern North Carolina and adjacent Virginia, Rose (1992) also found an ecological separation of *Blarina* species. He noted that the smaller *B. carolinensis* was more or less restricted to grasslands and other early successional habitat, whereas *B. b. telmalestes* tended to be found in shrubby or forested habitats. It must be noted, however, that other investigators (for example, Rhoads and Young 1897, Tate et al. 1980) have taken *B. carolinensis* and *B. brevicauda* together in this same area.

In Bastrop County in central Texas, Baumgardner et al. (1992) found *B. carolinensis* in close proximity with *B. hylophaga.* They interpreted their observations to mean that there could be microhabitat separation of the species, *B. carolinensis* preferring moist deciduous woods, various types of pine forests, brushy areas, and to a lesser extent meadows and oldfields, and *B. hylophaga* occupying more grassy areas in the proximity of stands of pine trees or wooded floodplains.

The distributions of the species of *Blarina* are unique in that the three currently recognized species occupy contiguous, but nearly allopatric, ranges across the eastern half of the United States and southern Canada, with the exception of eastern North Carolina where *B. brevicauda* and *B. carolinensis* are broadly sympatric. There are only a few areas of known syntopy between these species; however, these areas are limited geographically. There are no documented cases of hybridization among the species, although both Genoways and Choate (1972) and Tate et al. (1980) suggested that specimens of intermediate size might reflect hybridization along the zone of contact between species. The distributions of the species shifted during the Pleistocene and Holocene as environmental conditions fluctuated between glacial and interglacial periods (Handley 1971, Baumgardner et al. 1992). Handley (1971) proposed that *B. carolinensis* spread outward from the Floridian Refugium as the distribution of *B. brevicauda* retreated northward. This explanation may suffice for *Blarina* populations along the Atlantic Coast, but the movement of *B. carolinensis* into Texas and up the Mississippi Embayment seems to be more complex. Handley (1971) believed the current distributional patterns of *Blarina* are maintained by competitive exclusion, temperatures, and soil moisture. We agree that temperatures and soil moisture must have roles in maintaining this distributional pattern and that the distribution of the species suggests competitive exclusion, but to our knowledge no one has yet demonstrated actual mechanisms of competitive exclusion among these species.

POPULATIONS

Several different types of studies have been undertaken that have given estimates of the populations levels of the southern short-tailed shrew, although none of these studies has focused exclusively on this species. We found three studies that gave population density levels. These studies were conducted in Tennessee and South Carolina, so two distinct populations were involved. There are two general types of studies that give the relative abundance of *B. carolinensis*—removal trapping studies conducted on pre-set grids and general survey studies. The only studies that we have included in the latter group are those that actually mention relative abundance of small mammals, because there are too many factors in the laboratory and field that affect the results of this type of study. Also, a few of these studies give some insight into the population fluctuations of short-tailed shrews and the gender ratios in these populations, at least as revealed by investigations using trapping.

Population Density

Calhoun (1941), working in the vicinity of Reelfoot Lake in northwestern Tennessee, found a population density for the southern short-tailed shrew of 5.34 individuals per acre [= 13.2/ha] trapping with Museum Special traps. This made the population of short-tailed shrews the fifth most dense among small mammals, behind *Mus musculus, Peromyscus gossypinus, Peromyscus leucopus,* and *Oryzomys palustris.*

M.H. Smith et al. (1971) and Kaufman et al. (1971), working on small mammal populations in similar habitats on the Savannah River Site in South Carolina, found markedly different densities for southern short-tailed shrew populations. M.H. Smith et al. (1971), using one Museum Special and one Victor mouse snap-trap at each station, found *B. carolinensis* to be the most abundant small mammal on their grid. Other species trapped, in order of abundance, were *Ochrotomys nuttalli, Peromyscus gossypinus, Sorex longirostris, Microtus pinetorum, Oryzomys palustris,* and *Sigmodon hispidus.* Estimates of population densities of short-tailed shrews ranged from 6.11/ha to 17.01/ha. Kaufman et al. (1971), using one Museum Special and one Victor mouse snap-trap per station, found *B. carolinensis* to be the third most abundant small mammal on their grid behind *Peromyscus gossypinus* and *Ochrotomys nuttalli.* Estimates of population densities of short-tailed shrews ranged from just 1.3/ha to 2.2/ha. The primary difference in these two studies was that M.H. Smith et al. (1971) conducted their work in August and September and Kaufman et al. (1971) worked from January through April. The estimates by M.H. Smith et al. (1971) thus represent population levels after spring reproduction and the start of fall reproduction, whereas the estimates by Kaufman et al. (1971) represent low winter population levels before spring reproduction has had an effect (O'Farrell et al. 1977).

Relative Abundance from Removal Trapping

We found nine papers that used removal trapping from pre-set grids to estimate the relative abundance of small mammals, including southern short-tailed shrews. All of these studies were conducted on the Savannah River Site in South Carolina. These studies use relative numbers of individuals removed to estimate relative abundance and rate of removal to determine which are the dominant species. The dominant species were believed to be removed fastest from the grid and to have the largest home ranges. As seen in the discussion of Home Range, this latter assumption is incorrect for shrews.

Gentry et al. (1968), in a 27-day study conducted using two Victor mouse snap-traps per station in September and October, trapped 60 *B. carolinensis,* 27 *Peromyscus gossypinus,* 21 *Sorex longirostris,* 12 *Ochrotomys nuttalli,* 3 *Neotoma floridana*, and 1 *Scalopus aquaticus.* By the fifth day of the study, 63% of short-tailed shrews and 48% of the cotton mice had been captured. By the ninth day, 87% of the short-tailed shrews, 59% of the cotton mice, and 67% of the southeastern shrews (first trapped on the sixth day) had been captured. Although more female than male *Blarina carolinensis* were trapped in the study, the males were removed initially at a faster rate, with 90% of males and only 58% of females being removed by day 5. M.H. Smith et al. (1971) obtained similar results in an 18-day study conducted in August and September using one Museum Special and one Victor mouse snap-trap per station. *B. carolinensis* was the most abundant species, followed by *O. nuttalli, P. gossypinus,* and four species each represented by one or two specimens. They found that it took nine days to estimate the population of *O. nuttalli*, but only five days to estimate the populations of *B. carolinensis* and *P. gossypinus*. In a third study reported by Gentry et al. (1971b), based on 18 days of trapping in October and November using one Museum Special and one Victor mouse snap-trap per station, *B. carolinensis* was the most abundant species of small mammal, followed in order by *P. gossypinus*, *Microtus pinetorum*, and *O. nuttalli.* It took only two days to trap 50% of the shrews from a 5.1-ha inner grid and four days from a larger 14.1-ha grid. This was the fastest removal of any species on the grid. Smith et al. (1974), in a five-year study conducted on a 5.8-ha grid in a mature hardwood forest using one Museum Special and one Victor mouse snap-trap per station, found that *B. carolinensis* was caught in the highest numbers with 36.0 ± 12.3 (SE) being taken each year, followed by *O. nuttalli* at 24.7 ± 5.3, *P. gossypinus* at 21.2 ± 4.4, and *S. longirostris* at 4.0 ± 3.0.

Another series of papers, using similar techniques and also conducted at the Savannah River Site, indicated that *B. carolinensis* is a subordinate species in the small mammal community. Faust et al. (1971) concluded that *Peromyscus gossypinus* was the dominant species based on a 63-day trapping period in June to August, using one per station of equal numbers of Sherman and galvanized drop-door live traps. They captured 147 *P. gossypinus*, 90 *O. nuttalli*, and 32 *B.*

carolinensis. By the tenth day of the study, 50% of the *P. gossypinus*, 37% of the *O. nuttalli*, and 15% of the *B. carolinensis* had been captured. Kaufman et al. (1971) obtained similar results in a study conducted from January into April, using one Museum Special and one Victor mouse snap-trap per station, except that the numbers of *P. gossypinus* and *O. nuttalli* trapped were much higher (231 and 229, respectively), and just 55 *B. carolinensis* were taken. Fifty percent of the population had been sampled by day 10 for *P. gossypinus,* day 19 for *O. nuttalli*, and day 20 for *B. carolinensis* during a 28-day sampling period. Again, Gentry et al. (1971d), using three small Victor mouse traps per station, found similar results in a study conducted in summer (July to October) and winter (December to March). *B. carolinensis* was the third most abundant species of small mammal behind *P. gossypinus* and *O. nuttalli*, although the number of captures was much closer in the winter (40 and 36 versus 26). The average numbers of days until 50% of the species was captured during the 28-day trapping periods were 6.7 for *P. gossypinus*, 11.9 for *O. nuttalli*, and 12.3 for *B. carolinensis*. The difference in the rate of removal was significant between *P. gossypinus* and the other two species, whereas the difference in rates of removal of those species were not significant.

Gentry et al. (1971a), in a four-year study on a 5.8-ha grid using one Museum Special and one Victor mouse snap-trap per station, found that the number of *B. carolinensis* ranged from a high of 59 individuals in 1967 to 32 in 1968, 26 in 1969, and 7 in 1970. This made the southern short-tailed shrew the most abundant small mammal in 1967 and 1969 and the third-most abundant behind *O. nuttalli* and *P. gossypinus* in 1968 and 1970. They attributed these changes in relative numbers to at least four factors: season (trapping occurred in September–October, July–August, May–June, and April–May, respectively); a decline in total number of small mammals from 1967 to 1970; the fact that the length of trapping period varied from year to year; and movement of the small mammals.

In an interesting study of trap responses, G.C. Smith et al. (1971) found that the southern short-tailed shrew was caught equally well by Museum Special and Victor snap traps and by painted and unpainted traps. In the first year of a two-year study, they trapped during three 28-day periods beginning on January 24. The first year they caught a total of 224 *O. nuttalli*, 223 *P. gossypinus*, and 50 *B. carolinensis*. In the second year, the total number of captures was lower and *B. carolinensis* was the most abundant small mammal (98 individuals captured as compared with 82 *O. nuttalli* and 50 *P. gossypinus*).

Relative Abundance from Survey Trapping

We found seven papers that give information about the relative abundance of the southern short-tailed shrew based on survey trapping. We have included only those papers that give specific comparative information or comment on the relative abundance of small mammals. We have excluded those papers that do not present the information in a comparative fashion because we have no way of knowing if the methods involved were comparable.

Trapping in at least seven different habitat types on surfaced-mined areas in southern Illinois using two Museum Special and one Victor mouse snap-trap per station, Urbanek and Klimstra (1986) found the southern short-tailed shrew to be the fourth most abundant small mammal of 12 species trapped. *B. carolinensis* followed *Peromyscus leucopus*, *Microtus ochrogaster*, and *Peromyscus maniculatus* in abundance. Klimstra (1969), trapping in the Pine Hills–Wolf Lake–La Rue Swamp complex in southern Illinois using Museum Special traps, found *Peromyscus leucopus* to be the most abundant small mammal with *B. carolinensis* second in abundance, accounting for 41.9% and 16.1% of total captures, respectively. Rose and Seegert (1982) obtained almost identical results from studies conducted along the floodplain of the Ohio River in western Kentucky and adjacent Illinois using one Museum Special snap-trap and one pitfall trap per station, where these same species accounted for 44.7% and 21.3%, respectively, of the total captures from among 10 species of small mammals.

Schmidly (1983), working in the Big Thicket of East Texas, captured 57 *B. carolinensis* in 30,394 trap-nights, for a trap success percentage of 0.19. Schmidly suggested that these shrews were not common in the Big Thicket, but also commented on the difficulty of trapping this shrew. In 44,456 trap-nights in loblolly-shortleaf pine forest habitats in Louisiana, Hatchell (1964) captured 289 southern short-tailed shrews, for a trap success percentage of 0.65 using Havahart size 0 live traps. Based on trapping at four locations in this habitat, *B. carolinensis* was found to be the second most abundant small mammal, but its numbers almost equaled the more abundant *Ochrotomys nuttalli* (these species accounted for 35.2% and 34.6%, respectively, of the total captures, followed by *P. gossypinus* with 23.0% and *Reithrodontomys fulvescens* with 7.2%).

Two studies focused on the relative abundance of shrews alone. Gerard and Feldhamer (1990) compared the numbers of shrews captured in southern Illinois in pitfall traps and discarded bottles. Both methods captured more *B. carolinensis* than *Cryptotis parva* and *Sorex longirostris*, with southern short-tailed shrews accounting for 76% of the shrews captured. In Arkansas, Garland and Heidt (1989) found that the southern short-tailed shrew accounted for 70% of all shrews trapped using pitfalls.

Population Fluctuations

Populations of the southern short-tailed shrew undergo several types of fluctuations, none of which is fully understood. There appear to be annual fluctuations driven, at least in part, by the reproductive cycle and multi-year fluctuations caused at least in part by environmental conditions.

Briese and Smith (1974) presented monthly capture data for *Blarina carolinensis* and *Cryptotis parva* in South Carolina, using pitfall and live traps, that showed a bimodal annual population fluctuation in both of these species. For *B. carolinensis,* population lows were in August and February during the hottest and coldest periods of the year, when their numbers of monthly captures approached zero. Population peaks for *B. carolinensis* were recorded in June and November, toward the end of the spring and autumn breeding peaks, when 40 or more individuals were captured (O'Farrell et al. 1977). The peaks for *Cryptotis parva* were in May and October, one month earlier than for *Blarina.*

Gentry et al. (1971a) documented a multi-year decline in small mammal populations in South Carolina from 1967 through 1970 using one Museum Special and Victor mouse snap-trap per station. Much of this decline was in the population of *Blarina carolinensis*, which dropped from 52.2% of the small mammal population in 1967 to 18.9% in 1970. Smith et al. (1974) continued to monitor this population through 1972 using the same trapping method, by which time it had rebounded to a level above that of 1967 and *B. carolinensis* constituted more than 65% of the small mammal population. During this six-year period, the population level of *Blarina* had the highest coefficient of variation (54.8) of the three common species studied (*Ochrotomys nuttalli*, 53.0, and *P. gossypinus*, 28.0). Smith et al. (1974) performed linear correlation analyses among the population levels of the three common species and precipitation and temperature data. They found correlation between *Blarina* population levels and the following independent weather variables: summer precipitation (+); fall precipitation (+) and spring temperature (+); summer precipitation (–) and fall precipitation (+); fall temperature (+) and spring temperature (+). The authors concluded that summer precipitation in the year preceding trapping was the important weather variable because of its impact on soil organisms, which constitute much of the food of *Blarina.*

Gender Ratios

In a study conducted by Kaufman et al. (1971) from January into April, the gender ratio of male to female *B. carolinensis* was 1:1.16. This ratio did not differ significantly from the expected 1:1 ratio. In the three other studies giving data on gender ratios in this species, all differed significantly from the expected 1:1 ratio with more females than males captured: 1:2.2 (Gentry et al. 1971a, various trapping periods over four years); 1:2.5 (Gentry et al. 1971b, trapping in October and November); 1:5 (Gentry et al. 1968, trapping in September and October). Gentry et al. (1968) found that, although more females than males were captured, males were captured at a quicker rate than females, with 90% of males caught by day 5 but only 58% of the females taken by that day.

Population Conclusions

Blarina carolinensis is a relatively abundant member of the small mammal community throughout much of its geographic range. Population density estimates range as high as 17/ha. In some areas, however, such as the Big Thicket of East Texas, southern short-tailed shrews are rare, probably because they occur in less than ideal habitats (too dry or too wet). During the annual population cycle of the species, their levels may reach as low as one or fewer individuals/ha.

This species appears to undergo a bimodal annual cycle, with population highs in June and November and lows in August and February. Some of this cycle has been attributed to the bimodal reproductive cycle of the southern short-tailed shrew, but this does not seem to us to be a totally satisfactory explanation for this entire cycle. The winter low may result, in part, from harsh environmental conditions; however, these conditions certainly never reach the extent of conditions faced by the northern short-tailed shrew. Even more enigmatic to us is the low in population numbers during the hot summer months. We are not convinced that the population decreases in numbers at this time of year; rather, this low may represent a change in activity patterns or a change in response to traps.

Some of the studies reviewed considered the southern short-tailed shrew to be a dominant species or a subordinate species (see Calhoun 1963 for terminology). The status of this species appeared to change from one study to another and from one time of year to another. We prefer to avoid these terms and the implied social interaction between the southern short-tailed shrew and the other small mammals in the community. It is unclear to us that there is any significant social interaction between the rodents of the small mammal community and this small carnivorous species that prefers a diet of invertebrates. We prefer simply to consider the southern short-tailed shrew to be a predominate species in many small mammal communities—that is, it is one of the most abundant species.

A multi-year population cycle also has been documented for *B. carolinensis* in South Carolina. It appeared that this population decline over four years was the result of an extended drought. Droughts may affect shrew populations by lowering the amount of food available and the amount of ground cover to protect their movements. The investigators identified rainfall in the previous summer as the single most important factor in the recovery of these populations, probably by making more food available. Another interpretation of the population decline seen during drought is based on anecdotal observations that we made on *B. brevicauda*. We noted on several occasions that captive individuals of that species died after just a few hours of water deprivation (because the shrews spilled their water bowls) even if food was readily available. A possible explanation is that kidney function in this species with a diet high in protein (and which, therefore, theoretically requires a substantial amount of water to eliminate nitrogenous wastes) is inadequate for survival without access to free water. This hypothesis has not been tested, but it is possible that the availability of free water likewise may be essential to *B. carolinensis*.

Several of the available studies indicate that the gender ratio of the southern short-tailed shrew differs significantly from the expected ratio of 1:1. Whether this is real or an artifact of trapping methods is not clear at this time. It does suggest a useful direction for some future research activities. The gender ratio at birth must be determined for this species to see whether the ratio is skewed in favor of females at that point, and work must be undertaken to determine if the gender ratio of adults is truly skewed as suggested by these earlier studies. It also will be important to determine the longevity of members of this species. These data may help explain the skewed gender ratios and some parts of the annual population fluctuation.

REPRODUCTION

The most extensive study of reproduction in the southern short-tailed shrew was conducted between 1967 and 1973 at the Savannah River Plant near Aiken, South Carolina, by O'Farrell et al. (1977). The female reproductive cycle showed a distinctly bimodal pattern. Pregnant females were found beginning in March through early July. The peak of reproductive activity was in April, but the number of pregnant females remained high in May and June. There was little female reproductive activity in most of July and August. The second annual cycle of breeding of female southern short-tailed shrews began in September and lasted through November, with a

Table 4. Reproductive data for female *Blarina carolinensis*.

References and Date	N	Litter Size/Reproductive Activity
Audubon and Bachman 1854		
Unknown	2	5, 6
Brimley 1923		
March, April, July	3	3, 3, 5
Hoffmeister 1989		
April	7	3 pregnant, 4 lactating
May	1	pregnant
June	1	pregnant
September	3	1 pregnant, 2 lactating
October	1	lactating
overall litter size	6	5.4 (5–6)
Layne 1958		
April 3	1	3
Linzey 1970		
November 11	1	4
December 20	1	lactating
Moore 1946		
October 18	1	4
O'Farrell et al. 1977		
Spring, March–July	24	3.75 (2-6)
Fall, September–November	17	4.24 (3-5)

peak in October. The authors (O'Farrell et al. 1977) believed that two or possibly three litters could be produced during the first period of reproduction and one or two litters in the second. During the first period, 24 pregnant females were found to have litter sizes varying from two to six with a mean of 3.75, and during the second period 17 pregnant females had litters of three to five with a mean of 4.24. The female reproductive data from the remainder of the geographic range of *B. carolinensis* (Table 4) generally support the conclusions of O'Farrell et al. (1977). One possible exception is a lactating female taken in southwestern Alabama on December 20. This seems late in the season compared with the data from South Carolina. Six pregnant females from southern Illinois (Hoffmeister 1989) had litters of five or six with a mean of 5.4. This average litter size is considerably larger than those from South Carolina. Whether this represents simply a sampling error or a real difference in litter size, with larger litters being produced at more northerly latitudes, must await future studies of reproduction in the southern short-tailed shrew.

The male reproductive cycle, indicated by testicular length, duplicated the bimodal pattern of the females except that it proceeded it by about one month (O'Farrell et al. 1977). Peak testicular lengths were recorded in March and September. O'Farrell et al. (1977) believed that the decrease in testicular length in the summer was the result of an influx of juvenile males from the spring breeding season. They found that adult males did not exhibit regressed testes in the summer. There are only a few other brief comments on male reproduction in the literature. Pournelle (1950) reported "a breeding male" taken on October 14 in Alachua County, Florida. In southern Illinois, Layne (1958:222) noted that three males taken on April 3 "were fertile," but that males trapped in May and July "were not in breeding condition." These few observations do not seem to fall outside the range of data presented by O'Farrell et al. (1977).

Golley (1962, 1966) presented reproductive data for short-tailed shrews in Georgia and South Carolina, respectively. We have not included those data here because his samples from both states may have included *B. brevicauda churchi* from the southern end of the Appalachian Mountains. Reproductive data for *B. carolinensis* reported in some recent state lists (for example, Lowery 1974, Sealander 1979, Schmidly 1983, Webster et al. 1985, Sealander and Heidt 1990, Davis and Schmidly 1994) appear to represent data from some of the older, classical studies conducted on *Blarina brevicauda*, particularly in New York, and, therefore, should not be used for *B. carolinensis*.

MOVEMENTS AND HOME RANGE

Blarina carolinensis was found to have two well-developed peaks of activity during the year in studies at the Savannah River Site in South Carolina (Briese and Smith 1974). These peaks of activity were in the spring and fall, with peaks of movement probably being correlated with the end of the spring and autumn breeding periods. The least amounts of movement for this species occurred during the hottest and coldest periods of the year.

Gentry et al. (1971b) determined the mean minimum distances traveled by southern short-tailed shrews to reach isotope-labeled baits. This value was 41.9 ± 6.4 (SE) m when calculated using a 5.1-ha internal 16 x 16 grid, and was 40.6 ± 4.2 m when using a 14.1-ha 26 x 26 grid. Faust et al. (1971), using a similar grid arrangement, found that *B. carolinensis* (sexes combined) moved an average of 94.7 m between successive captures. The median distances between successive captures was 73.7 m and the maximum distances between successive captures was 603.7 m. The distribution of average distances between successive captures showed relatively more short-tailed shrews moving farther than cotton mice (*Peromyscus gossypinus*) and golden mice (*Ochrotomys nuttalli*). Faust et al. (1971) believed that this probably was related to the more carnivorous habits of the southern short-tailed shrew.

Using the minimum area method of calculating home range, Faust et al. (1971) found a home range of 0.96 ha for short-tailed shrews in South Carolina. Several other methods of calculating home range also were used for *B. carolinensis* by these authors with the following results: exclusive boundary strip method, 0.90 ha; inclusive boundary strip method, 1.17 ha; adjusted range length method, 4.46 ha; circular method, 10.72 ha. Although *P. gossypinus* was found to be the dominant species in this study and *O. nuttalli* and *B. carolinensis* were subordinate species, *B. carolinensis* was found to have the largest home range of the three species by all methods used. This led the authors (Faust et al. 1971, Smith et al. 1975) to reject Calhoun's (1963) hypothesis of the social organization of small mammal communities. According to Calhoun (1963), the dominant species in a small mammal community should be captured at a faster rate and have a larger home range than subordinate species.

NESTS AND RUNWAYS

John Bachman (Audubon and Bachman 1854) gave the best description of the nests and associated burrows of *B. carolinensis* based on observations of this species in the vicinity of Charleston, South Carolina. Bachman stated (1854:177), "On two occasions, their small but compact nests were brought to us. They were composed of fibers of roots and withered blades of various kinds of grasses. They had been ploughed up from about a foot beneath the surface of the earth, and contained in one nest five, and in the other six young. In digging ditches, and ploughing in moderately high grounds, small holes are frequently seen running in all directions, in a line nearly parallel with the surface, and extending to a great distance, evidently made by this species." The only other mention of the nest of this species that we have been able to find is by Easterla (1968:448), who, in Clay County, Arkansas, "collected from a leaf nest in a rotten log two *B. b. minima*." Other recent descriptions of the nests of this species in reports for several state mammal surveys (for example, Lowery 1974, Sealander 1979, Sealander and Heidt 1990) all appear to be based on earlier descriptions of the nests of *B. brevicauda* (Shull 1907, Hamilton 1929).

B. carolinensis moves in surface or subsurface runways. The surface runways almost invariably are under some type of ground cover, such as leaves, pine needles, or grass. Runways used by short-tailed shrews frequently are those used by mice or voles, and the shrews contribute little in runway maintenance (Webster et al. 1985). We believe that the bimodal annual population cycle of *B. carolinensis* may be explained at least during the summer months by the shrews confining their activity almost exclusively to subsurface runways. This would give the appearance of a population decline in trapping studies conducted during these months. Because shrews have a small body size and a concomitant large body surface area relative to mass making them unable to prevent overheating at temperatures above 30°C, it would seem reasonable that they would restrict their activities primarily to their subsurface runways and nests during the hot summer months.

DIET

There appears to be only two studies that give extensive information on the diet of *Blarina carolinensis*. One of these studies was conducted by Calhoun (1941) at the Reelfoot Lake Biological Station in northwestern Tennessee between 20 July and 1 September 1940. Of the nine southern short-tailed shrews that were caught during the study, eight had stomachs that could be examined for dietary contents. The following food items were found (percent occurrence indicated in parentheses): the pulmonate snail, *Deroceras agreste* (14); Hemiptera (14); Lepidoptera larvae (28); Coleoptera (total 57), represented by Scarabaeidae (28), larvae (14), and miscellaneous (28); Hymenoptera: Formicidae (28). The stomach of one individual contained 14% vegetable matter, which was not further identified.

Whitaker et al. (1994), studying 50 southern short-tailed shrews from the Savannah River Site in South Carolina, found that 45 individuals had stomach contents that could be analyzed to determine diet. Twenty-three different food items were found as follows (percent total volume in parentheses): slugs and snails (18.0), *Endogone* and related genera (16.3), earthworms (14.8), Coleoptera adults (9.6), Coleoptera larvae (5.8), spiders (4.6), Lepidoptera larvae (3.7), unidentified larvae (3.6), Diptera adults (3.0), Phalangida (2.4), Scarabaeidae larvae (2.4), Lepidoptera adults (2.3), crickets (2.1), Tipulidae (2.1), unidentified (1.8), muscoid Diptera (1.6), Hemiptera (1.3), vegetation (1.2), insects (1.1), vertebrates (1.0), Formicidae (0.6), Chilopoda (0.5), and Hemerobiidae (0.1). It was important to note that the hypogeous mycorrhizal fungus *Endogone* was a significant component of the diet of the southern short-tailed shrew in South Carolina. This small mammal–fungal relationship is an important component of many communities because the small mammals act as a dispersal agent for this valuable dietary item.

During the study of the use of American alligator (*Alligator mississippiensis)* nests as nest sites for freshwater turtles (*Chrysemys nelsoni, Trionyx ferox,* and *Kinosternon subrubrum*) in Alachua County, Florida, several predators on eggs of these species were identified. Among the predators, a *Blarina carolinensis* was observed eating the egg of one of the turtles (Dietz and Jackson 1979). This is probably not a particularly important (or wise) food source for these shrews.

Audubon and Bachman (1854:177) recorded the following observation on the food habits of *B. carolinensis* from the vicinity of Charleston, South Carolina: "We observed on the sides of one of these galleries, a small cavity containing a hoard of coleopterous insects, principally composed of the rare species (*Scarabeous* [= *Dynastes*] *tityus*), fully the size of the animal itself; some of them were nearly consumed, and the rest mutilated, although still living." This is the only record of which we are aware of food hoarding in this species, although it has been reported for *B. brevicauda* (Shull 1907, Hamilton 1930).

Davis and Schmidly (1994:20) reported data from "Analysis of more than 400 stomachs from East Texas . . . ." This clearly was a *lapsus* because Davis attributed those same data to the work of W.J. Hamilton in New York in two earlier publications (Davis 1960, 1974). Therefore, those data are for *B. brevicauda* rather than *B. carolinensis*.

Several recent authors have listed earthworms as an important part of the diet of *Blarina carolinensis*. This, however, was not conclusively shown to be true until the report of Whitaker et al. (1994). In their study, Whitaker et al. (1994) found that southern short-tailed shrew took earthworms less frequently than a comparative sample of northern short-tailed shrews from Indiana (14.8% versus 37.5%). They hypothesized that the difference might be caused by the lower earthworm populations in the sandy soils in South Carolina. Many authors have listed small vertebrates as a food item of the southern short-tailed shrew, but this was not proven until the report by Whitaker et al. (1994). They reported a frequency of vertebrates in the diet at 1.0%, but did not identify the species. The only other evidence that southern short-tailed shrews are willing to kill and consume small vertebrates comes from a study of predator avoidance behavior in juvenile skinks (Cooper and Vitt 1985). Adult southern short-tailed shrews did kill and consume several juvenile skinks (*Eumeces fasciatus* and *E. laticeps*) during that study. It is clear from these dietary data for the southern short-tailed shrew that there is much more to learn about their feeding habits.

PHYSIOLOGY

There are only three studies that include information on the physiology of the southern short-tailed shrew; therefore, much remains to be learned about this aspect of its biology. The three studies are on diverse topics and provide some insight into broad aspects of the physiology of these interesting little shrews.

Energy Expenditure

McNab (1991), in a well-documented study, reported on the rate of metabolism and temperature regulation in *B. carolinensis* and compared these results with those for other species of shrews. When inactive, southern short-tailed shrews maintained their body temperature at 36.8 ± 0.07°C between ambient temperatures of 10° and 31°C. At ambient temperatures above 30°C, body temperature increased, and below 12°C, body temperature decreased. The zone of thermoneutrality in the southern short-tailed shrew (average mass 10.2 g) extended from 30° to 34°C.

In the zone of thermoneutrality, the mean rate (basal rate) of oxygen consumption was 3.26 ± 0.058 $cm^3O_2/g{\cdot}h$, which is 1.70 times the value expected. Mean minimal thermal conductance was 0.375 ± 0.0086 $cm^3O_2/g{\cdot}h{\cdot}°C$, which is 1.20 times the standard value expected from mass. McNab (1991) found that the basal rate for *B. carolinensis*, but not for *B. brevicauda*, approached values for crocidurines, which are known to enter torpor. No torpor was observed in *B. carolinensis*.

Seasonal Changes in Brown Adipose Tissue

Interscapular brown adipose tissue is known to produce heat by non-shivering thermogenesis, which, in winter, is a less energy-demanding form of heat production than shivering thermogenesis. Non-shivering thermogenesis in *B. brevicauda* was documented more than a decade ago (Merritt 1986 and citations therein), but was first demonstrated in *B. carolinensis* by Dew (1992). Because heat production is related to the number of mitochondria, Dew (1992) measured the volume of brown adipose tissue cells occupied by mitochondria in summer-caught (June–August) and winter-caught (December–February) specimens of *B. carolinensis* from eastern Virginia. She found that 20.5% of the volume of brown adipose tissue cells was filled with mitochondria in winter specimens, as opposed to 5.65% in summer specimens. The mitochondria of winter specimens had increased their size and possibly increased their number, but Dew (1992) could not determine this for certain.

Standing Crop of Elements

Beyers et al. (1971), in a unique study, measured the standing crops of elements in a small mammal community in a lowland mesic-hardwood forest in South Carolina. The standing crop of elements contained within the bodies of three species of mammals (*Blarina carolinensis, Peromyscus gossypinus,* and *Ochrotomys nuttalli*) accounted for between 79 and 98% of the material contained within the entire small mammal community. The following mean values (ppm dry weight) were found for elements contained by *B. carolinensis*: calcium, 34,400;

potassium, 17,200; sodium, 4,220; magnesium, 1,438; iron, 500; zinc, 120. Standing crops of the six elements (g/ha) for southern short-tailed shrews from two sites were as follows: calcium, 0.508, 0.103; potassium, 0.224, 0.046; sodium, 0.060, 0.012; magnesium, 0.019, 0.004; iron, 0.007, 0.002; zinc, 0.002, 0.000. The primary difference among the species was the higher iron concentration in *Blarina*. This difference was attributed to the ratio of body size to blood volume in the smaller shrew.

Submaxillary Gland Toxin

Pearson (1942) demonstrated that a toxin produced in the submaxillary glands of *Blarina brevicauda* could kill mice (Ellis and Krayer 1955). No similar work has been done with *B. carolinensis*. We had initially included comments by Christenbury (1966) in this section, but the latest information indicated that the specimens she tested from Forsyth County, North Carolina, are *Blarina brevicauda* as she had originally stated.

PREDATORS

We found 13 predators of *Blarina carolinensis*, representing four vertebrate classes, documented in the literature (Table 5). Six of the species are raptors, with the most reports for the Barn Owl. The Barn Owl is a common raptor in the southeastern United States, and studies of its food habits in the literature far out-numbered those for other species. The southern short-tailed shrew formed a significant part of the diet of Barn Owls, with the shrews accounting for more than 20% of the diet in two of the studies (Adams et al. 1986, Chicardi et al. 1990). Given the nocturnal habits of short-tailed shrews, it is not surprising to find owls represented more heavily among the raptors than hawks. It is surprising to have only two mammalian predators represented, but it certainly is not the result of the lack of studies of the diets of most of the predators sharing the geographic range of the southern short-tailed shrew. It has been suggested in the literature for other species of shrews that their foul odor may give them some protection from mammalian predators, and that may well be what is happening with the southern short-tailed shrew. Four species of snakes have been reported as preying on the southern short-tailed shrew, but it should be noted that, in each of the five studies reported (Table 5), *B. carolinensis* was represented by just one individual. This work certainly establishes snakes as predators of short-tailed shrew, but more extensive, long-term studies are needed to fully assess their impact on shrew populations. Certainly the most unusual predator of the southern short-tailed shrew was the green sunfish. This report was based on the presence of a shrew in the stomach of one of 84 sunfish examined from Lake Glendale in southern Illinois (Huish and Hoffmeister 1947). The authors surmised that this shrew may have pursued an invertebrate prey item too near the edge of the lake.

Probably the most extensive study of predation involving *B. carolinensis* was conducted over an 11-month period in Ozan in southwestern Arkansas (Steward et al. 1988). Over this period, beginning in May 1987 and ending in March 1988, monthly collections were made of pellets from Barn Owls occupying an abandoned cotton gin. Remains of southern short-tailed shrews were recorded in only four months, with a high of four in both June 1987 and March 1988. Remains from this species also were found in July 1987 and February 1988. Remains of 11 species of mammals were identified throughout the study, with *Microtus pinetorum* and *Sigmodon hispidus* being the most abundant species in each month.

PARASITES AND DISEASE

A search of the available literature revealed that 57 species of parasites have been reported from *Blarina carolinensis* (Table 6). Of these, 44 species are ectoparasites—40 species of mites, two fleas, one tick, and one beetle. The other 13 species are endoparasites, including seven species of nematodes, four trematodes, one acanthacephalan, and one tapeworm.

Pascal (1984) presented an excellent survey of the ectoparasites of *B. carolinensis* and compared the ectoparasite faunas of *B. carolinensis* and several populations and subspecies of *B. brevicauda*. Of the 34 ectoparasites that Pascal (1984) considered to be regular associates of *Blarina,* 31 were recovered from both *B. brevicauda* and *B. carolinensis*. The three ex-

Table 5. Vertebrate predators of *Blarina carolinensis*.

Predators: Scientific Name	Predators: Common Name	Locality	Percent Occurrence of *Blarina* in Diet	References
Canis latrans	coyote	Arkansas	—	Gipson, 1974
		northwestern Louisiana	3.0%	Michaelson and Goertz, 1977
Vulpes vulpes	red fox	Union Co., IL	4.7%	Knable, 1970
Asio flammeus	Short-eared Owl	Roth Prairie, Arkansas Co., AR	7.6%	Smith and Hanebrink, 1982
Asio otus	Long-eared Owl	Jonesboro, Craighead Co., AR	4.6%	Lavers, 1990
		Pyatt, Perry Co., IL	0.6%	Birkenholz, 1958
Otus asio	Screech Owl	northeastern Arkansas	2.9%	Hanebrink et al., 1979
Tyto alba	Barn Owl	Auburn, Lee Co., AL	2.6%	Dusi, 1957
		Tuscaloosa, Tuscaloosa Co., AL	—	Wolfe and Rogers, 1969
		Arkansas State University, Craighead Co., AR	4.0%	Paige et al., 1979
		Ozan, Hempstead Co., AR	2.8%	Steward et al., 1988
		Garland, Miller Co., AR	1.3%	Westmoreland et al., 1994
		Paynes Prairie State Preserve, Alachua Co., FL	13.2%	Miller, 1994
		McIntosh, Marion Co., FL	1.0%	Trost and Hutchison, 1964
		Orlando Wilderness Park, Orange Co., FL	23.6%	Chicardi et al., 1990
		Norris City, White Co., IL	4.9%	Feldhamer, 1985
		Brunswick Co., NC	1.6%	Adams et al., 1986
		Chatham Co., NC	21.1%	Adams et al., 1986
		South Island, Georgetown Co., SC	0.7%	Feldhamer et al., 1987
		Carthage, Panola Co., TX	1.1%	Parmalee, 1954
Accipiter cooperii	Cooper's Hawk	northeastern Arkansas	6.3%	Hanebrink et al., 1979
Buteo jamaicensis	Red-tailed Hawk	northeastern Arkansas	21.4%	Hanebrink et al., 1979
Agkistrodon contortrix	copperhead	North Carolina/South Carolina	1.6%	Brown, 1979
Agkistrodon piscivorus	cottonmouth	Arkansas/Louisiana/Texas	1.9%	Burkett, 1966
		Atchafalaya River Basin, LA	4.0%	Kofron, 1978
Elaphe obsoleta	black rat snake	North Carolina/South Carolina	2.0%	Brown, 1979
Masticophis flagellum	coachwhip	Fort Benning, Chattahoochee/Muscogee counties, GA	2.2%	Hamilton and Pollack, 1956
Lepomis cyanellus	green sunfish	Lake Glendale, Pope Co., IL	1.2%	Huish and Hoffmeister, 1947

Table 6. Ectoparasites and endoparasites reported from *Blarina carolinensis*.

Parasites	References
Mites	
Androlaelaps fahrenholzi	Hays and Guyton 1958, Pascal 1984, Whitaker and Wilson 1974, Whitaker et al. 1994
Androlaelaps casalis	Whitaker et al. 1994
Bakerdania pluisetosa	Pascal 1984, Whitaker et al. 1994
Bakerdania	Pascal 1984, Whitaker et al. 1994
Blarinobia simplex	Pascal 1984, Whitaker et al. 1994
Comatacarus americanus	Whitaker et al. 1994
Cyrtolaelaps	Pascal 1984
Echinonyssus blarinae	Whitaker et al. 1994
Eucheyletia bishoppi	Pascal 1984
Eulaelaps stabularis	Hays and Guyton 1958, Pascal 1984, Whitaker and Wilson 1974, Whitaker et al. 1994
Euryparasitus	Pascal 1984
Euschoengastia ohioensis	Pascal 1984
Euschoengastia setosa	Pascal 1984
Glycyphagus hypudaei	Pascal 1984
Haemogamasus harperi	Hays and Guyton 1958, Whitaker and Wilson 1974
Haemogamasus liponyssoides	Pascal 1984, Whitaker et al. 1994
Haemogamasus longitarsus	Pascal 1984
Histiostoma	Pascal 1984
Hypoaspis	Pascal 1984
Myonyssus jamesoni	Pascal 1984
Orycteroxenus soricis	Pascal 1984, Whitaker et al. 1994
Proctolaelaps	Pascal 1984
Protomyobia americana	Pascal 1984
Protomyobia blarinae	Whitaker et al. 1994
Prowichmannia spinifera	Pascal 1984, Whitaker et al. 1994
Pygmephorus equitrichosus	Pascal 1984
Pygmephorus hamiltoni	Pascal 1984, Whitaker et al. 1994
Pygmephorus hastatus	Pascal 1984
Pygmephorus horridus	Pascal 1984, Whitaker et al. 1994
Pygmephorus johnstoni	Pascal 1984, Whitaker et al. 1994

(Table continues on the next page)

Table 6 continued

Parasites	References
Pygmephorus moreohorridus	Pascal 1984, Whitaker et al. 1994
Pygmephorus scalopi	Pascal 1984
Pygmephorus tamiasi	Pascal 1984, Whitaker et al. 1994
Pygmephorus whitakeri	Pascal 1984, Whitaker et al. 1994
Pygmephorus whartoni	Whitaker et al. 1994
Pymephorus wrenschae	Pascal 1984
Scutacarus	Pascal 1984
Xenoryctes latiporus	Pascal 1984, Whitaker et al. 1994
Xenoryctes nudus	Pascal 1984
Fleas	
Ctenophthalmus pseudagyrtes	Pascal 1984
Doratopsylla blarinae	Pascal 1984, Whitaker et al. 1994
Tick	
Dermacentor variabilis	Pascal 1984
Beetle	
Leptinus americanus	Pascal 1984, Whitaker et al. 1994
Acanthocephalan	
Centrorhynchus	Miller et al. 1974
Nematodes	
Capillaria plica	Miller et al. 1974
Capillaria	Barker 1986, Barker et al. 1987
Longistriata caudabullata	Miller et al. 1974
Physaloptera	Miller et al. 1974
Porrocaecum encapsulatum	Miller et al. 1974
Porrocaecum ensicaudatum	Barker 1986, Barker et al. 1987
Porrocaecum	Barker 1986, Barker et al. 1987
Tapeworm	
Cryptocotylepis anthocephalus	Barker 1986, Barker et al. 1987, Miller et al. 1974
Trematodes	
Brachylaima dolichodirus	Miller et al. 1974
Brachylaima thompsoni	Barker 1986, Barker et al. 1987, Miller et al. 1974
Brachylecithum	Miller et al. 1974
Panopistus pricei	Barker 1986, Barker et al. 1987, Miller et al. 1974

ceptions were taken from *B. brevicauda* only: *Corrodpyslla curvata, Neotrombicula cavicola,* and *Echinonyssus blarinae.* Pascal (1984) believed that the absence of *Echinonyssus blarinae* from *B. carolinensis* was the most significant exception because this blood-sucking nest parasite was recovered from all subspecies of *B. brevicauda.* Pascal (1984) also compared the frequency of occurrence of species of ectoparasites in populations of *B. carolinensis* and *B. b. kirtlandi* occurring within a 200-miles distance in southern Illinois and Indiana. He found that *Pygmephorus whitakeri* was the only species of ectoparasite with a frequency of occurrence that was significantly greater on *B. b. kirtlandi,* whereas six species of ectoparasites had a significantly higher occurrence on *B. carolinensis*: *Androlaelaps fahrenholzi, Myonyssus jamesoni, Olistrophorus blarina, Pygmephorus, Bakerdania plurisetosa,* and *Doratopsylla blarinae.* Obviously, the absence of *Echinonyssus blarinae* from *B. carolinensis* also was highly significant. Pascal (1984) was not able to demonstrate any morphological divergence between populations of ectoparasites occurring on *B. carolinensis* and *B. b. kirtlandi.*

Whitaker et al. (1994), studying 50 specimens of *B. carolinensis* from South Carolina, found that all shrews carried ectoparasites. They found 27 species of ectoparasites, including 25 species of mites representing eight families, one species of flea, and one of beetle (Table 6). The most frequently observed ectoparasites on *B. carolinensis* from this site were *Echinonyssus blarinae, Haemogamasus liponyssoides* (Laelapidae), *Asiochirus blarina* (Listrophoridae), *Orycteroxenus soricis* (Acaridae), and *Protomyobia blarinae* (Myobiidae). Unlike Pascal (1984), Whitaker et al. (1994) did find *Echinonyssus blarinae* occurring on the southern short-tailed shrew. It is unclear at this time whether Pascal (1984) simply missed the species in his Illinois survey or if there are geographic differences in the ectoparasite fauna occurring on *B. carolinensis*.

Studies of the endoparasites of *B. carolinensis* were undertaken in North Carolina by Miller et al. (1974) and in southern Illinois by Barker (1986) and Barker et al. (1987). Miller et al. (1974) found 44 of 46 (96%) shrews taken in the vicinity of Raleigh, North Carolina, to be infected by at least one of 10 species of helminths, including four species of trematodes, one tapeworm, four nematodes, and one acanthacephalan. They concluded that *B. carolinensis* from near Raleigh had few species and individuals of helminth parasites. Percent infestation of host individuals was as follows: *Brachylaima dolichodirus,* 61%; *B. thompsoni,* 28%; *Brachylecithum* sp., 4%; *Panopistus pricei,* 15%; *Cryptocotylepis anthocephalus,* 6.5%; *Capillaria plica,* 9%; *Longistriata caudabullata,* 17%; *Physaloptera* sp., 4%; *Porrocaecum encapsulatum,* 4%; *Centrorhynchus* sp., 4%. Barker (1986) and Barker et al. (1987) found 13 of 20 (65%) shrews from southern Illinois to be infected by at least one of six species of helminths, including two species of trematodes, one tapeworm, and three of nematodes. Their results also showed a relatively low rate of infestation of hosts, as follows: *B. thompsoni,* 20%; *P. pricei,* 15%; *C. anthocephalus,* 40%; *Capillaria* sp., 15%; *P. ensicaudatum,* 10%; *Porrocaecum* sp., 10%. In contrast to the studies in North Carolina and Illinois, which both found *Capillaria* present, Layne (1968) did not find *Capillaria hepatica* present in any of five specimens of southern short-tailed shrews from Alachua County, Florida.

Whitaker and Wilson (1974), in their review of mites from wild mammals of the United States and Canada, listed records of three species based on earlier reports that were erroneously attributed to *B. carolinensis.* They listed *Myonyssus jamesoni* based on the original description of the species by Ewing and Baker (1947), which included specimens from Greenbriar [Robertson County], Tennessee, and *Blarinobia simplex* based on the original description of the species by Ewing (1938), which included specimens from Smoky Mountains, Tennessee, and Terra Cotta, District of Columbia; both of these reports pertain to *Blarina brevicauda* and not *B. carolinensis.* The record of *Eulaelaps stabilaris* listed from Kansas by Whitaker and Wilson (1974), based on the report by Jameson (1947), and the record of *Stenoponia americana* listed from Kansas by Pascal (1984), based on the report by Poorbaugh and Gier (1961), are both properly attributed to *B. hylophaga* rather than *B. carolinensis.*

A random sample of 24 *B. carolinensis* from southern Illinois was tested for rabies by Pearson and Barr (1962). Tests of brain and salivary tissues from all specimens tested negative.

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