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The Biology of the Soricidae

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PREFACE

SARAH B. GEORGE, GORDON L. KIRKLAND, JR., AND JAMES S. FINDLEY

The papers published in this volume were originally presented in a symposium entitled "The Biology of the Soricidae" at the 67th annual meeting of the American Society of Mammalogists, held in June 1987 at the University of New Mexico in Albuquerque. When we organized the symposium, we had two goals in mind. First, we wished to assemble speakers currently studying diverse aspects of soricid biology to enable us to survey the breadth of ongoing research on this relatively little-studied group of small mammals. Second, we hoped to stimulate further research on soricids by highlighting problems and raising questions that can and should be addressed in the future. The papers in this volume deal with current research on the ecology, behavior, physiology, biogeography, and systematics of shrews.

Williams examines the distribution of soricids along an altitudinal transect on the western slope of California's Sierra Nevada, where five species of *Sorex* occur. He found that in each major vegetational zone, one species dominated the soricid community. This contrasted with the situation on the eastern slope of the Sierra Nevada and in other forest communities in North America, where soricid communities may consist of up to five species. Kirkland examines this phenomenon further, seeking to explain the high species richness of many soricid communities. He concludes that, although the small size of shrews may facilitate coexistence by permitting shrews to exploit resources in a more coarse-grained fashion, environmental moisture is the factor that determines resource availability and ultimately the potential richness of soricid communities. Churchfield confirms this observation with a fine-grained analysis of soricid communities consisting of species with varying foraging techniques. Her data also suggest that in more diverse communities dietary generalists may outnumber dietary specialists.

McNab contrasts metabolic rates in crocidurine and soricine shrews, demonstrating that soricines are capable of far more precise body temperature regulation than crocidurines. He suggests that this is a direct reflection of the respective distributions of these largely allopatric subfamilies. The predominantly tropical and warm-temperate crocidurines face considerably less environmental stress than soricine shrews, which are largely temperate and sub-boreal in distribution. Merritt and Adamerovich explore the winter physiology of a soricine shrew, *Blarina brevicauda,* and confirm that this species does not employ torpor or communal nesting to deal with cold winter temperature; however, winter survival is facilitated by prey-caching behavior and the construction of elaborate networks of tunnels at depths that insulate these shrews from cold temperatures.

The systematic works examine morphologic variability in two species complexes of *Sorex.* In an analysis of populations of *Sorex cinereus* from North America and eastern Siberia, van Zyll de Jong divides the species into three subgroups. The biogeographic history of this species corresponds well to vicariance models of the Pleistocene history of North America and Beringia. George and Smith examine cranial variability in two commonly confused species, *Sorex vagrans* and *S. monticolus,* in the Pacific Northwest of North America. They quantify cranial variability within and among populations of each species, documenting an increase in cranial size in populations of *S. vagrans* on the Gulf and San Juan Islands between Vancouver Island and the mainland.

Shrews occupy a broad spectrum of habitats throughout the Holarctic and much of the Old World tropics. They commonly coexist in multispecies communities, despite the fact that (to us) they appear to vary little in size, overall morphology, and ecological strategy. Compared to many other small mammals, shrews are difficult to catch, maintain, and manipulate. As a consequence, relatively little research has been conducted to answer basic questions regarding their ecology, physiology, and systematics. The seven papers included in this volume attempt to explore a few of these questions. We hope that these papers will stimulate the reader to undertake further research in these areas as well as on aspects of soricid biology not addressed in this volume.

ACKNOWLEDGMENTS

The preparation of this volume involved the help of many colleagues. The role of Rayann Robino, U.S. Fish and Wildlife Service, was central. She dealt with style and technical editing, proofreading, correspondence, acted as a liaison with the University of New Mexico Printing Services, and in general tried, with varying degrees of success, to keep the Editors abreast of their responsibilities. James Brown, James Findley, Robert Hoffmann, Karl Koopman, David Nagorsen, Eric Toolson, John Whittaker, Bruce Wunder, and David Zegers each kindly consented to review one or more of the contributions. Editing and proofreading tasks were carried out by Joseph Cook, Forrest Davis, Jennifer Frey, William Gannon, Scott Gardner, Gregory Hartman, Douglas Kelt, and Norman Scott. Irene Farmer and Kelly Burks typed the manuscripts into a word processing program. Some travel was underwritten by the Department of Biology, University of New Mexico, Donald Duszynski, Chairman, and by the James Herbert Smith Estate. Publication of the symposium would not have been possible without the generous support of Paul Risser, Vice President for Research at the University of New Mexico.

James S. Findley
Terry L. Yates

Habitats of Shrews (Genus *Sorex*) in Forest Communities of the Western Sierra Nevada, California

DANIEL F. WILLIAMS

Abstract

The distribution and habitat associations of shrews (*Sorex*) in forest communities of the western slope of the southern Sierra Nevada were determined from captures in pitfall traps placed in eight successional stages of ponderosa pine, mixed conifer, and red fir forests, and their corresponding riparian communities. Data from this and ancillary studies in mixed conifer, red fir, and lodgepole pine forests and digger pine/blue oak woodlands show that each major forest zone is dominated by a single species of shrew: *S. ornatus* in the pine/oak woodland and ponderosa pine communities, *S. trowbridgii* in mixed conifer forests, and *S. monticolus* in red fir and lodgepole pine forests. *Sorex palustris* is relatively uncommon in the riparian zone of mixed conifer, red fir, and lodgepole pine forests. *Sorex tenellus* was captured at a single site in red fir forest. Within each forest type, shrews were most common in riparian zones with abundant shrubs, and in the brushy successional stages of forests. Occurrences of coexisting species of shrews were rare, almost always limited to two species, and primarily confined to the interdigitating forest communities along canyon bottoms and slopes in the transitional elevations between forest types. This contrasts markedly with the eastern slope of the Sierra Nevada, where as many as five coexisting species of shrews may be found, and with most other temperate North American forests where from two to five coexisting forest species are characteristic.

INTRODUCTION

Shrews of the family Soricidae are prominent members of woodland and forest communities throughout the northern hemisphere. In deciduous hardwood and conifer forests of the north temperate latitudes, from one to six species may be found (Spencer and Pettus 1966, Fleming 1973, Kirkland 1985). In some forest communities, and in others at periods during the year, shrews may be the most abundant small-mammal species. Invertebrates are the staple food for most species of shrews, although many also eat seeds, which may comprise the bulk of their diets seasonally (Criddle 1973, Whitaker and Maser 1976, Terry 1978, French 1984). Shrews impact forest communities through the consumption of insects, other small animals, and seeds, which can influence plant succession, reforestation, and irruptions of forest pests.

Although considerable information on small mammals of the western Sierra Nevada is available, there is little detailed information on shrews or other species of small mammals, and few published studies provide more than anecdotal information on distributions and habitats. Despite the lack of data derived from field studies in the Sierra Nevada for most mammalian species, the U.S. Department of Agriculture, Forest Service, developed accounts of the distributions and habitat associations of mammals for the western slope of the Sierra Nevada, California, as part of a program for providing land managers with quantitative information to predict responses of wildlife species to forest and rangeland management alternatives (Verner and Boss 1980). Each major forest type was divided into four successional stages (grass/forb, shrub/seedling/sapling, pole/medium tree, and large tree), and each tree stage was further divided into three classes based on canopy cover (<40%, 40–69%, 70–100%), for a total of eight stages. Streamside communities were treated separately as low-, medium-, and high-elevation riparian/deciduous zones, and meadows were classified as wet and dry. Thus, for a given forest type there were 11 potentially distinct habitats for wildlife.

In the western Sierra Nevada of central California, forest communities are strongly zoned by altitude. In the Sierra National Forest of Fresno County, digger pine (*Pinus sabiniana*) and blue oak (*Quercus douglasii*) woodlands occupy the lowest zone, between about 450 and 915 m. Chaparral is a fire disclimax of this community. Between about 915 and 1,525 m, ponderosa pine

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(*Pinus ponderosa*) is the predominate tree species. Above about 1,525 m, and extending to about 2,100 m, the mixed conifer forest consists of ponderosa pine (lower elevations), sugar pine (*P. lambertiana*), white fir (*Abies concolor*), Douglas fir (*Pseudotsuga menziesii*—rare, found at only one site in the study area); incense cedar (*Libocedrus decurrens*), Jeffrey pine (*P. jeffreyi*—at higher elevations), and black oak (*Q. kelloggii*). Above about 2,100 m to about 2,550 m, red fir (*A. magnifica*) is the dominant climax species; in this zone, Jeffrey pine occupies dry, southward-facing slopes and lodgepole pine (*P. contorta*) is a sere and fire disclimax of red fir forest. Above about 2,600 m, lodgepole pine is the dominant forest tree. Klyver (1931) provided details of the major plant communities on a transect through the Sierra Nevada in the region of the studies reported here.

According to the Wildlife Habitat Relationships Program (WHRP) for the western Sierra Nevada, six species of *Sorex* occur on the western slopes (White et al. 1980). As a test of the predictions of the WHRP for small mammals of the three principal forest communities of the western Sierra Nevada, a sampling program for the four successional stages and three canopy cover classes of ponderosa pine, mixed conifer, and red fir forests, and the corresponding riparian zones, was instituted. Prerequisite studies to determine the most efficient type of traps (Williams and Braun 1983) and spacing of traps (Braun-Hill and Williams 1986) and studies of small mammals in the foothills of the western Sierra Nevada (unpubl. report, U.S. Bureau of Land Management; and unpubl. data), together with the test of the WHRP, provide substantial data on distributions and habitats of shrews, which are presented and interpreted here.

METHODS AND MATERIALS

Study Sites and Trapping Programs

Data used herein are from eight separate studies, seven of which employed pitfall traps and another which used a combination of Museum Special and Victor rat traps. Two of these tests were described in detail by Williams and Braun (1983; tests of trap design) and a third was described by Braun-Hill and Williams (1986; test of trap spacing on transect lines). All elevations are in meters above sea level. Locations and experimental procedures for each test are elaborated below.

Two separate experiments of trap design were conducted for 10-day periods in July, August, and September 1979 in the mixed conifer and red fir forest zones within the Sierra National Forest, Fresno County, California (Fig. 1). Elevations ranged from 1,830 to 2,300 m. In one test, 50 pitfall traps (7.6 l) were positioned 15 m from a pair of traps consisting of a Museum Special snaptrap and a Sherman livetrap. The other experiment tested efficiency of drift fences used with pitfall traps, and employed 30 sets of 3 pitfall traps arranged in an equilateral triangle with 15 m between traps. Refer to Williams and Braun (1983) for additional details. Each station of three traps was separated by ≥30 m from other stations. Trap stations were characterized in terms of forest type,

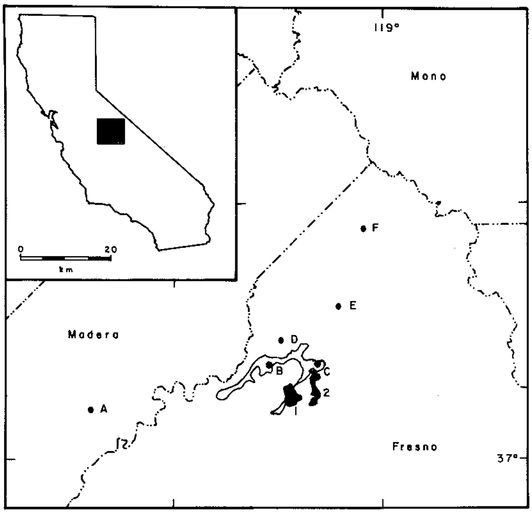

Figure 1. Location of study sites in central California. Shading shows approximate area covered by 49 pitfall transects on the Sierra National Forest. Solid black shows sites of studies of trap design (1) and drift fences (2). Other sites are: A = San Joaquin Experimental Range; B = trap spacing study in mixed conifer forest; C = trap spacing study in red fir forest; D = transect employing 18.1-l pitfall in mixed conifer forest; E = transect employing 18.1-l pitfall in high-elevation lodgepole pine forest (Kaiser Pass); and F = sampling site in subalpine pine community.

ground, shrub, and canopy cover and amount of downed woody material (litter). Only captures in pitfall traps are used in this report (Table 1).

Tests of trap spacing on line transects also employed 7.6–l pitfalls and were conducted at two sites in the Sierra National Forest during summer 1980 (Fig. 1). One site, in mixed conifer forest, was at approximately 1,675 m; traps were arranged in 30 lines of four traps each (120 total) and operated for a continuous 23-day period. At the second site, in red fir forest, at about 2,300 m, the same number and arrangement of traps were operated continuously for 14 days (Braun-Hill and Williams 1986). The areas along four-trap transects were characterized by forest type, ground, shrub, and canopy cover, distance to water, and amount of litter.

On the San Joaquin Experimental Range, 460 m, Madera County, California (Fig. 1), 7.6-l pitfall traps were spaced at 15-m intervals on eight 10-trap transects in a blue oak/digger pine woodland, and operated continuously for 13 days during January 1982. Features of the plant community were characterized for each transect.

At two sites in the Sierra National Forest, 18.9-l pitfall traps were placed irregularly, with minimum intertrap spacing of 15 m, in mixed conifer at 2,100 m (10 traps) and lodgepole pine forests at about 2,745 m (15 traps) and operated continuously for 37 and 16 days, respectively, during June and July 1979 (Fig. 1).

In the Stanislaus National Forest in a ponderosa pine forest at approximately 915 m, N. Fork of Merced River, near Bower Cave, Mariposa County, 14 7.6-l pitfalls, spaced at 15-m intervals were operated for a 14-day period in May 1979.

At 49 sites on the Sierra National Forest, Fresno County, between about 930 and 2,470 m, 10-trap transects (7.6-l pitfalls with 15-m intertrap spacing) were established in the eight successional stages of ponderosa pine, mixed conifer, and red fir forests and their associated riparian communities (Fig. 1). Two transects at separate sites were established in each stage, except for four cases where appropriate stages, uniform enough to meet the definitions of Verner and Boss (1980) and to contain a 150-m straight-line transect with no trap falling within 30 m of another successional stage could not be found. Successional stages represented by a single transect or unsampled are indicated in Table 2. There were no recent clearcuts in ponderosa pine and mixed conifer forests within the study area, so powerline right-of-ways were substituted for the grass/forb stage in these communities. Traps on transects at elevations between 930 and about 1,670 m (lower transects) were operated for a continuous 7-day period in July 1980. Traps on transects above 1,670 m (upper transects; approximately equal numbers of transects were located above and below this elevation) were operated for a continuous 7-day period in August 1980. Traps at all sites were checked daily. At the end of the sampling period, water was pumped from traps and they were covered with plywood squares, weighted down with rocks and covered with soil. The original intent was to operate the traps periodically over a 3-year period, sampling for 28-day periods in each season. Due to reduced funding to the U.S. Forest Service, however, traps were not operated during 1981. In 1982, all traps were uncovered, cleaned, and refilled with water, then recovered. When all traps had been reconditioned, covers were removed from traps on the lower transects on one day, and on the upper transects the next day. Traps were checked on alternate days for a continuous 28-day trapping period (distances between transects precluded servicing all traps on a single day); thus, traps on all 49 transects were operated simultaneously except for a day at the beginning and end of the 28-day sessions. One Victor rat trap and one Museum Special snaptrap were set at each pitfall station after pitfalls were removed on eight transects representing seven of the eight seres of mixed conifer forest plus its riparian zone (grass/forb stage was not sampled). Traps were operated for 4 days commencing with the cessation of pitfall trapping in 1982.

Measurements of 55 aspects of the structure and composition of the plant community were made on two separate plots on each transect. Data on plant communities are used here only to confirm classification of forest stages by tree size and canopy cover class, and to generally characterize the features of stages. They will be reported and analyzed in greater detail in a separate report on small mammal communities of the western Sierra Nevada.

Twenty pitfall traps (1.9 l) were placed in irregular lines along a stream, around the edge of

Table 1. Captures of shrews per unit effort of pitfall trapping in woodland and forest communities of the western Sierra Nevada. Number of shrews caught are given in parentheses. Elevation range refers to minimum and maximum elevations, in meters above sea level, of study sites for each forest type. Values of X^2 are from goodness-of-fit tests; values for *Sorex* spp. test a null model assuming no preference for a particular forest community, are corrected for unequal sampling efforts, and do not include data from blue oak/digger pine communities (d.f. = 2). Comparisons within communities test a null model assuming that there are no differences in abundance among species (d.f. = 4). Significant values of X^2 are marked with an asterisk (*).

	Forest Community				
	Fir/Lodgepole	Mixed Conifer	Ponderosa Pine	Oak/Pine	X^2
Elevation range	2,196–2,745	1,482–2,105	933–1,684	460	
Total trap nights	8,610	10,205	5,446	1,040	
Sorex monticolus	0.0184	0.0010	—	—	347.02*
	(158)	(10)	—	—	
Sorex tenellus	0.0012	—	—	—	25.37*
	(10)	—	—	—	
Sorex palustris	0.0015	0.0006	—	—	22.47*
	(13)	(6)	—	—	
Sorex trowbridgii	0.0023	0.0417	0.0013	—	808.61*
	(20)	(442)	(7)	—	
Sorex ornatus	—	0.0008	0.0110	0.0010	175.52*
	—	(8)	(60)	(1)	
Total *Sorex* spp.	0.0233	0.0457	0.0123	0.0010	550.38*
	(201)	(466)	(67)	(1)	
X^2	347.42*	1,259.16*	170.80*	—	

Table 2. Captures of shrews by successional stages within forest communities of the western Sierra Nevada. Stages follow definitions of Verner and Boss (1980): GF = grass/forb; SSS = shrub/seedling/sampling; PMA = pole-medium tree with <40% canopy cover; PMB = pole-medium tree with 40 to 69% canopy cover; PMC = pole-medium tree with >69% canopy cover; LTA = large tree with <40% canopy cover; LTB = large tree with 40 to 69% canopy cover; LTC = large tree with >69% canopy cover; RD = riparian deciduous zone. Stages indicated by 10 traps were sampled at only one site; the closed canopy, large tree stage of ponderosa pine (LTC) could not be found within the study area. Trap nights per trap were equal across all forests and successional stages. Values of X^2 are from goodness-of-fit tests of null models assuming that there were no differences in captures by species across successional stages, and no differences in captures among species within stages, respectively. Significant values of X^2 are marked by an asterisk (*).

Species	GF	SSS	PMA	PMB	PMC	LTA	LTB	LTC	RD	X^2
					RED FIR					
Number of traps	20	20	20	20	20	20	20	10	20	d.f. = 8
S. monticolus	15	12	2	2	4	5	4	6	33	76.50*
S. trowbridgii	0	0	0	0	2	6	4	2	1	25.58*
S. palustris	0	0	0	0	0	0	0	0	5	21.47*
X^2 (d.f. = 2)	32.96*	26.37*	4.39	4.39	5.55	9.01*	6.49*	8.58*	46.80*	
					MIXED CONIFER					
Number of traps	10	20	20	20	20	20	20	20	20	d.f. = 8
S. monticolus	0	6	3	0	0	0	0	0	0	28.09*
S. trowbridgii	1	66	11	27	25	30	30	21	60	8.79
S. palustris	0	0	0	0	0	0	0	0	5	127.98*
S. ornatus	0	0	0	0	0	0	0	0	2	21.97*
X^2 (d.f. = 3)	2.77	158.32*	24.27*	74.86*	69.31*	83.18*	83.18*	58.22*	147.89*	
					PONDEROSA PINE					
Number of traps	20	20	20	20	20	20	10	0	20	d.f. = 7
S. trowbridgii	1	0	3	0	2	1	0	—	0	52.46*
S. ornatus	6	3	6	2	5	0	5	—	23	11.23
X^2 (d.f. = 1)	3.96*	4.16*	1.02	2.77	1.33	1.39	6.93*	—	31.88*	

a wet meadow, and in talus in a subalpine pine community (mainly whitebark pine, *Pinus albicaulis*) near Frog Lake at approximately 3,310 m, and operated for 3 days.

Trapping sessions were also conducted at 33 sites in six plant communities at elevations between about 300 and 1,100 m on the western slopes of the central Sierra Nevada, in Amador, Calveras, Mariposa, Nevada, Placer, and Tuolumne Counties, California, during 1978 and 1979. Each trap station on line transects consisted of two Museum Special snaptraps and one Victor rat trap. Trap spacing and trapping effort were not uniform among all transects; total trap nights on the 33 transects was 19,824. Plant communities included annual grassland, chaparral, blue oak/digger pine, ponderosa pine, mixed conifer, and low- and mid-elevation riparian deciduous (Verner and Boss 1980). The plant community was classified and characterized at each site. Data on captures of shrews are used here solely to further document their altitudinal distributions and habitats.

Except for less than 20 that were discarded because of excessive damage, specimens were preserved by standard methods and deposited in the Carnegie Museum of Natural History.

Analysis of Data

Data on captures of shrews from all trapping studies employing pitfalls in red fir, lodgepole pine, mixed conifer, and ponderosa pine forests and blue oak/digger pine woodland were used to determine distributions of *Sorex* spp. by forest types. Data on captures were transformed by dividing captures by total trap nights to produce a value on catch per unit effort to compare captures by species across communities with unequal sampling efforts (Table 1). For within-community comparisons of captures by species, raw data on captures were used because the model being tested assumed equal probability of capture by species. In the across-community comparisons by species, log-ratio goodness-of-fit tests (Sokal and Rohlf 1969) tested null models assuming that there were no preferences for a particular forest type. Within-community comparisons tested null models assuming that there were no differences in probabilities of captures among species (Table 1). Goodness-of-fit tests were also used to measure preference by successional stages by species within a forest type (Table 2). Significant values of X^2 require rejection of the null models. The method of Sokal and Rohlf (1969) for computing goodness-of-fit values (X^2) from data that includes cells with values of zero was used, except that zeros were assigned values of 0.0001 instead of 0.01.

The statistical method of Price and Kramer (1984) was used to estimate dissimilarity in use of successional stages between species coexisting in the same general forest type. This index of microhabitat dissimilarity is:

$$H_{ij} = \sum_{k} \left| \frac{n_{ki}}{N_i} - \frac{n_{kj}}{N_j} \right|$$

where n_{ki} and n_{kj} are the number of captures of species i and j, respectively in successional stage k; and where N_i and N_j are total captures over all successional stages of species i and j, respectively. Values of H range from 0 (no dissimilarity or identical use of successional stages by species i and j) to 2 (maximum dissimilarity in use of stages by species i and j).

RESULTS

Captures in snaptraps out of 20,964 trap nights totaled six shrews, including 1 *Sorex monticolus* at the upper edge of mixed conifer zone at 2,075 m, 1 *S. ornatus* in chaparral at about 640 m, and 4 *S. trowbridgii* in mixed conifer forests. Captures of shrews in pitfall traps are summarized in Table 1. Captures in lodgepole pine and red fir forests were combined because lodgepole pine represents a successional stage and fire-maintained disclimax in the red fir climax forest. Above the red fir zone, lodgepole pine forest was sampled only at one site (15 traps operated for 16 days) and 10 *S. monticolus* were captured. Three *S. monticolus* were taken in the subalpine community. Values of X^2 are highly significant for all across-community comparisons by species and all within-community comparisons across species ($P < 0.00001$), requiring rejection of the null models (Table 1).

Captures by species by forest type across nine successional stages are given in Table 2. All but two within-community, across-stages comparisons of captures by species are highly significant ($P < 0.006$). Indices of habitat dissimilarity for captures by successional stage in three forest types are presented in Table 3. Only data from studies on the 10–trap transects operated simultaneously during 1980 and 1982 were used in Tables 2 and 3.

Blue Oak/Digger Pine Woodland

Sorex ornatus was the only species captured in the blue oak/digger pine woodlands; its rate of capture in pitfalls was approximately an order of magnitude lower than its rate of capture in ponderosa pine forest (Table 1). Its rarity in the foothills chaparral and oak/pine zone is further demonstrated by captures in snaptraps: a single specimen was captured in a brushy successional stage of oak/pine woodland out of 7,947 trap nights in chaparral and oak/pine communities on transects employing three snaptraps per station. Its occurrence in this zone is too rare to allow determination of habitat. The one ornate shrew captured in a pitfall was taken among large rocks on a steep slope, away from the riparian zone.

Ponderosa Pine Forest

In ponderosa pine forest, captures of *S. ornatus* were greater than eight times as numerous as *S. trowbridgii*. *Sorex trowbridgii* was captured in ponderosa pine communities only on transects above 1,245 m. Ornate shrews were captured in small numbers in most habitat stages, but they were common only in the riparian zone, although the differences in captures across successional stages were not significant (P = 0.13; Table 2).

Mixed Conifer Forest

Four species of shrews were captured in the mixed conifer zone (Tables 1 and 2), with captures of *S. trowbridgii* outnumbering those of other species by more than 40 to 1. *Sorex ornatus* was taken in mixed conifer only in the riparian zone at a single locality at about 1,670 m, near the lower limit of this forest type, on a northward-facing slope. Although both *S. ornatus* and *S. palustris* were captured only in the riparian zone and have an index of habitat dissimilarity of 0 (Table 3), the two species occupied qualitatively different types of riparian zones. *Sorex ornatus* was found along a small, seasonal stream with an open canopy of conifers and an understory of a diverse mix of woody shrubs, and was not closely associated with water. *Sorex palustris* was found at the same general elevation along the edges of a larger, permanent stream in a riparian community with a closed canopy predominately consisting of deciduous hardwoods. There were few understory shrubs.

Dusky shrews (*S. monticolus*) were captured in the mixed conifer zone at a single locality in a shrub-dominated clearcut and a nearby open, pole stage of mixed conifer, dominated by shrubs (Tables 1 and 2). This site, at about 2,074 m, was on a northward-facing slope of a small canyon, near the ecotone between mixed conifer and red fir forests.

At the majority of sites in mixed conifer forest, and at all sites between about 1,670 and 2,070 m, only Trowbridge shrews (*S. trowbridgii*) were captured. *Sorex palustris* occurred along

Table 3. Values for H (habitat dissimilarity index; Price and Kramer 1984) based on captures of shrews in pitfall traps in successional stages of forest and riparian zones in three forest types of the western Sierra Nevada, California. Index values range from 0 (identical habitat) to 2 (maximum dissimilarity in habitat).

	Forest								
	Red Fir			Mixed Conifer			Ponderosa Pine		
	S. t.	*S. p.*	*S. o.*	*S. t.*	*S. p.*	*S. o.*	*S. t.*	*S. p.*	*S. o.*
S. monticolus	1.41	1.20	—	1.41	2.00	2.00	—	—	—
S. trowbridgii	—	1.87	—	—	1.54	1.54	—	—	1.38
S. palustris	—	—	—	—	—	0.00	—	—	—
S. ornatus	—	—	—	—	—	—	—	—	—

permanent streams throughout the mixed conifer zone, but was rare (captures in the riparian zones at two sites were five in 700 trap nights for a relative capture rate of 0.007). *Sorex trowbridgii* was common in all successional stages except grass/forb (Table 2). The single site representing the grass/forb stage was in a powerline right-of-way, and was maintained in this successional stage by use of herbicides. The site differed qualitatively from clearcuts in a number of important features, especially in the lack of litter, duff, and humus, and in the type of herbaceous cover. Thus, a scarcity of shrews at this site might not be representative of their use of recent clearcuts. Trowbridge shrews were not captured in dry meadows during studies of trap design, however, suggesting that they avoid the grass/forb sere of forests. Sites with the greatest abundance of Trowbridge shrews were the shrub stages of forest and the riparian zones. Riparian zones are in perpetual succession due to periodic floods and support a diversity of woody shrubs, except along heavily eroded streambeds.

Red Fir/Lodgepole Pine Forest

In the red fir and lodgepole pine zone, four species of shrews were captured (Table 1). Ten Inyo shrews (*S. tenellus*) were captured at a single site in a closed-canopy, old-growth red fir forest, and along a small, permanent stream about 50 m away. There was no tree canopy along the segment of the stream where some Inyo shrews were captured [Williams (1984) gave other details]. It is not possible to determine its habitat on this basis. Water shrews (*S. palustris*) were captured in small numbers along permanent streams in this zone; their relative abundance was about twice as great as in mixed conifer (Table 1). A single water shrew was captured in a wet meadow, near a tiny, ephemeral stream.

Trowbridge shrews were captured in small numbers at several sites in the red fir zone, primarily in the older stages of forest and on dry, southwest-facing slopes supporting Jeffrey pine. Trowbridge shrews were not captured in shrub stages and only one was captured in the riparian zone of red fir forest, stages where *S. monticolus* was common (Table 2). *Sorex trowbridgii* was not taken above about 2,320 m.

Sorex monticolus was the dominant shrew throughout the red fir zone and the only shrew captured above 2,320 m in red fir, lodgepole pine, and subalpine pine forests. It was most common in the riparian zone and in the grass/forb and shrub stages of forest. Most captures in the grass/forb stage were from along a small stream in a 2-year old clearcut. Herbaceous cover and downed woody material were sparse, but partly burned logs and large limbs were scattered over the clearcut.

DISCUSSION

The pattern of captures over all forest types (Tables 1 and 2) is one of altitudinal zonation of shrew species, with each forest zone dominated by a single species (Fig. 2). *Sorex ornatus* was the only species found in the blue oak/digger pine forest and chaparral zone at the lowest elevations; it was also the sole shrew in ponderosa pine forest below about 1,200 m, and the dominant shrew species in the ponderosa pine zone between about 1,200 and 1,500 m, where it was found most commonly in riparian communities. *Sorex trowbridgii* ranged from the upper portion of the ponderosa pine forest above about 1,230 m, where

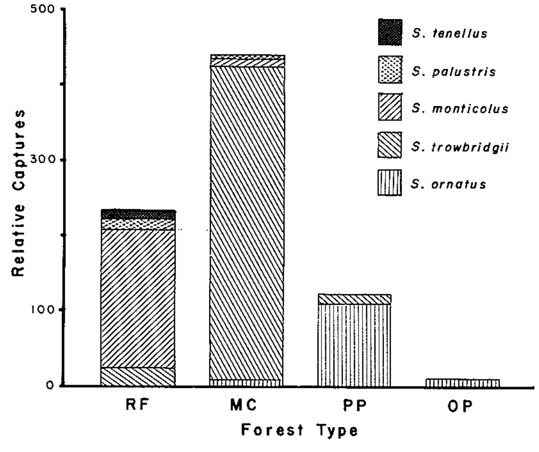

Figure 2. Histogram of captures per 10,000 trap nights in pitfalls by species of *Sorex* in five forest types in the western Sierra Nevada, California. Data are from Table 1, except for 10 captures of *S. monticolus* in a high-elevation lodgepole pine forest (see Methods and Materials). Forest types are: LP = lodgepole pine; RF = red fir (LP and RF combined under RF); MC = mixed conifer; PP = ponderosa pine; and OP = blue oak/digger pine.

it was rarely captured, through the mixed conifer zone where it was abundant, and into the red fir zone to about 2,300 m; it was scarce above about 2,100 m. *Sorex monticolus* was rare in the upper mixed conifer zone above about 2,070 m and was the most common shrew in the red fir/lodgepole zone. Dusky shrews were most abundant in riparian communities, but were not limited primarily to wetlands and sites close to water, in contrast to the report by Ingles (1961) based on studies in the vicinity. *Sorex palustris* occurred sparsely throughout the mixed conifer and red fir/lodgepole pine zones in association with streams. *Sorex tenellus* was captured at a single site in a red fir forest (Fig. 3). *Sorex tenellus* was not known to occur on the western slopes of the Sierra Nevada (White et al. 1980), and the prediction of the WHRP that *S. vagrans* would be common within the study area above about 1,680 m proved to be false—it was never captured.

Although four species of shrews were captured in both red fir and mixed conifer forests, no more than two shrews were captured at any site, with two exceptions (see below). Two of the four species occupy only the lower and upper ecotones between mixed conifer and ponderosa pine (*S. ornatus*) and red fir forest (*S. monticolus*), respectively. Thus, no more than three species, one common forest shrew (*S. trowbridgii*), one rare forest shrew (*S. monticolus* or *S. ornatus*), and the rare water shrew potentially coexist in ecotones along streams in the mixed conifer zone (Fig. 3).

In the red fir zone, four species were taken in the same general area only at the site of the trap-spacing study (Braun-Hill and Williams 1986). *Sorex monticolus* was the most common species (captures in 1,680 trap nights were: *S. monticolus* 52, *S. palustris* 7, *S. tenellus* 10, and *S. trowbridgii* 3) and was widely distributed in riparian, red fir, and lodgepole pine stands. *Sorex trowbridgii* was primarily found on dry, southwestern-facing slopes among Jeffrey pine and dense clumps of ceanothus (*Ceanothus cordulatus*). *Sorex palustris* was limited to the streamside community where it was captured in association with *S. monticolus* and *S. tenellus*. Elsewhere in the red fir forest, *S. monticolus* and *S. trowbridgii* were found to coexist at a few sites below about 2,300 m in about equal numbers, and these two species were taken in traps on a transect in the riparian zone that also captured *S. palustris* (Table 2).

Although the broad patterns of distribution and habitat of shrews of the western slopes of the southern Sierra Nevada are abundantly documented, the specific features of the communities determining occupancy are not resolved. Because the main trapping program was designed as a test of the WHRP, a priori selection of potential habitats and habitat features to test were those represented within blocks of forest communities that met the definitions of the successional stages of the WHRP (Verner and Boss 1980). Overall, no microcommunity went unsampled; however, the experimental design diffused efforts among several stages that probably are unrecognizable as qualitatively different by shrews and generally unacceptable as habitat. This resulted in too few

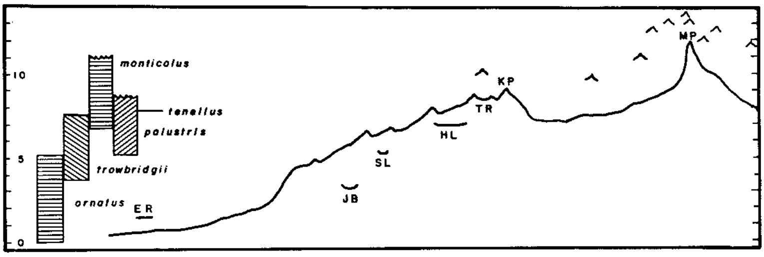

Figure 3. Elevational profile through the Sierra Nevada in the region of the study sites; scale is in thousands of feet above sea level. Jose Basin (JB) marks the sites at the lowest elevation where transects were placed in ponderosa pine forest; Tamarack Ridge (TR) marks the highest elevations where transects were placed in red fir. The east slope of Kaiser Pass (KP) was the site of the transect in high-elevation lodgepole pine forest. Other abbreviations are: ER = San Joaquin Experimental Range; HL = Huntington Lake; MP = Mono Pass; and SL = Shaver Lake. Cross-hatched bars show approximate altitudinal distribution of shrew species on the western slope as determined from these studies. Broken bars indicate that upper elevational limits were not determined.

captures in most seres to statistically test features of the microcommunity associated with most species. Detailed analyses of small mammal captures associated with structure of the plant communities will be reported elsewhere. In general, however, those features that define the riparian zone (exposed rocks, an abundance of shrubs, and nearness to water) were most often significantly associated with captures of shrews.

Captures of shrews by species between tree stages of forest (pole through large-tree seres) generally were not significant (Table 2). Except for *S. trowbridgii,* shrew species were most abundant in riparian communities but otherwise not necessarily associated with water. *Sorex trowbridgii* was equally abundant in dense patches of shrubs without a tree overstory and far from water and in the riparian zone. The common feature of both seres is an abundance of woody shrubs. Unlike other species, *S. trowbridgii* also was common in the tree stages of forest, a finding in agreement with reports of studies of this species elsewhere (Dalquest 1941, Gashwiler 1959, Hooven 1973, Terry 1981).

Single species of shrews occupying large areas of temperate zone conifer forests with diverse plant associations was unexpected at the start of these studies and in marked contrast to virtually all other areas in temperate, North American forest and riparian communities (Table 4). Data in Table 4 represent numbers of coexisting species reported from the same general area or on the same trapping grid. The coexistence of all species at a single site within the general area usually would be rare and limited to ecotones. Apparent from these reports, however, is that two or more coexisting forest shrews are typical of temperate forest communities, including the eastern slopes of the central and southern Sierra Nevada (in this context forest shrews do not include water shrews, but *S. palustris* was counted in totals in Table 4 when it was reported as coexisting with other species).

That the conifer forests of the western slopes of the central (Grinnell and Storer 1924) and southern Sierra Nevada are so depauperate in numbers of coexisting shrew species may relate to the summer aridity, lack of snow cover in winter, or both. The climate on the western slope exhibits a pronounced Mediterranean pattern: cool, wet winters and hot, dry summers. Below about 2,075 m, little precipitation falls between about May and October. At higher elevations, irregular summer thunderstorms provide a small amount

Table 4. Numbers of coexisting species of shrews (Soricidae) in forest and woodland communities of North America north of 32 degrees N latitude. "Lat." is degrees N latitude. "Other" refers to number of species of genera other than *Sorex* (i.e., *Blarina* and/or *Cryptotis*). Elevation is in meters above sea level. Authors cited typically reported some habitat segregation among coexisting species.

Locality	Community	Lat.	Elev.	Numbers *Sorex*	Numbers Other	Reference
Alaska	birch/willow	68	900	3		Douglass 1984
Alaska	tundra	65	250	1		Quay 1951
Yukon Terr.	conifer/riparian	61	900	2		Krebs and Wingate 1976
British Columbia	conifer	50	200	3		Sullivan and Sullivan 1982
Manitoba	conifer/wetland	50	300	4	1	Buckner 1966
Washington	conifer/oldfield	49	200	2		Newman 1976
Washington	conifer	48	30	2		Dalquest 1941
Ontario	conifer/wetland	48	300	4	1	Nagorsen and Peterson 1981
Idaho	conifer	48	700	3		Hoffman 1960
Michigan	conifer/hardwood	47	300	2	1	Mannville 1949
Washington	conifer	47	400	3		Terry 1981
Minnesota	conifer/wetland	47	500	4		Quimby 1943
Idaho	conifer	47	880	3		Rickard 1960
Nova Scotia	conifer/hardwood	46	150	2	1	Kirkland and Schmidt 1982
Ontario	conifer/wetland	46	200	4	1	Fowle and Edwards 1954

Table 4 (continued)

Locality	Community	Lat.	Elev.	Numbers *Sorex*	Numbers Other	Reference
Washington	conifer	46	900	5		Bury and Corn 1987
New Brunswick	conifer/hardwood	45	170	4	1	Kirkland and Schmidt 1982
Michigan	hardwood/riparian	45	300	1	1	Fleming 1973
Montana	riparian/Pine, sage	45	330	3		MacCracken et al. 1985
Maine	conifer/hardwood	45	370	4	1	Richens 1974
Quebec	hardwood	45	600	1	1	Grant 1976
Oregon	conifer/riparian	44	100	2		Hooven et al. 1975
New York	conifer	44	700	3	1	Kirkland and Griffin 1974
Oregon	conifer	44	900	3		Hooven and Black 1976
Oregon	conifer	44	900	5		Bury and Corn 1987
Oregon	conifer	44	980	2		Gashwiler 1959
Wyoming	shrub wetland	44	1,920	3		Clark 1973
S. Dakota	riparian wetlands	43	500	2	1	Findley 1956
New York	conifer/hardwood	43	520	2	1	Jameson 1949
Oregon	conifer forest	43	600	3		Hooven 1973
Iowa	hardwood riparian	42	300	1	1	Geier and Best 1980
Pennsylvania	hardwood	42	650	2	1	Kirkland 1978
Nevada	riparian	41	2,040	3		Ports and McAdoo 1986
California	conifer/wetland	41	2,350	4		Williams 1984 and unpubl.
Colorado	conifer/meadow	41	2,940	5		Spencer and Pettus 1966
Wyoming	subalpine talus	41	3,190	3		Brown 1967
Pennsylvania	conifer/hardwood	40	350	3	1	Richmond and Grimm 1950
Pennsylvania	hardwood	40	490	2	1	Kirkland et al. 1985
West Virginia	conifer	39	1,300	3	1	Kirkland 1977
California	conifer/wetland	39	2,500	6		Williams 1984 and unpubl.
California	conifer	38	2,430	4		Howell 1924
N. Carolina	conifer/hardwood	36	730	2	1	Linzey and Linzey 1973
N. Carolina	conifer/hardwood	35	1,160	3		Whitaker et al. 1975
N. Carolina	hardwood	33	60	1	2	Golley et al. 1965
Alabama	hardwood	33	300	1	2	French 1980

of precipitation (totaling less than 3 cm between June and October at 2,135 m). Daytime maximum temperatures range to over 38°C in the lower elevation ponderosa pine forests with mean maximums above 36°C. In the red fir zone, mean July maximums are about 25°C with an upper range of 30°C. In winter, daytime temperatures at 2,135 m average about 10°C with occasional highs to 15°C in the red fir zone, and a mean January high of about 13 to 14°C at about 1,586 m with occasional highs to about 24 or 25°C (National Oceanic and Atmospheric Administration 1974). During prolonged periods of high pressure and drought in winter, snow in all but the most protected sites may melt at elevations below 1,600 m. Even in years of typical weather, winter snowpack at elevations below about 1,500 m is not dependable, and areas unprotected by forest canopy may be without snow periodically during winter. In the red fir zone above about 2,135 m, winter snows are typically deep and wet, usually exceeding 3 m in depth and weighing as much as 448 kg per cubic meter (Storer and Usinger 1963). Nighttime temperatures are usually below freezing at elevations above 1,200 m in winter, but minimum temperatures average above 0°C during all winter months in the blue oak/digger pine zone and lower elevations of ponderosa pine forest, and monthly normal temperatures are above freezing during all months of the year below the red fir zone. In the red fir zone, only the months of January and February have normal temperatures below freezing. Under these conditions much of the forest may be too hot and arid in summer and lack sufficient snow cover in winter for most species of *Sorex*. In sites with continuous snow cover in winter, the snow may be so wet and heavy that little subnivean space is available except under cover of dense, woody shrubs and in areas with deep layers of logs, litter, and duff.

Riparian sites typically have more continuous canopy cover, are located in bottoms of canyons, and support an abundance of woody shrubs. The microclimate there is probably less extreme in both summer and winter, being especially cooler and more moist in summer than exposed slopes. Snow would be less exposed to sun and less likely to melt during warm periods in winter in riparian sites. Dense shrubs hold snow off of the ground, providing more subnivean space for small animals to live and move about.

Although the forest plant communities are well developed, they apparently are poor habitat for most species of *Sorex*, except in the more climatically moderate and mesic riparian zones. That only a single species of forest shrew is generally found even in riparian communities suggests that the best shrew habitats are poor in comparison to those in typical North American conifer communities. The absence of shrew-moles (*Neurotrichus gibbsii*) and the red backed vole (*Clethrionomys californicus*) from all but the northern edge of the Sierra Nevada (White et al. 1980) lends additional support to this argument. Shrew-moles occupy a niche that is similar to shrews (Terry 1978); they and California red backed voles are associated with relatively cool, mesic, coastal forests. Red backed voles in general require mesic surroundings. Odum (1944) measured daily water consumption in *C. gapperi* at about six times the rate of other similar-sized forest rodents. These things suggest that summer aridity may be the principal factor in limiting diversity of *Sorex* species in the western Sierra Nevada.

ACKNOWLEDGMENTS

This paper is dedicated to James S. Findley, whose publications on the *Sorex vagrans* group stimulated my early interest in mammalogy and in the biology of shrews.

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Competition and Coexistence in Shrews (Insectivora: Soricidae)

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Abstract

Diverse assemblages of up to six or more species of soricids have been reported for moist, forested habitats of the Holarctic and Old World tropics. Because of their high within-habitat diversity, shrews have the potential for yielding important insights into the nature of competitive interactions and coexistence in small mammals. Interspecific competition in soricids is inferred on the basis of an overwhelming body of indirect evidence relating to size, behavioral, temporal, microspatial, and trophic relationships of syntopic soricids; however, such competition in shrews has not been tested experimentally under field conditions. Compared to other equally diverse guilds of small mammals, such as desert granivores, shrews evince less variation in size, locomotion (e.g., no quadrupedal-bipedal dichotomy), foraging patterns (e.g., no open sites versus under shrub pattern), and physiology (e.g., no differential expression of seasonal torpor). Such comparisons suggest that mechanisms to reduce competition and facilitate coexistence in shrews may be more subtle than those of other guilds of small mammals. Species-rich assemblages of soricids consistently are associated with cool, moist, forested habitats that are characterized by an abundant, diverse, and dependable food resource base in the form of soil invertebrates. Because of the high moisture requirements of most soricids and the influence that environmental moisture has on the size, diversity, and reliability of the food resource base exploited by shrews, environmental moisture may be the ultimate determinant of within-habitat soricid diversity. In addition, the extremely small size of many soricids may facilitate coexistence by permitting shrews to exploit their environment in a more course-grained fashion than that of larger species.

INTRODUCTION

Shrews (Insectivora: Soricidae) are important constituents of small mammal communities in forested ecosystems throughout the Holarctic and in the Old World tropics. Within-habitat species richness can be high with as many as six species of shrews, including five *Sorex,* inhabiting individual habitats in parts of North America (Kirkland, unpubl. data; Spencer and Pettus 1966; Wrigley et al. 1979). In the Old World, equal or greater species richness has been reported for *Sorex* in Siberia (Yudin 1962, Okhotina 1977) and central Asia (Yudin et al. 1979), *Soriculus* in China (Hoffmann 1986), and *Crocidura* in West Africa (Dieterlen and Heim de Balsac 1979). In North America, alpha diversity of shrews often rivals that of desert granivorous rodents and generally exceeds the diversity of small rodents in grasslands and forests (Kirkland 1985). Because of their high within-habitat diversity, shrews have the potential for yielding important insights into the nature of competitive interactions and coexistence in small mammals, but they remain relatively unstudied in this regard as compared to granivorous rodents in the deserts of the American Southwest (e.g., Brown and Lieberman 1973, Brown 1975, Schroder and Rozenzweig 1975, Mares and Williams 1977, Price 1978, Brown et al. 1979, Munger and Brown 1981, Price and Brown 1983, Brown and Munger 1985), and in rodents inhabiting North American grasslands (Koplin and Hoffmann 1968, Stoecker 1972, Petersen 1973, Abramsky et al. 1979, Cameron et al. 1979, Cameron and Kincaid 1982, Kincaid and Cameron 1982, Linzey 1984) and forests (Chappell 1978; Dueser and Shugart 1978, 1979; Wolff et al. 1983; Barry et al. 1984; Parren and Capen 1985). This may reflect the inherent difficulties of working with endotherms as small as shrews. Nevertheless, researchers such as Michielson (1966), Hawes (1977), Ellenbroek (1980), and Churchfield (1984a, 1984b) have successfully carried out long-term live-trapping studies that have yielded important insights into interspecific competition and coexistence in shrews.

Research on niche differentiation in soricids has been carried out under the assumption that sympatric species are, or have been, in compe-

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tition. Given the morphological and ecological similarities of many coexisting shrew species, this assumption is logical; however, interspecific competition in shrews has not been tested experimentally under field conditions. Instead, competition in soricids has been inferred on the basis of indirect evidence relating to the size, behavioral, temporal, trophic, and spatial/microspatial relationships of syntopic soricids. Although competition theoretically should be intense among syntopic soricids, in general they do not manifest many of the characteristics that facilitate resource partitioning and coexistence in other guilds of small mammals. For example, shrews evince relatively little differentiation in size, locomotion, adaptive physiology, habitat segregation, and temporal activity (Table 1). Nevertheless, shrews exhibit subtle patterns of interspecific differentiation that may be interpreted as serving to reduce competition and facilitate coexistence. The objective of this paper is to review the pertinent literature on competition in soricids and to provide an assessment of our current knowledge regarding interspecific competition and coexistence in soricids.

FACTORS INFLUENCING COMPETITION AND COEXISTENCE IN SHREWS

Body Size

Size differentiation between closely related coexisting species has been proposed as a major evolutionary mechanism leading to a reduction in competition, particularly when that size differentiation fosters trophic differentiation (Lack 1971). In comparison to other guilds of North American terrestrial small mammals, shrews evince little variation in size (Table 1). Although chipmunks also exhibit a relatively small degree of size variation (Patterson 1981, Brown and Bowers 1984), the tendency for sympatric chipmunks to manifest contiguously allotopic distributions (Heller 1971, Chappell 1978, Brown and Bowers 1984) clearly distinguishes them from soricids, which frequently occur in syntopy (Table 1).

In portions of eastern North America characterized by high soricid diversity, shrews sort into three general size classes: small ($\bar{x}$ = 3–4 g), medium ($\bar{x}$ = 5–7 g), and large ($\bar{x}$ = 12–20 g). In each of these size classes, there are two species, one of which is common, the other being

Table 1. Comparison of mechanisms to facilitate coexistence in four guilds of terrestrial small mammals.

Guild/ Characteristic	Desert Rodents[1]	Forest Rodents[2]	Soricids[3]	Chipmunks[4]
Trophic Specialization	Granivores	Omnivores	Insectivores	Omnivores
Number of Species	1 to 10	2 to 6	1 to 6	1 to 2
Body Mass (Max./Min.)	7 to 150 g (21X)	18 to 160 g (9X)	3 to 28 g (9X)	25 to 125 g (5X)
Locomotion	Quadrupedal/ Bipedal	Quadrupedal/ Bipedal	All Quadrupedal/	All Quadrupedal
Adaptive Physiology	Seasonal torpor in some species	Seasonal torpor in some species	No seasonal torpor	Seasonal torpor
Spatial Segregation	Open vs. Shrubby Habitats	Terrestrial vs. Arboreal	No conspicuous 2-dimensional pattern/limited vertical stratification of foraging	Habitat segregation (contiguous allopatry)
Temporal Segregation	None—all nocturnal	Diurnal vs. Nocturnal	None—all active throughout 24-hr day	None—all diurnal

[1] Source: J.H. Brown (in litt.), Brown (1973), Brown and Bowers (1984)
[2] Source: Kirkland (1985).
[3] Source: Present study.
[4] Source: Brown and Bowers (1984), Chappell (1978), Heller (1971), Kirkland (1985).

uncommon (Table 2). In an analysis of community structure in soricids at 41 localities in eastern North America, Fox and Kirkland (unpublished; see Fox 1989) found that soricid communities were not random assemblages of species but appeared to follow a species-assembly rule which predicts that each of the three size niches should be filled before a second species of the same size is present. These authors identified interspecific competition as the most likely mechanism responsible for the non-random association observed in these 41 soricid communities.

The phenomenon of character displacement has been interpreted as an evolutionary response to interspecific competition (Brown and Wilson 1956, Pianka 1983). Malmquist (1985) recently described character displacement between *Sorex araneus* and *S. minutus* in Europe. Crania of the smaller *S. minutus* were larger when in allopatry. This would be predicted if their smaller size when in sympatry is influenced by competition with the larger *S. araneus;* however, *S. araneus* did not evince smaller cranial size in the absence of *S. minutus*. This suggests that *S. minutus* may derive thermoregulatory and trophic benefits from larger size in allopatry, whereas *S. araneus* would derive no similar benefits from evolving a smaller body size in allopatry.

A key aspect of size in shrews is the role that small size per se may play in permitting syntopic soricids to exploit their environments in a more coarse-grained fashion than would be possible in larger species (MacArthur and Wilson 1967, Pianka 1983). For example, Hawes (1977) found consistent microhabitat differences (based on soil and associated vegetation) between the distributions of *Sorex vagrans* and *S. obscurus* (= *monticolus*) on a 1 ha study plot. If small size facilitates coexistence in soricids, this may help to explain why the size ratio between the smallest coexisting species of soricids often approaches unity, while it is substantially greater between pairs of medium-sized and larger species (Table 2; see also, Wrigley et al. 1979).

Behavior

Behavioral differences in foraging may enhance dietary differentiation by exposing competitors to different portions of the food resource spectrum (Brown and Lieberman 1973). The question is whether the foraging behaviors of syntopic shrews differ to such an extent that individual species exploit the food resource spectrum in slightly different fashions. The most frequently reported example of differences in foraging behavior among syntopic shrews is vertical stratification of foraging activity (Michielsen 1966, Abe 1968, Ellenbroek 1980, Yoshino and Abe 1984). This difference in foraging behavior is re-

Table 2. Guild of forest-dwelling shrews from northeastern North America.

Relative Size	Species	Weight* Mean (Range)	Relative Abundance	Habitat Spectrum	Ratio of Mean Weights
Small	*Sorex hoyi*	3.6 g (2.5–5.4)	Uncommon	Generalist (?)	1.0
	Sorex cinereus	3.6 g (2.2–5.4)	Common	Generalist	
Medium	*Sorex dispar*	5.2 g (3.5–8.3)	Uncommon	Specialist	1.3
	Sorex fumeus	6.7 g (5.8–8.0)	Common	Generalist	
Large	*Sorex palustris*	12.9 g (8.5–17.9)	Uncommon	Specialist	1.5
	Blarina brevicauda	19.8 g (16.8–28.6)	Common	Generalist	

*From van Zyll de Jong (1983).

flected in dietary differences between species such that the more fossorial member of the species pair has a higher proportion of worms (Lumbricidae) in its diet (Pernetta 1976, Bauerova 1984, Churchfield 1984a). In a comparison of foraging activity between *Sorex caecutiens* and *S. unguiculatus* in Japan, Yoshino and Abe (1984) described the latter species as having a large body with relatively short tail, small hind feet, short ears, and large forefeet with long claws. These general morphological characters are reminiscent of those of *Blarina brevicauda,* which is semi-fossorial (George et al. 1986) and also includes a high proportion of earthworms in its diet (Whitaker and Ferraro 1963, Mumford and Whitaker 1982). Similar morphological, behavioral, and trophic adaptations characterize *Soriculus nigrescens* (Abe 1971, 1982; Hoffmann 1986). The fact that semi-fossorial soricids often are characterized by a particular morphology suggests that behavioral differences between shrews constitute part of a suite of integrated adaptations that foster niche differentiation and accompanying reduction in interspecific competition.

Temporal Variation

The small body mass of soricids and accompanying high energetic demands (Pearson 1948) dictate that shrews have minimal opportunities for temporal subdivision of foraging activity, such as those between diurnal and nocturnal omnivorous rodents in temperate forests (Kirkland 1985). Nevertheless, in homeotherms of the size of soricids, small differences in body mass should be reflected in pronounced differences in metabolic rate (Pearson 1948), which in turn could influence the length of intervals between feeding bouts. In comparing the activity of *S. unguiculatus* and *S. caecutiens,* Yoshino and Abe (1984) documented that the smaller *caecutiens* tended to have a shorter periodicity in its activity cycle and spent a higher proportion of their active time foraging. Whether such differences are of sufficient magnitude to influence competition and coexistence is unknown.

Trophic Relationships

Considerable research has focused on food habit studies in shrews with the objective of demonstrating dietary differences between sympatric soricids. Dietary differences related to size have been recorded for syntopic shrew species, and as expected, there tends to be a positive relationship between the mean size of a shrew species and the size of the dominant food items in the diet (Pernetta 1976, Whitaker and French 1984). In general, however, dietary overlap between syntopic soricids is high (Pernetta 1976, Whitaker and Maser 1976, Butterfield et al. 1981, Bauerova 1984, Churchfield 1984a, French 1984, Whitaker and French 1984, Ryan 1986). Although soricids may be viewed as dietary generalists on the basis of the broad spectrum of orders or families represented in gut or fecal samples, individuals species tend to specialize on a limited number of food items, such that two or three dietary components may constitute in excess of 50% of dietary volume (Whitaker et al. 1983, Bauerova 1984, French 1984, Kuvikova 1986). To the extent that their diets tend to mirror available food resources (Rudge 1968, Pernetta 1976, Churchfield 1982), shrews also may be viewed as opportunistic feeders, and, given the energetic constraints under which they live, shrews probably cannot afford to ignore potential food items. Nevertheless, some potential food items may not be readily consumed because they either are unpalatable or resistent to predation (Rudge 1968, Churchfield 1982).

Spatial-Microspatial Relationships

One mechanism of reducing interspecific competition is for potential competitors to occupy different habitats/microhabitats (Grant 1969, Morris 1969, Heller 1971, Morris and Grant 1972, Chappell 1978). Although sympatry is common in shrews, habitat segregation between species may occur on a local scale (Spencer and Pettus 1966, Brown 1967, Choate and Fleharty 1973, French 1984). Assemblages of shrews often consist of a mix of habitat generalists, which tend to be common, and specialists, which tend to be uncommon (Table 2). Some habitat specialists have morphological specializations which may contribute to competitive superiority within preferred habitats. Examples would be hygrophilous species, such as *Sorex bendirii, S. palustris,* and *Neomys* spp., and saxiphilous species, such as *Sorex alpinus, S. dispar,* and *S. gaspensis.*

EVIDENCE OF COMPETITION IN SHREWS—NUMERICAL RELATIONSHIPS

Competition theory predicts higher population density in allopatric populations as a result of relaxed competition (Malmquist 1986). In a study of density compensation in *Sorex araneus* and *S. minutus,* Malmquist (1986) documented higher population levels of *S. minutus* in allopatry; however, because allopatric populations of *S. araneus* were not sampled, the reciprocal effect of the absence of *S. minutus* on *S. araneus* could not be assessed. It should be noted, however, that Ellenbroek (1980) found no evidence of density compensation in populations of *S. minutus* in Ireland (allopatry) compared to populations in the Netherlands, where this species is sympatric with *S. araneus*. Although Buckner (1966) reported an inverse numerical relationship between *Sorex cinereus* and *S. arcticus* in tamarack bogs in Manitoba, Canada, this relationship may have been mediated by the independent responses of these two species to an environmental moisture gradient.

In general, research on the numerical relationships of syntopic soricids has lagged behind that dealing with other facets of competition and coexistence in shrews. Long-term live-trapping studies are needed in order to document the numerical, as well as spatial, relationships of syntopic soricids, and research on competition in soricids will remain incomplete until controlled removal studies are carried out to test experimentally for numerical and/or spatial responses to the removal of presumed competitors.

ROLE OF MOISTURE IN FACILITATING COEXISTENCE IN SHREWS

Any review of competition in soricids would be incomplete without some consideration of extrinsic factors that might influence the severity of competition and facilitate the coexistence of species. Soricids manifest considerable regional variation in diversity. In North America, soricids are most diverse in regions characterized by cool, moist forests (Kirkland 1985). They are conspicuously less diverse in drier and/or warmer habitats, such as grasslands, deserts, and the forests of the Southeast. This pattern of geographic variation in soricid diversity suggests that moisture is a principal factor in determining regional diversity, and by extension, local diversity of shrews. This is exemplified by the work of Wrigley et al. (1979), who found that hydric habitats in Manitoba, Canada, yielded an average of 4.7 species of shrews per habitat type, compared to 3.5 species in mesic habitats and only 1.8 soricid species per habitat type in xeric habitats. Environmental moisture may be viewed as both a direct and an indirect determinant of soricid diversity. Because many species of shrews have high moisture requirements (Manville 1949, Getz 1961), limits of tolerance for this environmental factor may directly influence the local abundance and diversity of soricid species. Equally important is the role that environmental moisture plays in supporting an abundant, diverse, and relatively stable soil invertebrate fauna on which soricids depend (Kirkland 1985). The relationship between precipitation and soricid diversity parallels the positive correlation between precipitation and within-habitat species diversity in granivorous desert rodents (Brown 1973, 1975). In both cases, increased local diversity is mediated through the effect of water availability on the food resource base. In this regard, the diversity patterns of both groups would appear to conform to the predictions of the productivity hypothesis of species diversity (MacArthur 1965, 1972; Pianka 1971).

An important corollary to the pattern of variation in soricid diversity in North America is the fact that regions of low diversity are characterized by sympatric soricids which tend to differ markedly in size. Examples are *Blarina brevicauda* and *Sorex longirostris* in forests of the Southeast, and *B. hylophaga* and *Cryptotis parva* in the prairies of the Midwest. In such regions, the comparatively small food resource base, or seasonal variation thereof, may limit the morphological similarity of syntopic species.

EVIDENCE OF INTRASPECIFIC COMPETITION IN SHREWS

Although interspecific competition in soricids has not been demonstrated experimentally, behavioral studies by Barnard and co-workers (Barnard and Brown 1981, 1982; Barnard et al. 1983) have examined the impact of intraspecific interactions on foraging behavior in *Sorex ara-*

neus. The presence of a confined but detectable conspecific in the laboratory arena led to shifts in foraging patterns of test animals (Barnard and Brown 1981, Barnard et al. 1983); however, these behavioral changes were influenced by prior residency and food abundance (Barnard and Brown 1982). The experimental procedures employed in this research on intraspecific competition should be adaptable for use in studying interspecific competition in shrews under laboratory conditions.

SUMMARY AND CONCLUSIONS

In reviewing the evidence relating to competition and coexistence in shrews, it is evident that size plays a role, either directly or indirectly, in virtually every mechanism proposed to facilitate the coexistence of shrews. Size differences between competitors may be reflected in dietary, behavioral, and temporal differentiation of niche parameters. Furthermore, the small size of shrews permits them to exploit their habitats in a more coarse-grained fashion, thereby fostering higher within-habitat diversity than is possible in larger species. However, regardless of whatever differences or adaptations shrews might possess to reduce competition, the ultimate determinant of within-habitat soricid diversity will be environmental moisture and the role it plays in supporting a food resource base of sufficient size, diversity, and reliability to permit coexistence.

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Niche Dynamics, Food Resources, and Feeding Strategies in Multispecies Communities of Shrews

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Abstract

Many soricid species are not only sympatric but also syntopic. Since shrews are voracious predators, active all year-round, it is difficult to imagine how such multispecies communities operate. It has been suggested that the generalized habits of shrews and their abundant, diverse, and constantly renewable food resources have permitted coexistence but only now is an attempt being made to quantify the food resource base and correlate it with population numbers and niche dynamics in coexisting soricids. Studies on communities of shrews show that, despite adaptations to different foraging modes, syntopic species show a convergent response in exploiting common food sources and the major shared prey are high in biomass and food value. Niches expand with few soricid species present but niche overlap decreases with the addition of species, and ecological separation is then achieved in subtle ways. Shrews are highly flexible in habits both on a spatial and a temporal basis but generalists are numerically dominant over specialists in multispecies communities.

INTRODUCTION

Many soricid species are not only sympatric but also syntopic. Typically, two or three species coexist in the same habitat but there are many examples of communities comprising six or more species. Over much of Europe, for example, *Sorex araneus, S. minutus*, and *Neomys fodiens* frequently coexist in forests and grasslands (e.g., Aulak 1967, Churchfield 1984a) and these three species are in places joined by *S. caecutiens* and *N. anomalus* (Aulak 1970). Communities of five species have been found in grassland in France, including *S. coronatus, S. minutus, N. fodiens, Crocidura russula*, and *C. leucodon* (Yalden et al. 1973). Turning to North America, in Manitoba, Buckner (1966) and Wrigley et al. (1979) commonly found *S. cinereus, S. arcticus*, and *Blarina brevicauda* together in marshlands and these were often accompanied by *S. hoyi, S. palustris*, and *S. monticolus*. In Colorado, Spencer and Pettus (1966) found communities of five species of soricids coexisting in marshlands. In the tropics, soricid communities are even more complex. For example, Dieterlen and Heim de Balsac (1979) caught 25 different species belonging to five different genera in part of the Kivu region of Zaire, with 8–10 species occurring together in primary forest and swamp. In all these communities it is usual for one or two species to be dominant in terms of population numbers and the others to be much less numerous: in Europe, *S. araneus* and *C. russula* are usually the dominant species; and in North America, *B. brevicauda, S. cinereus*, and *S. vagrans* are frequently dominant.

It is interesting to speculate on how these voracious, nonhibernating small mammals are able to coexist in multispecies communities. Michielsen (1966), Ellenbroek (1980), and Malmquist (1985) have investigated interspecific competition and character displacement in one- and two-species communities of shrews but the degree of overlap and ecological separation in multispecies communities has not been studied in detail. It has been suggested that the generalized habits of shrews and their abundant, diverse, and constantly renewable food resources have permitted coexistence but there has been little attempt to quantify the food resource base and correlate it with population numbers and niche dynamics in coexisting shrew species.

The present paper is an attempt to formulate such a model for investigating ecological separation, using a simple two- and three-species community of shrews.

METHODS

The Soricid Communities

The two communities of shrews are in central and southern England. One included *Sorex*

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araneus and *S. minutus* occupying 1.5 ha of grassland-scrub where Longworth live-traps were set in pairs at 15 m intervals. The other community included these two species plus *Neomys fodiens* inhabiting 2.5 ha of grassland-scrub, watercress beds, and streams. Here, Longworth traps were placed singly at 4–10 m intervals amongst the terrestrial vegetation on the banks adjacent to the streams and watercress beds. Traps were examined at approximately 3-hour intervals during the trapping periods and all captures were marked and released. Trapping was carried out for 3 days and nights at 4–6 week intervals over a period of 2 years. The feeding habits of shrews were investigated by analysis of fecal pellets collected from the traps. Identification of prey and their size ranges was facilitated by the use of a reference collection of invertebrates taken from the study areas. For a full description of the study site and methods see Churchfield (1982a, 1984a).

Niche Dimensions

For small mammals which have high metabolic rates, remain active all year, share the same breeding seasons, and have similar demands for foraging areas and nesting sites, the resource which may provide greatest scope for ecological separation is food, particularly as this resource is multidimensional. All shrews feed primarily on invertebrates but these come in different types, sizes, and locations. The dimensions of the food resource continuum that were selected as a basis for the study of niche separation in soricid communities are: 1) diversity of prey eaten and the number of shared prey, 2) dietary composition, 3) prey location, 4) prey size, and 5) shrew size.

Calculation of Niche Breadth and Overlap

The amount of overlap between species in the different food resource dimensions was expressed using modifications of indices of niche overlap and niche breadth in common use as follows:

Niche Breadth

Diversity Index (Shannon-Weaver function)

$$H = -\Sigma\, p_i \log_e (p_i)$$

where p_i = the proportion of each food type in the diet of each species.

Niche Overlap

1. Sørensen's Quotient

$$QS = \frac{2j}{a+b}$$

where a = total number of prey taxa in the diet of Species A,
b = total number or prey taxa in the diet of Species B,
j = total number of prey taxa common to both species.

2. Niche Overlap (after Schoener 1968)

$$0 = 1 - 0.5 \sum_{i=1}^{n} p_{xi} - p_{yi}$$

where p_{xi} = the proportion of prey type x in resource state i and
p_{yi} = the proportion of prey type y in resource state i and
n = the total number of resource states.

Food Resources

Since the availability of prey probably has an important influence on the feeding habits of shrews, the food resource base was quantified in terms of the biomass, food value, and location of prey by a program of monthly qualitative and quantitative invertebrate sampling. Ten pitfall traps (diameter 75 mm) were set for 3 days and nights during each shrew-trapping period in order to assess invertebrates active amongst the vegetation and soil, 5–10 cores (diameter 300 mm) were taken of vegetation and the top 80 mm of soil at monthly intervals (for full details, see Churchfield 1982a). Invertebrates were identified, categorized according to size and type, and counted. They were dried at 60°C to constant weight to obtain biomass estimates and were placed in a bomb calorimeter to obtain calorific values.

RESULTS AND DISCUSSION

Foraging Habits and Modes of Ecological Separation in Soricid Communities

Diversity of Prey and the Number of Shared Prey

Shrews eat a wide variety of commonly occurring invertebrates from small collembolans to large tipulid larvae and lumbricids (e.g., Hamilton 1940; Pernetta 1976; Bever 1983; Churchfield 1984b, 1985; Whitaker 1984). They are essentially opportunists, feeding within limits on whatever is available and there are few invertebrates which are not preyed upon by shrews. For these reasons, the diversity of prey items in the diet of all shrew species is high, as shown in the example in Table 1. Here, percentage composition refers to the number of occurrences of a named item divided by the total number of occurrences of all items. While this does not take account of the sizes of different prey types and so may bias the data towards the very small items, there was no evidence of such a bias.

Niches are broad for all species (Table 2). *Neomys fodiens* took the greatest diversity of prey because it includes both terrestrial and aquatic items in the diet, and *S. minutus* took the smallest diversity of prey. The small size of this shrew may have an important bearing on its dietary diversity, and this will be discussed later. Only four prey types out of a total of 29 terrestrial taxa identified were not shared by all three shrews. It is notable that *S. minutus* does not feed on lumbricids, although they are a common resource (Pernetta 1976, Grainger and Fairley 1978, Churchfield 1984b). Size may be a factor here, with most earthworms being simply too large for these small shrews to tackle. All the prey types eaten by *S. minutus* were also taken by both the other species. The amount of overlap between

Table 1. An example of the diversity of prey taken by shrews: the percentage composition of items found in the diet of *N. fodiens*, *S. araneus*, and *S. minutus*.

	Three-species Community			Two-species Community	
	N. fodiens	*S. araneus*	*S. minutus*	*S. araneus*	*S. minutus*
N =	169	242	35	219	27
Terrestrial prey					
Carabidae	1.9	1.6	1.6	2.1	2.2
Staphylinidae	2.7	2.5	2.4	12.3	13.3
Chrysomelidae	0.5	3.0	2.4	4.1	6.6
Other Coleoptera, adults	4.0	5.9	15.9	6.6	5.5
Coleoptera, larvae	0.8	2.1	0.8	2.8	0
Hemiptera	2.3	4.0	7.1	3.6	8.8
Culicidae, adults	0	0	0	0.1	1.0
Tipulidae, adults	0	0	0	0.9	0
Tipulidae, larvae	0.7	2.4	0	9.1	5.5
Other Diptera, adults	—	—	—	5.5	8.8
Other Diptera, larvae	2.5	3.5	9.5	1.4	0
Lepidoptera, larvae	0.7	2.0	3.2	6.1	8.8
Hymenoptera	0.2	0.2	0	0	0
Dermaptera	0.2	0.1	0	0.4	0
Formicidae	2.0	3.4	2.4	0.5	0
Collembola	0.2	0.4	1.6	2.0	2.2
Acari	3.2	8.3	7.9	3.1	2.1
Araneae	3.4	6.7	16.6	9.2	17.6
Opiliones	1.3	3.4	5.6	1.4	7.7
Isopoda	2.5	6.3	14.2	9.0	4.4
Geophilomorpha	1.8	4.5	1.6	2.7	1.1
Lithobiomorpha	0.5	0.7	3.2	1.1	4.4
Diplopoda	1.8	0	0	0.3	0
Gastropoda	5.7	18.0	4.0	3.9	0
Lumbricidae	5.7	21.0	0	11.8	0

Table 1. (continued)

	Three-species Community			Two-species Community	
	N. fodiens	*S. araneus*	*S. minutus*	*S. araneus*	*S. minutus*
N =	169	242	35	219	27
Aquatic prey		0	0	0	0
Coleoptera	1.2				
Hemiptera	0.3				
Trichoptera	11.4				
Plecoptera	4.5				
Ephemeroptera	0.5				
Diptera	8.8				
Asellus	19.0				
Gammarus	7.2				
Gastropoda	0.2				
Ostracoda	2.0				
Osteichthyes	0.3				

species was therefore considerable, as calculated by Sørensen's Quotient (Table 3) which takes into account all dietary items. Greatest overlap occurred between the two most terrestrial species, *S. araneus* and *S. minutus*.

Dietary Composition

When the proportions of prey types in the diet of different shrew species were examined, a more significant area of separation is apparent, for different species took different amounts of shared prey. This is demonstrated in the trophic spectrum in Fig. 1 where the composition of major prey types in the diets of the three coexisting species of shrews is shown. The major differences were: 1) approximately 50% of the diet of *N. fodiens* was aquatic in origin and consequently this shrew took smaller quantities of all terrestrial prey than did *S. araneus* or *S. minutus;* 2) *S. araneus* took large proportions of lumbricids and gastropods; and 3) *S. minutus* relied heavily upon araneids, coleopterans, and isopods compared with the other shrews. It is notable that *N. fodiens,* although adapted for underwater foraging, still took some 50% of its diet from the land where it is then in direct competition with the strictly terrestrial shrews.

If niche overlap is recalculated on the basis of the proportions of different prey types in the diets rather than simply on the diversity of prey eaten (as given by Sørensen's Quotient) then, as Table 3 indicates, overlap between all species is substantially reduced. This is so regardless of whether all prey taxa or only major prey types

Table 2. Food niche breadth in a two- and three-species community of shrews.

	N. fodiens	*S. araneus*	*S. minutus*
	Three-species Community		
Number of prey taxa	38	25	18
Diversity Index	3.01	2.67	2.58
	Two-species Community		
Number of prey taxa	—	29	18
Diversity Index	—	2.82	2.23

Table 3. Food niche overlap in a two- and three-species community of shrews.

	S. araneus } *S. minutus* }	*S. araneus* } *N. fodiens* }	*S. minutus* } *N. fodiens* }
		Three-species Community	
Sørensen's Quotient	0.84	0.79 (0.98)*	0.64 (0.88)*
Niche Overlap	0.58	0.45	0.36
		Two-species Community	
Sørensen's Quotient	0.8	—	—
Niche Overlap	0.73	—	—

*Terrestrial prey only.

are considered. Schoener's (1968) index of overlap and the index derived from Pianka (1973) give almost identical results. This, then, provides one means of achieving ecological separation, but on a quantitative rather than a qualitative basis, and it suggests that although shrews are opportunists in terms of the number of different prey eaten, they tend towards specialization by selecting for particular prey types. Note that all three species ate large proportions of coleopterans, particularly the small *S. minutus*.

The amount of overlap appears to differ in this niche dimension according to the number of soricid species present in the community. Overlap between *S. araneus* and *S. minutus* decreased from a value of 0.73 in the two-species community to 0.58 in the three-species community suggesting that, as might be predicted, niches are compressed when more species are present but expand when competition is reduced.

The diets of shrews do vary from one location to another, probably as a result of the availability of different prey. For instance, the diversity of prey taxa eaten remained similar in the two- and three-species communities exemplified here, but the proportions of certain prey types taken differed. Gastropods, for example, were one of the major prey types for both *S. araneus* and *S. minutus* in the three-species community but were relatively unimportant as prey in the two-species community. This may have been due to their greater abundance in the damper habitat surrounding the watercress beds.

Some seasonal differences were apparent in the diets of all three species, but again, these were

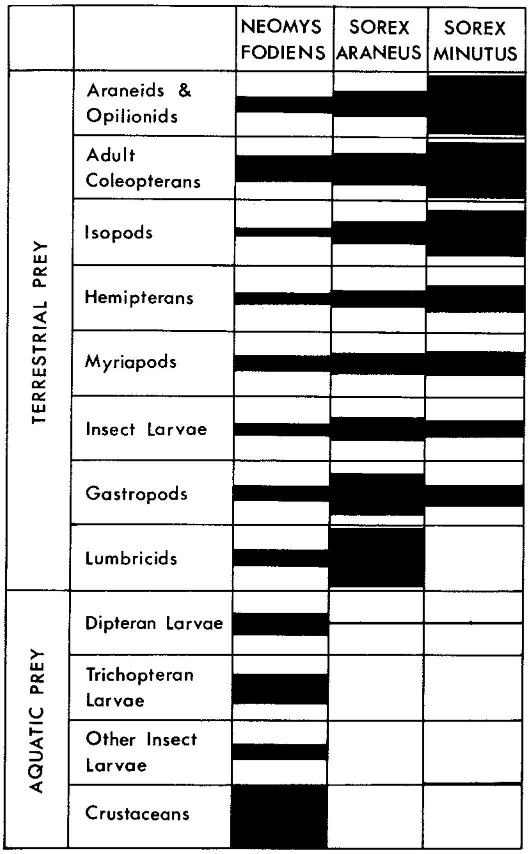

Figure 1. Trophic spectrum showing the composition of major prey types in the diets of three species of coexisting shrews. Each complete block represents a maximum of 30%. (Reproduced by permission of the Editor, Journal of Zoology, London.)

reflected not in the diversity of prey taken but in the proportions of certain major prey types eaten. Contrary to expectation, *S. araneus* and *S. minutus,* the most similar species, showed least overlap in winter (0.47) compared with summer (0.62) in the three-species community. This indicates that, either prey are not in short supply at this time of year, or that the decrease in the population numbers of shrews in autumn and winter reduced competition for resources. While the activity of invertebrates on the ground surface is reduced in winter, results of the vegetation/soil cores revealed that large numbers of invertebrates, including coleopterans, insect larvae, and isopods remained associated with the soil throughout winter, reaching densities of some 1,500 per m^2 which surpassed midsummer densities.

Location of Prey

Terrestrial invertebrates occupy various microhabitats and so niche separation may be achieved by adopting different foraging strategies in relation to the location of prey. Michielsen (1966) recognized this as a possible means of ecological separation of *S. araneus* and *S. minutus* and drew attention to the predominantly hypogeal habits of *S. araneus* and the epigeal habits of *S. minutus* but with little supporting evidence beyond the seasonal pitfall captures of shrews.

While many invertebrates are active in a variety of vertical strata from below ground to aerial vegetation, the majority of prey of shrews can be assigned to particular locations. For example, lumbricids, geophilomorph centipedes, and many dipteran larvae are soil-dwelling except for occasional emergences to the surface; carabid and staphylinid beetles, being fast-running predators, are inhabitants of the ground surface; and chrysomelid beetles and plant-feeding hemipterans are essentially inhabitants of aerial vegetation. The vertical distribution of prey such as these were confirmed by different methods of field sampling of invertebrates.

Figure 2 shows the proportions of prey of *N. fodiens, S. araneus,* and *S. minutus* in the three-species community from various locations and reveals certain differences in the foraging strategies of these shrews. While each species

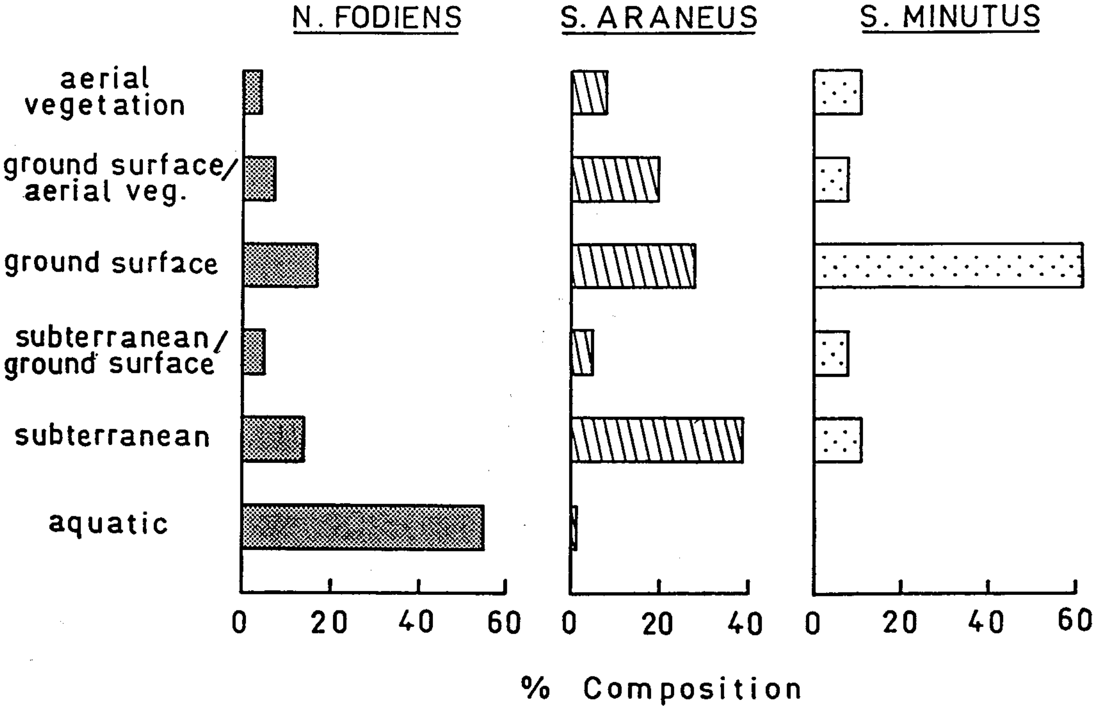

Figure 2. The percentage composition of prey taken from different locations by three species of coexisting shrews.

took some prey from all the terrestrial locations identified, notable differences were as follows: 1) *N. fodiens* caught a large proportion of its prey in freshwater and consequently took small amounts from all terrestrial locations; 2) subterranean prey were the most important food source for *S. araneus* and were exploited little by *S. minutus;* and 3) while both *S. araneus* and *S. minutus* took many prey from the ground surface, these comprised over 60% of the diet of *S. minutus* but only 30% for *S. araneus,* indicating differences in foraging modes between coexisting species, even amongst strictly terrestrial shrews. *Sorex minutus,* although small and a good climber, does not forage much amongst aerial vegetation.

Similar trends were apparent where *S. araneus* and *S. minutus* occurred in the absence of *N. fodiens,* but the differences between these shrews were not as clear. Calculated niche overlap was greater in the two-species community (0.77) than in the three-species community (0.60), again indicating that niches may expand in the absence of competing species.

Prey Size

All soricid communities comprise species of a range of body sizes (Table 4). In Europe, *N. fodiens* and *N. anomalus* are relatively large species, intermediate species include *S. araneus* and *C. russula,* and very small species are *S. minutus, S. minutissimus,* and *Suncus etruscus.* Similarly, in North America, the most abundant large species is *Blarina brevicauda* (16–29 g), intermediate are *Sorex vagrans* and *S. arcticus* (4–9 g), and *S. cinereus* and *S. hoyi* are smaller species (2–6 g). Tropical forest communities of soricids include the large *Crocidura turba* (14–30 g), intermediate *C. kivuana* and *C. hildegardae* (5–16 g), and small *C. bicolor* and *Sylvisorex megalura* (3–8 g). In most communities it is the intermediate species which are dominant in terms of number of individuals.

This suggests a further mode of ecological separation which may operate in a variety of ways but most obviously in the sizes of prey exploited, with a correlation between body size of shrew and prey size taken. Such a relationship has been demonstrated in lizard communities (Pianka 1973), and there is some evidence that this is the case both in shrews (Ackefors 1964, Platt and Blakely 1973) and in small rodents (Brown 1975).

Comparing the sizes of prey eaten by wild shrews with reference collections of invertebrates revealed that each species took a range of prey sizes. This is clearly indicated in Fig. 3 for the three-species community. *Neomys fodiens,* though large, takes a lot of small prey and *S. minutus,* though very small, is capable of dealing with large prey such as tipulid larvae over 20 mm in body length. However, although all three species took most of their prey around 6–10 mm in body length, 82% of prey of *N. fodiens* and *S. araneus* was 6–10 mm or larger, while 86% of prey of *S. minutus* was 6–10 mm or smaller. So, *S. minutus* does indeed take predominantly smaller prey (with the emphasis on small coleopterans, araneids, and isopods) than the larger shrews which feed on the bulkier earthworms and gastropods (see Fig. 1). The technique of assessing dietary composition may have underemphasized the importance of larger items in the diet, as previously mentioned, so the differences between shrews in the prey sizes eaten may be greater than suggested here.

Where *S. minutus* and *S. araneus* occurred in the absence of *N. fodiens* (see Fig. 4), the former still fed predominantly on small prey while

Table 4. Size differences of shrews in a community of *Neomys fodiens, Sorex araneus,* and *Sorex minutus.*

		N. fodiens	*S. araneus*	*S. minutus*
Body weight (g)	Mean	11.9	8.2	3.5
	Range	9.0–16.0	5.0–13.0	2.3–5.5
Body length (mm)		61–72	48–71	40–55
Mean length of Maxillary tooth row (mm)		0.91	0.79	0.59

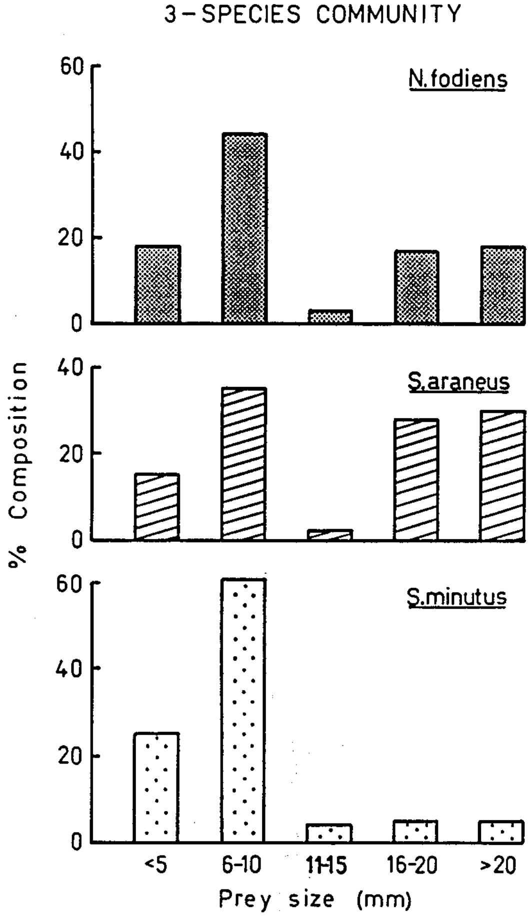

Figure 3. The percentage composition of prey of different size ranges in the diets of three species of coexisting shrews.

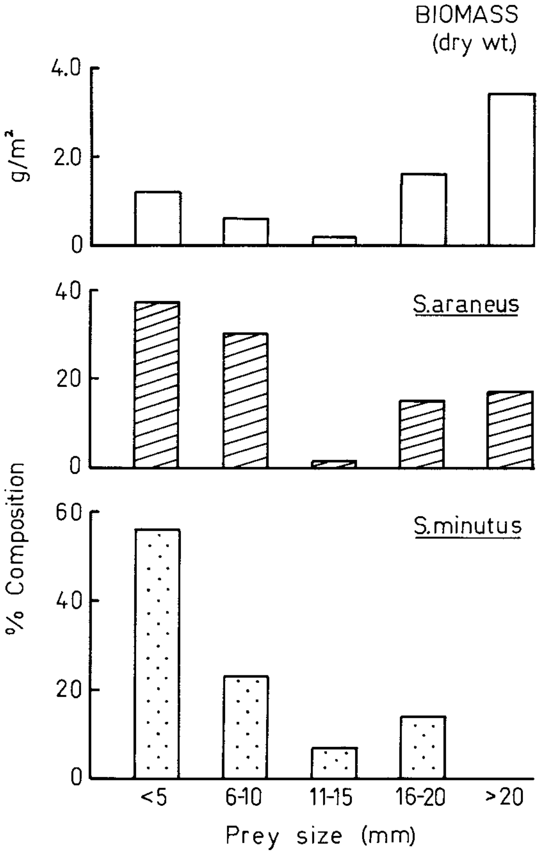

Figure 4. Size ranges of prey taken by a two-species community of shrews and the mean biomass (g dry weight/m^2 over the whole year) of prey available in different size categories.

the latter fed on large prey. But, *S. araneus* extended its niche to include a larger proportion of small prey and *S. minutus* took a larger quantity of large prey.

Studies of prey choice with captive *S. araneus* and *S. minutus* so far confirm these findings. Shrews provided with pieces of *Tenebrio molitor* larvae in a mixture of sizes (3 mm, 10 mm, and 25 mm in length) ad libitum showed no consistent preference for prey of any size. Both shrews took prey of all sizes and *S. minutus* exhibited no greater preference for smaller prey than did *S. araneus*.

As demonstrated by Wilson (1975), the exploitation of prey by shrews of different sizes has certain implications. Large predators may have a competitive advantage over small predators because they can utilize a wider range of prey sizes. However, small predators may have the advantage that they can utilize smaller prey more efficiently than can large predators. But, exploitation of food resources will depend on the distribution and occurrence of prey of different sizes. Although optimal foraging theories may predict that shrews should show preferences for prey of certain types and sizes, in the wild these predators seem to take whatever prey they encounter, within the constraints imposed by their body dimensions.

Combined Niche Overlap

Table 5 provides a summary of the overlaps calculated for different dimensions of the food

Table 5. Summary of food niche overlaps in two communities of shrews.

Food Niche Dimension	Three-species Community *S. araneus* } *S. minutus* }	 *S. araneus* } *N. fodiens* }	 *S. minutus* } *N. fodiens* }	Two-species Community *S. araneus* } *S. minutus* }
Prey diversity*	0.84	0.79	0.64	0.80
Dietary composition	0.58	0.45	0.36	0.73
Prey location	0.60	0.42	0.46	0.77
Prey size	0.57	0.82	0.75	0.76
Combined Niche Overlap	0.65	0.62	0.55	0.77

*Sørensen's Quotient; all others after Schoener (1968).

resource niche in two- and three-species communities of soricids on a scale of 0.0 (no overlap) to 1.0 (complete overlap). It also includes an estimate of full niche overlap which combines the effects of the different dimensions. As the niche dimensions here are not completely independent, the combined niche overlap is derived from the arithmetic mean of the component dimensions (May 1975).

Different areas of niche separation have been identified but in some dimensions overlap is still considerable (up to 0.82). However, the combined effect of many small differences between species in their exploitation of resources in different dimensions was reduced total overlap and a means of effective ecological separation. Niche overlap was reduced where more coexisting species were present but niches expanded when fewer species were present. For example, overlap between *S. araneus* and *S. minutus*, the most similar species, was reduced in all but one dimension when the number of coexisting species increased from two to three.

Models of niche overlap such as that developed by MacArthur and Levins (1967) have indicated a limiting overlap between niches of approximately 0.54, beyond which competition would lead to exclusion of one or the other species, assuming that resources are limited. The soricid communities considered here exceeded this value for food niche overlap. However, in practice the maximum tolerable overlap must depend upon the number of species in the community, the pattern of species packing, and, probably most importantly, the resource base.

Niche Overlap and Food Availability

Niche size and shape much depend upon the resources available as well as the presence of inter- and intraspecific competition. If resources are in short supply or are unpredictable then the niche must remain broad. So the niche occupied is not only a product of the effects of competing species but also of resource availability.

The feeding habits of all shrews probably reflect the relative abundance of prey of different types, sizes, and locations and there is some evidence to suggest that the diets of shrews and food availability are correlated (Ackefors 1964, Pernetta 1976, Churchfield 1982a). Any conclusions drawn about niche overlap and possible modes of ecological separation must, therefore, include a consideration of the resource base.

Prey Sizes and Biomass

The sizes of prey taken by shrews do reflect the relative abundance of invertebrates in different size categories. The availability of prey in different size categories is shown in Fig. 4 in terms of the mean biomass in gram dry weight per meter^2 estimated from vegetation/soil core samples in the grassland-scrub study area. Prey sizes were assessed for individual items, not for whole taxa, since certain taxa (notably coleopterans) contained both small and large representatives.

Figure 4 indicates that the greatest biomass of prey was available as large items such as lumbricids and large insect larvae which are suitable for *S. araneus* and *N. fodiens* but which are not as favored by *S. minutus*. Few prey actually occurred in the 11–15 mm category which would explain why few prey of this size were eaten by shrews. There were many small prey available, both in terms of biomass and diversity. The greatest diversity of prey types occurred in smaller sizes, between 3–10 mm in body length, which includes the majority of coleopterans, an important food source in many shrew communities, as well as isopods and araneids. Although large shrews may have a competitive advantage over small shrews in being able to exploit larger prey more effectively, the size distribution of prey available suggests that small shrews also have an advantage. The encounter rate with small prey is considerably greater than for large prey, and small shrews probably forage more efficiently for small prey than do large shrews. Medium-sized shrews may have the greatest advantage since they can probably exploit the widest size range of prey most efficiently. This may account for the dominance of intermediate species such as *S. araneus* and *S. vagrans* in soricid communities.

The greatest contributors to prey biomass were lumbricids and coleopterans, as indicated in Fig. 5. Coleopterans were mostly small in size (5 mm or less) but were extremely abundant and easy to locate; lumbricids were generally over 20 mm but were less numerous. Other major prey items had a much lower availability (see Fig. 5). It is not surprising, then, that coleopterans form an important component of the diet of many shrews (e.g., Hamilton 1940; Whitaker and Mumford 1972; Grainger and Fairley 1978; Churchfield 1982a, 1982b, 1984b, 1985; Whitaker 1984; Rowe-Rowe 1986). Araneids were the third most abundant food source; they were generally 5 mm or less in size, forming a major prey item for small shrews such as *S. minutus*.

Vegetation/soil cores and pitfall samples showed that some invertebrates, such as myriapods, were never very abundant, while others such as araneids, hemipterans, and insect larvae underwent marked seasonal fluctuations in numbers (see Churchfield 1982a). The most dependable food resources were 1) coleopterans, which were usually superabundant (mean = 340 per m^2, maximum = 890 per m^2); 2) lumbricids, which were usually abundant but may be inaccessible

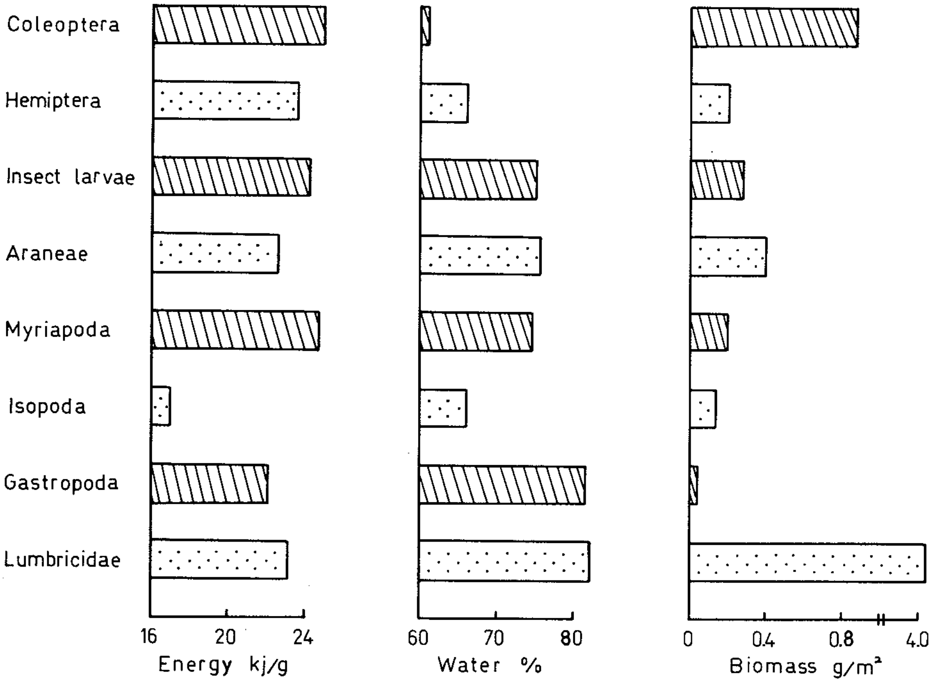

Figure 5. Relative food value and biomass of the major prey available to shrews as determined from vegetation/soil cores taken in the grassland-scrub study area. Biomass estimates (g dry weight/m^2) represent mean values for the whole year.

during freezing or hot, dry conditions; and 3) isopods, which were never very numerous but were available throughout the year.

Food Value

Invertebrates show relatively small differences in terms of energy content (see Fig. 5). Coleopterans, lumbricids, and araneids rate high as do less numerous prey such as insect larvae and myriapods. Isopods have the lowest energy content of those tested. Total food value may be reduced by high water content and indigestible chitin. The latter has not been taken into account here since so many prey of shrews have chitinous exoskeletons, but Fig. 5 shows that isopods and coleopterans have the lowest percentage water content of all prey types, while lumbricids have the highest.

In conclusion, it is not surprising that coleopterans form a major component of the diet of many shrews since they are relatively more abundant and have a higher availability throughout the year and a greater food value than any other terrestrial invertebrate prey.

Prey Exploitation at the Population Level

Shrews remain essentially opportunistic generalists with broad niches. Where specialization does occur, as in *N. fodiens* and *S. palustris,* generalized habits are retained. This suggests that resources are, or have been, in short supply. While more information is required on the seasonal biomass of invertebrate prey in northern continental areas, estimates of prey availability and food consumption by populations of shrews in Britain suggest that food is not limiting. For example, Churchfield and Brown (1987) showed that combined populations of *S. araneus* and *S. minutus* of 74 per ha in summer may clear up to 1.1 m^2 per day of insects alone, but this represented only 0.01% of the total insects available as prey. Even in winter, shortages of certain, seasonally active prey are compensated for by an abundance of other invertebrate prey. The minimum number of known prey items occurring in winter months during 2 years of investigation was approximately 700 per m^2 (Churchfield 1982a). Even if shrews maintained populations at summer levels, predation rate would only reach 0.09% of the prey available.

Hence, niche overlap in shrews may be a product of abundant food supply and/or the effects of intra- rather than interspecific competition. Where competition with other species is not severe, intraspecific competition may encourage individuals to exploit those parts of a resource where competition with conspecifics is reduced, and so individuals will diversify and broaden their niche. This seems most likely since soricid communities invariably comprise one or two abundant species and other much less numerous, even rare, species. For example, in the three-species community exemplified here, 52% of individuals belonged to *S. araneus,* 31% to *N. fodiens,* and only 17% to *S. minutus*. It should be remembered that shrews are not the only predators to exploit invertebrates as prey. Also, the effects of past climatic events on food resources cannot be ignored. While there may be little ecological pressure on many present-day temperate and tropical soricids to reduce niche overlap, this may not always have been the case.

CONCLUSIONS

Habitats can support several similar, coexisting species because they provide multidimensional resources which can be exploited in different ways by different species in the community. Hence, overlap can be high in certain dimensions as long as niches are sufficiently separate along some other dimension. Sharing a resource, however, still may reduce the potential population size of coexisting species which is reflected in the relative abundance of different soricids. Studies by Malmquist (1986) showed that population densities of *S. minutus* in allopatry are higher than those in sympatry with *S. araneus*. Selection will favor ways of reducing overlap and in many cases this has produced marked differences in adaptations, as in the aquatic foraging mode of *N. fodiens* and *S. palustris*. But, the distribution and availability of a resource, particularly food, may provide an opportunity for exploitation by many species, despite the possibility of competition. A uniformly abundant resource such as beetles may, therefore, produce a convergent response in foraging strategy in different soricids: even the more specialized species retain a generalized foraging mode to exploit food in a variety of dimensions. Hence, soricids remain flexible both on a spatial and temporal basis.

In summary, shrews remain generalized small mammals which are adapted to exploit a common resource (invertebrates) in a multitude of dimensions but where ecological separation increases or decreases according to the availability of resources and the presence of potential competitor species.

Using two- and three-species communities as examples, this paper has attempted to highlight aspects of the niche dynamics of shrews in the context of resource availability. Even in these relatively simple communities, niches are not distinct or exclusive and ecological separation may occur in quite subtle ways. The niche dynamics of more complex multispecies communities, such as those occurring in tropical forests, still require detailed investigation and would well repay further study.

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The Energy Expenditure of Shrews

BRIAN K. MCNAB

Abstract

Measurements of rate of metabolism and temperature regulation in two North American shrews, *Cryptotis parva* and *Blarina carolinensis,* are presented along with a general reexamination of the energy expenditure of members of the eutherian family Soricidae. By general mammalian standards, all members of this family have high basal rates, but some have much higher basal rates than others. The highest basal rates are found in red-toothed shrews (Soricinae) that do not enter daily topor. White-toothed species (Crocidurinae) and soricines that enter daily topor have lower basal rates. Whether the apparent connection between a low basal rate and propensity to enter torpor is obligatory or not is unclear because the soricines *C. parva* and *B. carolinensis* have basal rates that approach those of crocidurines, but neither species is known to enter torpor. Many data reported in the literature on rates of metabolism in shrews are much too high to be standard because the measurements were made at temperatures well below the lower limit of thermoneutrality.

Temperate and arctic shrews avoid entrance into torpor by combining a small body mass, and a low total rate of metabolism and food requirement, with use of an abundant, high-quality food. Some cold-climate soricines further reduce energy requirements by a seasonal reduction in body mass. Why crocidurine shrews have a lower rate of metabolism and thus are prone to enter torpor is unclear. In terms of energetics, a New World tribe of soricines, the Blarini, appears to be intermediate to the Soricini and the Crocidurinae. All soricids have higher basal rates than are found in the marsupial equivalents of shrews, the smallest members of the Dasyuridae, a difference that may be related to the different form of reproduction found in marsupials and eutherians.

INTRODUCTION

Shrews, small eutherian mammals that feed predominantly on soil invertebrates, belong to the family Soricidae. They are often said to have such high rates of metabolism that they will starve to death within an hour or two if not fed. Shrews, however, show some diversity in energetics: white-toothed shrews (Crocidurinae) have lower basal rates than red-toothed shrews (Soricinae) of the same size (Dryden et al. 1974, Vogel 1976) and crocidurines, unlike soricines, upon occasion enter daily torpor (Vogel 1974).

These conclusions summarized knowledge up to 1980, but were fraught with various conceptual and empirical difficulties. In absolute terms, shrews have high rates of metabolism only if one assumes that the effective rate is mass-specific; shrews actually have very low total rates of metabolism because they are so small. Shrews, however, have high basal rates when compared to a "standard" curve, such as the Kleiber (1961) relation. The problem faced by shrews is not a high rate of metabolism, but rather a high turnover rate, i.e., a high rate of metabolism relative to the size of energy stores. As a consequence, shrews are required to feed often during a day because their energy stores are continuously threatened by exhaustion. Experience, however, indicates that many shrews, even those weighing a few grams, can withstand starvation for a few hours as long as they are permitted to rest and are not exposed to cold ambient temperatures.

Many of the measurements available on shrew energetics have a questionable significance. 1) A complete metabolism-temperature curve was often not measured, so that no assurance can be given that the measurements reported, often at "room" temperature, were within thermoneutrality. 2) Out of concern for the high turnover rates of shrews, some investigators included food during the measurement of oxygen consumption. This may have led to the inclusion of the heat increment of metabolism (= specific dynamic action) in the estimate of rate of metabolism. In compensation, some investigators reduced the measured rate of metabolism by an arbitrary amount to compensate for the assumed heat increment. These manipulations have produced confusion as to what the "true" basal rate of shrews is.

A further complication in the energetics of

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shrews was the discovery by Lindstedt (1980a, 1980b) that the desert soricine *Notiosorex crawfordi* has a basal rate and propensity to enter torpor similar to that of crocidurine shrews. These observations suggest that the correlation of energetics with subfamilial affiliation may reflect an ecological correlation.

In this paper I will: 1) present data collected on two species of shrews found in Florida, *Cryptotis parva* and *Blarina carolinensis,* both belonging to the tribe Blarini of the subfamily Soricinae; 2) review the data available on shrews in an attempt to separate those measurements that estimate the mean rate of energy expenditure at various ambient temperatures from those estimates of the standard (= basal) rates of metabolism; 3) examine the factors associated with the variation in basal rate and the propensity of some soricids to enter torpor; and 4) compare the energy expenditure of shrews with their ecological equivalents among marsupials. Even at this stage one can conclude that many more data on the standard energetics of shrews are needed before any clear understanding of soricid energetics can be obtained.

ANIMALS AND METHODS

Rates of oxygen consumption and body temperatures were measured as a function of ambient temperature in two least shrews (*Cryptotis parva*) and five short-tailed shrews (*Blarina carolinensis*). These shrews were collected in central Florida, most of them near Micanopy and Gainesville, Alachua County. *Cryptotis* was found in grassy flats near water and *Blarina* was usually found in, or near, wooded tracts.

Oxygen consumption was measured in an open system with an Applied Electrochemistry oxygen analyzer that was placed in the gas stream after CO_2 and H_2O were removed and after flow rate was measured. The minimally recurring rate of oxygen consumption was used in each experiment; this rate was corrected to dry gas at STP. A shrew was placed in a chamber submerged in a water bath to control ambient temperature. At the end of a run, rectal temperature was measured usually within 0.25 minute of completing an experiment. The mean minimal thermal conductance was estimated as recommended by McNab (1980a). A few runs were conducted with mealworms given to the shrews but, because shrews can survive several hours without food, most experiments were made without such supplements. These data permitted an evaluation of the consequence to rate of metabolism of adding food. Data are reported as a mean ± SE (n, measurements).

RESULTS ON *CRYPTOTIS* AND *BLARINA*

Measurements of body temperature and rate of metabolism in *Cryptotis parva* at temperatures between 6 and 36°C are presented in Fig. 1. Mean body mass in this species was 6.2 g. *Cryptotis* maintained body temperature at 37.0 ± 0.07 (39)°C between ambient temperatures of 5 and 33°C; at higher ambient temperatures, body temperature increased (ΔT equals 2.5°C). Basal rate in this shrew equals 3.06 ± 0.101 (17) $cm^3O_2/g{\cdot}h$, which is 1.41 times the value expected from the Kleiber (1961) relation. The zone of thermoneutrality extends, approximately, from 32 to 36°C. Pfeiffer and Gass (1962) suggested that a rate of 7.0 $cm^3O_2/g{\cdot}h$ was basal in a 6.4 g *Cryptotis,* but given that the measurement was made at 27°C, it surely is not basal. In fact, this value is similar to those presented here at 26°C (Fig. 1). Thermal conductance is 0.477 ± 0.0092 (20) $cm^3O_2/g{\cdot}h{}^\circ C$, which is 1.19 times the value expected from mass (McNab and Morrison 1963). No evidence of torpor, or of low body temperatures, was found in *Cryptotis;* however, Layne and Redmond (1959) recorded 35.0°C as the mean body temperature with the range extending from 31.9 to 39.1°C, which suggests a thermal lability in *Cryptotis*.

Data on the body temperature and rate of oxygen consumption in *Blarina carolinensis* as a function of ambient temperature are found in Fig. 2. *Blarina* maintained body temperature at 36.8 ± 0.07 (73)°C between 10 and 31°C, as long as the shrew was inactive. With activity, body temperature increased 1–2°C. Body temperature increased at ambient temperatures above 30°C (ΔT equalled about 5°C), and decreased at temperatures below 12°C. At ca. 6°C, body temperature in inactive individuals varied between 33.1 and 36.6°C. Such body temperatures were measured in all individuals exposed to 6°C. Torpor was not observed in any of these experiments.

The zone of thermoneutrality in *B. carolinensis* (average mass 10.2 g) extended from 30

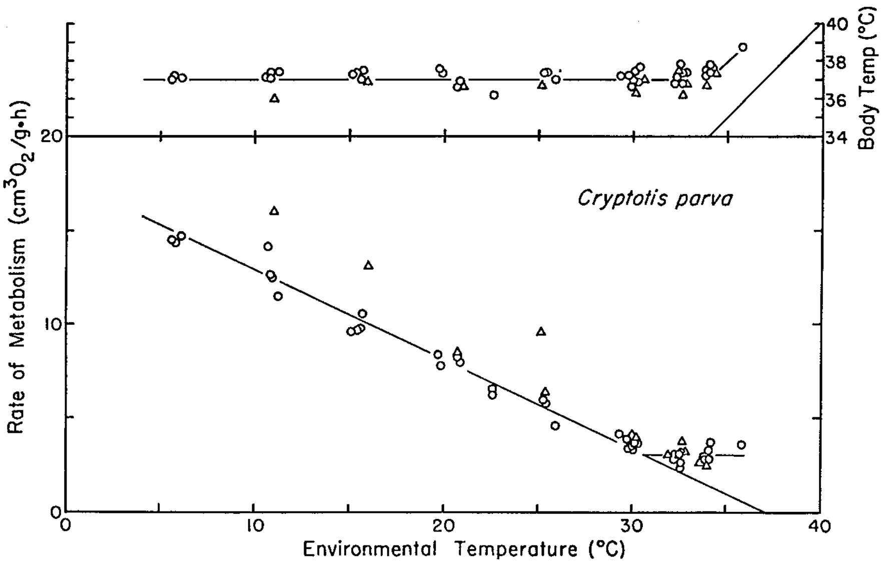

Figure 1. Body temperature and mass-specific rate of oxygen consumption as a function of environmental temperature in two *Cryptotis parva*. Each individual is given a different symbol.

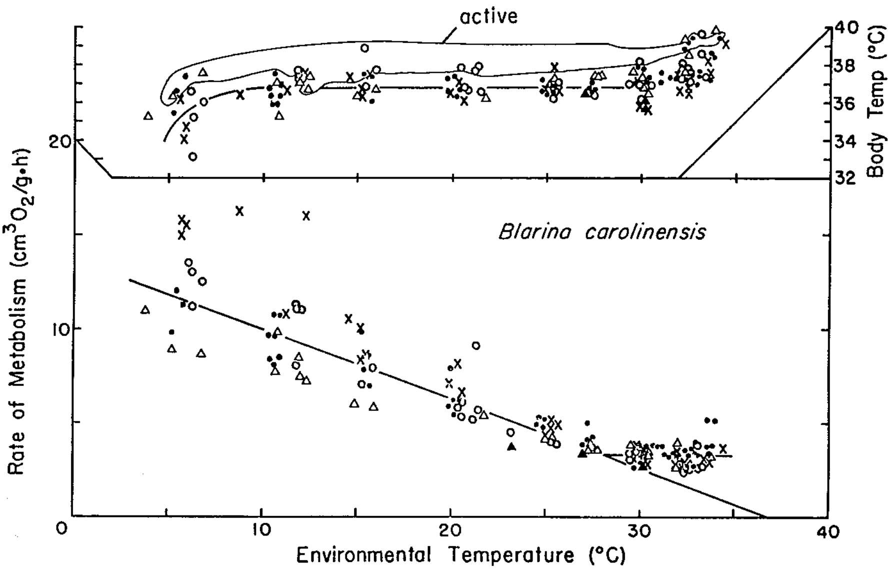

Figure 2. Body temperature and mass-specific rate of oxygen consumption as a function of environmental temperature in five *Blarina carolinensis*. Each individual is given a different symbol. Those individual measurements of body temperature associated with activity are indicated.

to 34°C. At these temperatures the mean rate of oxygen consumption was 3.26 ± 0.058 (55) $cm^3O_2/g{\cdot}h$, which is 1.70 times the value expected from the Kleiber relation. This rate is basal (or standard), not only because the shrews were within thermoneutrality and were inactive, but because it was not influenced by feeding before a run, by placing up to five–six mealworms in the chamber (Fig. 3), or by completely withholding food for up to 6 hours (in a sequence of three 2-hour runs). Giving up to five mealworms also had no effect on rate of metabolism in *C. parva* (Fig. 3). Mean minimal thermal conductance in *Blarina* equals 0.375 ± 0.0086 (54) $cm^3O_2/g{\cdot}h°C$, which is 1.20 times the standard value expected from mass.

ANALYSIS

The data available on rate of metabolism in shrews are often difficult to interpret. They are potentially complicated by the influence of ambient temperature, by activity, by the addition of food during measurement, and by selective occurrence of daily torpor in certain species. These complications are exaggerated by the use of techniques that depend on the integration of rate of metabolism over some extended time period (e.g., Pearson 1948, Fons and Sicart 1976), and therefore permit the incorporation of activity, rather than using techniques that permit continuous measurements to be made (e.g., Morrison et al. 1959, Lindstedt 1980a, Nagel 1985, this study). The influence of these secondary factors must be clarified before an understanding of soricid energetics can be attained.

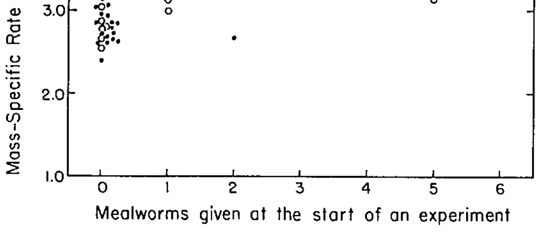

Figure 3. Mass-specific rate of oxygen consumption of *Cryptotis* and *Blarina* within the zone of thermoneutrality as a function of the number of mealworms given at the start of an experiment.

Standard Energetics in Shrews

A basal (or "standard") rate of metabolism is a rate measured during the normal period of rest in an endotherm within thermoneutrality when the animal maintains a normal body temperature, is inactive, and is postabsorptive. In contrast, many shrews have had energy expenditures measured at ambient temperatures from 20 to 25°C, which are well below the lower limit of thermoneutrality in endotherms that weigh from 3 to 10 g. This limit is usually between 30 and 32°C (Morrison et al. 1959, Gebczynski 1965, Lindstedt 1980a, Tomasi 1985; Figs. 1 and 2). Notice that the lower limit *measured* by Morrison et al. (1959) in *Sorex cinereus* is ca. 29°C, not as *drawn* (their Fig. 7) down to 22°C. The available measurements on shrews can be grouped into those that potentially represent basal rates (because they were made within thermoneutrality) and those that represent mean rates at some temperature below thermoneutrality. This distinction is drawn in Fig. 4, although sufficient information is often lacking on whether those species measured in thermoneutrality were inactive and post-absorptive, i.e., whether the measurements in thermoneutrality were "standard" or not. Some measurements on soricines [e.g., *Sorex araneus* (Gebczynski 1965, Nagel 1985), *Neomys anomalus* (Gebczysnka and Gebczynski 1965), and *N. fodiens* (Gebczynska and Gebczynski 1965)] and on crocidurines [*Suncus etruscus* and *Crocidura russula* (Fons and Sicart 1976)] apparently were made in thermoneutrality, but are unusually high (Fig. 4), which may have reflected the inclusion of activity. Observations summarized in Fig. 3 make it unlikely that moderate amounts of food given before or during an experiment markedly increase rate of metabolism, probably because food is processed within a 2–3 hour experimental period. The best estimates of basal rate in soricids are assembled in Table 1.

The distinction between measurements made in thermoneutrality and those made at lower tem-

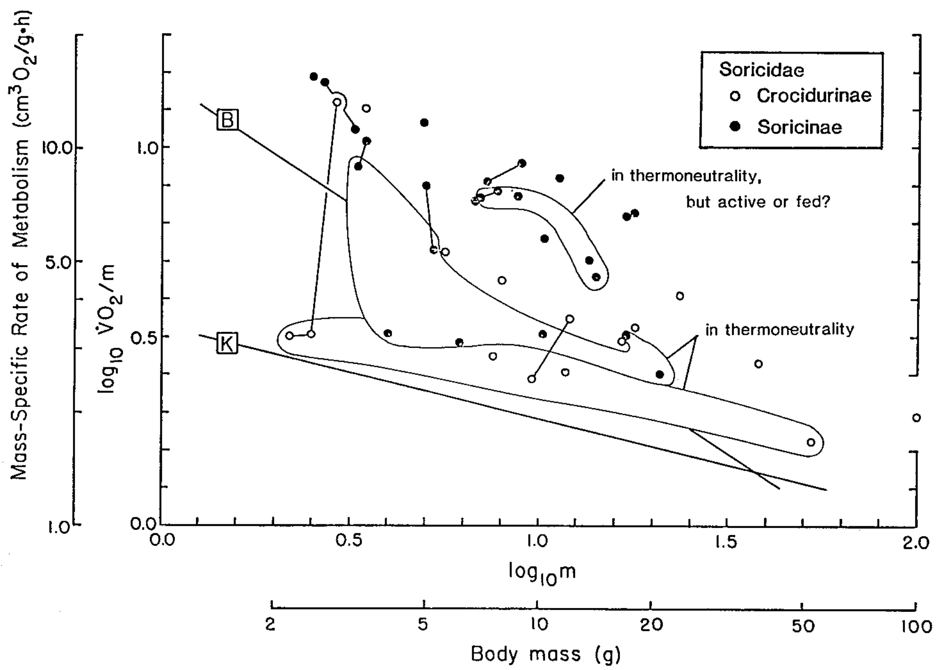

Figure 4. Log mass-specific rate of oxygen consumption as a function of log body mass in shrews within the zone of thermoneutrality (data taken from Table 1) and at cooler temperatures (data taken from Pearson 1948, Gebczynska and Gebczynski 1965, Gebczynski 1965, Fons and Sicart 1976, Vogel 1976, and Hanski 1984). The scaling relation of Kleiber (1961) and the boundary curve for endothermy (McNab 1983) are indicated by K and B, respectively. Values for the same species derived by different workers are connected.

Table 1. Basal rates of shrews.

Species	Mass (g)	Basal Rate (cm³O₂/g·h)	Basal Rate f_m*	Torpor	Sources
Crocidurinae					
Suncus etruscus	2.5	3.60	0.43	+	Nagel 1985
Crocidura suaveolens	7.5	2.81	0.70	+	Nagel 1985
Crocidura russula	9.6	2.45	0.72	+	Nagel 1985
Crocidura leucodon	11.7	2.55	0.85	+	Nagel 1985
Suncus murinus	52.0	1.68	1.52	+	Dryden et al. 1974
Soricinae					
Soricini					
Sorex cinereus	3.3	9.00	1.29	o	Morrison et al. 1959
Sorex vagrans	5.2	5.41	1.05	o	Tomasi 1985
Neomyini					
Notiosorex crawfordi	4.0	3.27	0.53	+	Lindstedt 1980a
Neomys fodiens	17.1	3.22	1.39	o	Nagel 1985
Blarini					
Cryptotis parva	6.2	3.06	0.67	?	this study
Blarina carolinensis	10.2	3.26	0.99	?	this study
Blarina brevicauda	21.0	2.50	1.24	o	Platt 1974

*f_m = (measured basal rate)/(15.56 $m^{-0.67}$) (McNab 1983).

peratures is indicated in Fig. 4 in both crocidurine and soricine shrews. In white-toothed shrews, standard rates are slightly higher than the values expected from the Kleiber curve. Measurements made at temperatures between 20 and 25°C, however, are appreciably higher, as is to be anticipated from a lower limit of thermoneutrality equalling ca. 32.5°C. This difference in rate between measurements made in thermoneutrality and at lower temperatures is most marked, as expected, at smaller masses.

The measurements of rate of metabolism in soricine shrews are higher than equivalent measurements found in crocidurines. Basal, or standard, rates in red-toothed shrews appear to be highly variable, depending on the species. Some, namely *Sorex cinereus, S. vagrans, Neomys fodiens,* and *Blarina brevicauda,* have basal rates that equal, or exceed, the "minimal boundary curve for endothermy" described by McNab (1983). Others, namely *Notiosorex crawfordi, Cryptotis parva,* and *B. carolinensis,* have basal rates that are higher than the Kleiber curve, but lower than the boundary curve, and similar to crocidurines. Although some doubt exists on whether all of the rates in thermoneutrality described here in some smaller soricines are standard with reference to activity, little doubt exists that crocidurines have lower basal rates than most, or even all, soricines, especially at masses less than 10 g (Fig. 4). These data confirm the conclusions of Vogel (1974, 1980).

Body Size, Dehnel's Phenomenon, Bergmann's Rule, and the Low Rate of Metabolism of Shrews

As noted in the Introduction, many biologists consider shrews to have exceedingly high rates of metabolism. This view is justified only if mass-specific rates are used. Shrews, however, have the lowest total basal rates of all mammals because they are the smallest continuous endotherms. Total basal rates have been argued to be the only ecologically relevant rates (McNab 1971), yet this suggestion has met with some resistance, principally as a result of a confusion between rate of metabolism (i.e., power = energy/time) and turnover "rate" (i.e., time for the storage or consumption of a given quantity of energy or matter). Kleiber (1970) concluded that mass-specific rate has ". . . no proper physical or physiological meaning," a view that he later (1974, 1975) modified to conclude that mass-specific rate is a measure of turnover rate. The relation between turnover time and mass-specific rate deserves attention here because of the many erroneous statements on the implication of body size for energy exchange, especially with respect to shrews.

The time period for energy consumption or storage can be approximated by

$$t\ (\mathrm{h}) = \frac{\textit{energy store}\ (\mathrm{kJ})}{\textit{rate of energy expenditure}\ (\mathrm{kJ/h})}$$

(McNab 1980c). If the energy store is proportional to body mass (i.e., $m^{1.0}$) and if energy expenditure is proportional to $m^{0.75}$, then time is proportional to $m^{0.25}$, which is what has been specifically (Morrison 1960, McNab 1980c) and generally (Lindstedt and Calder 1981) argued. Thus, turnover time (or as Lindstedt and Calder called it, "physiological" time) increases with body mass. Mass-specific rate of metabolism is, simply, an approximate means of calculating turnover time. For example, when rate of metabolism ($\dot{Q}$, kJ/h) is divided by mass (m, g), then $\dot{Q}$/m (kJ/g·h) is generally acknowledged to be proportional to $m^{-0.25}$ Yet, the mass of the endotherm has an equivalence in energy (i.e., g $\approx$ kJ), so the units kJ/g·h can be replaced by kJ/kJ·h = 1/h (turnover "rate"). In other words, mass-specific rate of metabolism is simply equivalent to the inverse of turnover time, and that is why turnover time scales proportionally to $m^{0.25}$ and mass-specific rate scales proportionally to $m^{-0.25}$.

The above analysis suggests that two conflicting factors influence energy expenditure in mammals: the need to reduce energy expenditure would force a *reduction* in mass because rate of metabolism is proportional to $m^{0.75}$, whereas the utility of an extended period of starvation in a variable environment (Lindstedt and Boyce 1985) would require an *increase* in mass, which itself would require an *increase* in energy expenditure. Herein lies the comparative significance of Dehnel's phenomenon and Bergmann's rule.

Adams (1912), Dehnel (1949), Pucek (1964), Mezhzherin (1964, 1969), Mezhzherin and Melnikova (1966), Genoud (1984), and Hyvarinen (1984) have shown that shrews are smaller in winter than in summer, that some of the reduction in size involves a decrease in skeleton and skull size, and that such a decrease may be under endocrine control mediated by photoperiod. The reduction in size is greatest in colder climates (Mezhzherin 1964, Hyvarinen 1984) and the smallest species of *Sorex* are generally found in colder climates (Mezhzherin 1964). These observations suggest that the *reduction* in mass is a means of reducing energy expenditure during a period when the availability of soil invertebrates is reduced (Mezhzherin 1964, Genoud 1984, Hyvarinen 1984, Aitchison 1987). This interpretation is in accord with the interpretation that the fundamental rate of metabolism is the total rate, and that the reduction in mass is a reflection of a winter food shortage.

Bergmann's rule, which describes an increase in body mass at higher latitudes and which has on occasion erroneously been said to reduce energy expenditure, in fact requires an *increase* in energy expenditure (McNab 1971). An animal cannot increase mass unless food availability permits such an increase. Merritt (1986) argued that *B. brevicauda,* in contrast with the reduction of mass found in *Sorex araneus,* increases mass in winter by 39%, which implies an increase in basal rate of 28% ($[1.39]^{0.75} = 1.28$); he measured a 38% increase in rate of metabolism in association with the larger mass. Such increases in body mass and rate of metabolism mean that food availability is not limiting. Genoud (pers. comm.), however, suggested that the increase in rate of metabolism described by Merritt actually reflected a seasonal variation in rate and not a change in body mass, an interpretation, which if correct, also means that food availability is not limiting.

So the rationale for an increase in mass in a cold climate must be other than energy conservation (remembering always that no animal—other than humans—can appreciate a *proportional* savings of energy). One such rationale, as stated, is an increase in starvation time in a physically variable and hostile environment. This rationale, however, has little value for a small *Sorex*. Thus, if a 5 g shrew can starve for 2 hours at a cold temperature, then one can estimate the increase in mass required for starvation time to be doubled (given that all other physiological characters remain the same):

$$2 = t_2/t_1 = (m_2/m_1)^{0.25}$$
$$m_2/m_1 = 16,$$

where m_1 and m_2 are body masses. That is, the *Sorex* would have to weigh $5 \times 16 = 80$ g—an absurd increase in size, which would be associated with a $(m_2/m_1)^{0.75} = (16)^{0.75} =$ eightfold increase in basal rate! The 39% increase in mass found in *Blarina* translates into a 9% increase in starvation time, although starvation time may be further increased if all of the increase in mass is an energy store. So 9% is a minimal estimate of the increase in starvation time.

Clearly, shrews have low basal rates and short turnover times in association with their small masses, and often respond in harsh climates to a food restriction by a reduction in body mass. This response is typical of Holarctic soricine shrews. But another response is possible: shrews can theoretically respond to a food shortage by entrance into torpor.

The Occurrence of Torpor in Shrews

Torpor, which occurs on a daily, rather than a seasonal, basis in shrews, has been widely found among crocidurines (Vogel 1974, 1976; Nagel 1977; Frey and Vogel 1979), but in soricines it has been described only in the North American desert shrew (*Notiosorex crawfordi*) by Lindstedt (1980b).

McNab (1983) argued that the occurrence and absence of daily torpor in small endotherms is correlated with basal rate of metabolism. Small endotherms that do not enter daily torpor have, at a given mass, higher basal rates than those that enter daily torpor, even if those that enter torpor have basal rates as high as the values expected from the Kleiber curve. These two relationships intersect at a mass of about 36 g (Fig. 5). Thus, all small crocidurine shrews have basal rates that are less than those required by the "boundary curve" for continuous endothermy, and (as a consequence) all enter torpor on occasion (Table 1). The propensity to enter daily torpor, in fact, is greatest in *Suncus etruscus,* befitting its small mass and low basal rate relative to the boundary curve. The much larger *Suncus murinus* apparently enters torpor (Frey and Vogel 1979), but with what frequency is unclear; nevertheless it has a basal rate above both the boundary and Kleiber curves (Dryden et al. 1974).

In contrast, most soricine shrews have basal rates that equal, or exceed, the boundary curve

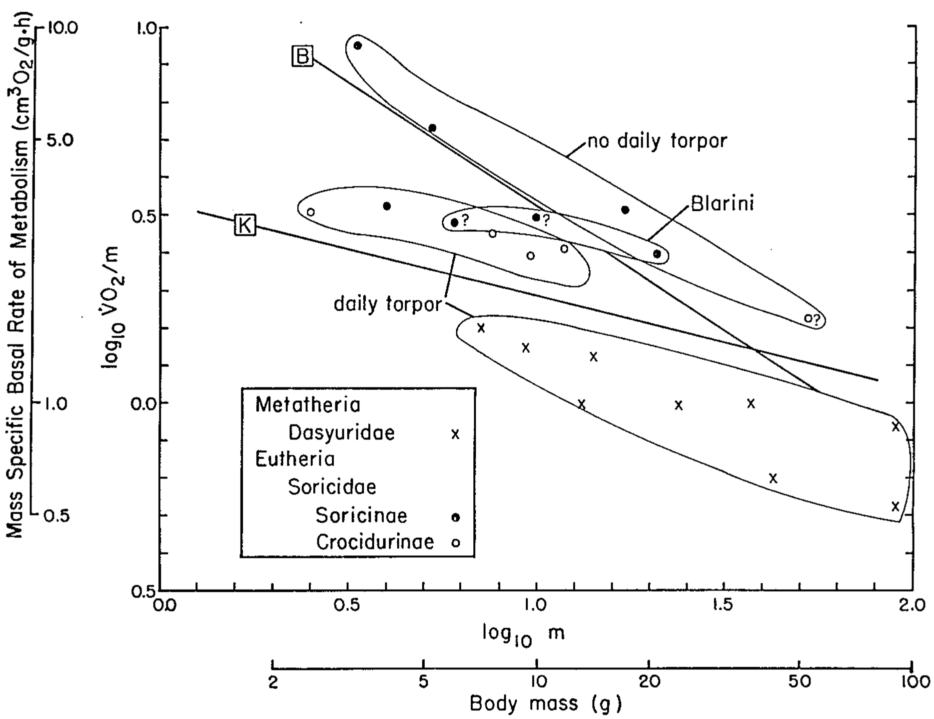

Figure 5. Log mass-specific basal rate of oxygen consumption as a function of log body mass in shrews (data taken from Table 1) and in small dasyurid marsupials [data taken from MacMillen and Nelson (1969) and Dawson and Hulbert (1970)]. Question marks indicate uncertainty whether a particular species enters daily torpor at all, or on a regular basis. Other symbols as in Fig. 4.

and do not enter daily torpor (Fig. 4, Table 1). This condition is most noticeable in *S. cinereus, S. vagrans, N. fodiens,* and *B. brevicauda.* Three other soricines, however, deserve special attention. 1) *Blarina carolinensis* has a basal rate that is approximately equal to that expected from the boundary curve and well above that expected from the Kleiber curve. The principal difference between this species and its congener, *B. brevicauda,* is that it has a mass that is only one-half that of *B. brevicauda.* The increase in mass-specific basal rate associated with this reduction in mass is modest, so that the basal rate of *B. carolinensis* falls slightly below the boundary curve (Fig. 5), which implies that this shrew might enter torpor. No direct evidence of torpor was found in *B. carolinensis,* but body temperature was more variable at ambient temperatures below 10°C, which may, or may not, be associated with the low relative basal rate and a propensity to enter daily torpor.

2) *Cryptotis parva* has a basal rate that falls intermediate to the boundary and Kleiber curves (Fig. 5). This soricine is similar in size and basal rate to *Crocidura suaveolens,* which is known to enter daily torpor (Nagel 1985). No evidence of daily torpor or of a limited capacity to regulate body temperature (Fig. 1), however, was found in this species, although some hint of this behavior might have been found by Layne and Redmond (1959). I predict that daily torpor will be found in this species with future work. The comparatively low basal rate and hypothesized propensity to enter torpor may be typical of all small Blarini (Fig. 5).

3) *Notiosorex crawfordi,* a soricine, has a basal rate that is similar to those found in crocidurines. The low basal rate coupled with a small mass (4 g) means that *Notiosorex* falls well below the boundary curve for endothermy (Fig. 5). As is to be expected, *Notiosorex* enters daily torpor (Lindstedt 1980b).

The occurrence of daily torpor is clearly related to the interaction between basal rate of metabolism and body mass, but it may well be more fundamentally related to the interactions among mass, basal rate, food habits, and climate. Soricine shrews generally are small, have low total rates of metabolism, and feed on a high-quality food that is abundant relative to the requirements of shrews; this combination permits them to maintain continuous endothermy. Torpor occurs principally in shrews that live either in the tropics or in deserts. For example, crocidurines are principally found in Africa or in Southeast Asia. They enter southern Eurasia and Europe, where they coexist with soricines. Genoud (1984) examined their coexistence in Switzerland. He showed that *Sorex* responds to winter by defending an exclusive territory and by reducing energy expenditure through a seasonal reduction in mass (the Dehnel phenomenon), whereas *Crocidura* reduces energy expenditure through huddling and entering torpor. Thus, although soricines face the most severe climates of any shrews, they are the least likely to enter torpor, which may well mean that the principal difference between these two subfamilies is related in some manner to differences in their food supplies, as is reflected in the levels of their basal rates.

The low basal rate of *Cryptotis parva* suggests a parallel with the low basal rates found in *Crocidura*. This species is one among many congeneric species that range through Central America into northern South America. Much of this distribution is at higher elevations, but the question does arise whether the comparatively low basal rate in *C. parva* and its hypothesized propensity to enter torpor might in some way be related to the southern distribution of this genus. Furthermore, one might ask whether *C. parva*, itself, might be a northern extension of a Central American radiation, either in the genus *Cryptotis* or even in the tribe Blarini, carrying with it a "tropical" or "subtropical" shrew niche and physiology, just as the European *Crocidura* appear to be a northern radiation derived from Asian or African sources, carrying with them an ecological niche and attendant physiology that is most highly developed in tropical regions. Some significant differences in physiology may exist between *Crocidura* and *Cryptotis* because *Crocidura*, unlike *Cryptotis*, is found at low elevations in the tropics.

An independent development of comparatively low basal rates and entrance into torpor has apparently occurred in North American deserts, presumably attuned to a restricted food quality and availability. This appears to be the situation in *Notiosorex*. Other shrews, of course, also live in the arid regions of North America, including *Sorex merriami* and *S. preblei*, both of which are very small, especially *S. preblei*. They live in dry sagebrush grasslands, and may, like *Notiosorex*, have Kleiberian basal rates and enter daily torpor. Whether soricine shrews have made similar adjustments to deserts in Eurasia, or whether these habitats have been preferentially occupied by crocidurines, is unknown.

Differences in the Energetics of Marsupial and Eutherian "Shrews"

Some Australian biologists have raised the question whether shrews really have as high a basal rate and energy expenditure as reported, given the apparently lower basal rate measured in the marsupial equivalents of shrews, the small members of the Dasyuridae. As shown above, the estimates of basal rates in soricids have been often exaggerated by measurement at ambient temperatures below thermoneutrality and by the inclusion of activity. An examination of Fig. 5, however, clearly demonstrates that dasyurids have much lower basal rates than are found in all soricids. Soricine shrews that do not enter torpor have basal rates that are 2.5 to 3.0 times above those found in dasyurids of the same mass, while crocidurines (and soricines that enter, or are suspected to enter, torpor) have basal rates that are about 1.5 to 2.0 times above those of dasyurids. Because crocidurines have significantly higher basal rates than dasyurids, the tendency to enter torpor may be greater among dasyurids than in crocidurines of the same mass.

The difference between the level of energy expenditure in shrews and dasyurids may reflect the suggestion of McNab (1980b) that eutherians have as high a basal rate as is possible to maximize reproductive output. Marsupials apparently do not couple reproductive output to the level of maintenance energy expenditure and do not adjust energy expenditure at small masses to assure avoidance of torpor, two functions that may be associated with each other (McNab 1986) and that combine to produce the low basal rates found in the marsupial counterparts of soricid shrews.

CONCLUSIONS

An examination of the energy expenditure of shrews indicates that a small body mass coupled with the use of an abundant, rich food resource permits most species to maintain continuous endothermy. The integrity of endothermy in cold-temperate species is preserved during the rigors of winter by a reduction in rate of metabolism through a decrease in body size. Shrews that are characterized by lower rates of metabolism, especially crocidurines, often enter daily torpor. Whether this difference between continuously endothermic shrews and those species that enter torpor is fundamentally based in ecological relations or whether it has a large historical component is presently unclear. The occurrence of torpor in the soricine *Notiosorex,* however, argues for an important ecological component.

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Winter Thermoregulatory Mechanisms of *Blarina brevicauda* as Revealed by Radiotelemetry

JOSEPH F. MERRITT AND ARLYNN ADAMEROVICH

Abstract

Blarina brevicauda is a common inhabitant of eastern deciduous forests of North America and exhibits good winter survivorship. In response to increased cold and reduced food and water availability during winter, *Blarina* has evolved a unique suite of behavioral, anatomical, and physiological adaptations that enhance overwinter survival. This study examined the role of two mechanisms hypothesized to contribute to the winter thermoregulatory constitution of *B. brevicauda:* the ability to exhibit physiological heterothermy and the potential for energy conservation by exhibiting communal nesting. Shrews implanted with temperature-sensitive radio transmitters were monitored in a natural outdoor enclosure, in a sheltered observation chamber, and in a minihabitat and were subjected to food deprivation trials under simulated natural conditions. Mean daily body temperatures for the 90–day winter study within the outdoor enclosure averaged 38.3°C, ranging from 36.8 to 39.7°C. Body temperatures recorded four to six times daily revealed no significant correlation between body temperature and time of day. Results of the shrew observation chamber experiment indicated that *B. brevicauda* readily hoarded arthropod prey in a minimum of eight different underground caches located in small chambers radiating from major burrows and reaching a depth of 55 cm below the surface. During the study, ambient temperatures ranged from −21.5 to 21.0°C. Snow cover was intermittent, reaching a maximum depth of only 23 cm. Subsurface temperatures showed minimum fluctuations ranging from 0.5 to 2.0°C during the study period. Results derived from field studies coupled with laboratory food deprivation experiments indicated that *B. brevicauda* does not possess the physiological capability to undergo a state of adaptive heterothermy during winter. Further, radiotelemetry techniques demonstrated that *Blarina* does not display communal nesting as a means of energy conservation during winter.

INTRODUCTION

The overwinter survival of small, nonhibernating mammals is largely contingent on their ability to cope with extreme cold coupled with a reduced availability of food. In north temperate and boreal regions of North America the winter period may last up to 7.5 months with minimum temperatures frequently reaching −40°C (Merritt 1984). In response to these harsh selection pressures, small mammals have evolved behavioral, anatomical, and physiological adjustments which optimize their overwinter survival (Wang and Hudson 1978; Feist 1984; Hanski 1984; Hyvarinen 1984; Madison 1984; Merritt 1984, 1986; Wunder 1984; Heller et al. 1986).

Blarina brevicauda, the largest of all North American shrews, is distributed throughout much of the eastern half of North America, where it is one of the most abundant mammals. This semifossorial insectivore is most common in mesic forests possessing a well-developed layer of leaf litter and humus, but it can be found in a diverse array of plant communities (George et al. 1986). Microhabitat selection is strongly influenced by soil moisture, stable microclimatic temperatures, and the availability of invertebrate prey (Pruitt 1959, Getz 1961, Martinsen 1969, Randolph 1973, Platt 1974, Deavers and Hudson 1979). Research on the population dynamics of *B. brevicauda* derived from field studies in Ontario, Manitoba, Minnesota, and Pennsylvania (Buckner 1966; Randolph 1973; Yahner 1983a; Merritt, unpubl. data) reveals good overwinter survival in regions characterized by ambient temperatures reaching −40°C (Buckner 1966).

The apparent success of *B. brevicauda* in coping with harsh winter climates derives from a complex suite of behavioral, anatomical, and physiological mechanisms which contribute to their thermoregulatory constitution. Table 1 summarizes year-round field and laboratory studies that suggest possible mechanisms adaptive for the overwinter survival of *B. brevicauda*. Some hypotheses have been examined in earlier research

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Table 1. Winter survival adaptations of *Blarina brevicauda* in seasonal environments.

Adaptation	Reference
A. *Behavioral*	
1. Communal nesting	Rood 1958
2. Construction of an elaborate nest	Shull 1907; Hamilton 1929, 1930; Ingram 1942; Eadie 1944; Rapp and Rapp 1945; Martinsen 1969; Platt 1976; Martin 1982, 1983; present study
3. Food hoarding and/or utilization of high energy food during winter	Merriam 1884; Shull 1907; Hamilton 1930; Ingram 1942; Platt 1976; Tomasi 1978; Martin 1981a; present study
4. Winter foraging confined to a stable thermal regime	Pruitt 1953, 1959; Randolph 1973; Platt 1974; Yahner 1983a, 1983b; Merritt 1986; present study
5. Decreased level of activity during periods of severe cold	Mann and Stinson 1957; Osterberg 1962; Martinsen 1969; Randolph 1973; Platt 1974; Merritt 1986; present study
B. *Anatomical/Physiological*	
1. Minimize thermal conductance by increasing hair density and length during winter	Findley and Jones 1956
2. Abandon homeothermy for torpor or hibernation	Martin 1983*
3. Increased thermogenic capacity during winter	Randolph 1973, 1980; Platt 1974; Merritt 1986

*Hypothesized due to decreased activity in cold (Martin 1983).

efforts (Merritt 1986) while others are pending investigation. The objective of the present study was to evaluate the role of two survival attributes presented in Table 1: initially, our objective was to assess the ability of *B. brevicauda* to abandon homeothermy for torpidity or hibernation in response to cold and/or lack of food; and secondly, to evaluate the potential for social thermoregulation in the form of communal nesting as an adaptation for energy conservation during the winter period.

METHODS

Physiological heterothermy and the proclivity for communal nesting of *B. brevicauda* were evaluated by employing radiotelemetry techniques under both field and laboratory regimes. Shrews implanted with temperature-sensitive transmitters were monitored during winter months (mid-December to mid-March) in a natural outdoor enclosure, sheltered observation chamber and in a minihabitat under simulated natural conditions in the laboratory.

Description of the Study Area

Northern short-tailed shrews (*B. brevicauda*) were live-trapped from the field station of the Carnegie Museum of Natural History (Powdermill Biological Station), southeastern Westmoreland County, Pennsylvania (Merritt 1986). The specific collection site was located at an elevation of 400 m and encompassed a secondary growth forest of hawthorn (*Crataegus sp.*), crab apple (*Pyrus coronaria*), black locust (*Robinia pseudoacacia*), sugar maple (*Acer saccharum*), and black cherry (*Prunus serotina*). Within this forest-type, abundant rock piles provided excellent habitat for securing specimens of *B. brevicauda* for the experimental procedures described below. Upon capture, shrews were marked by toe clipping, sexed, weighed, and reproductive status was recorded if evidenced by external criteria.

Surgical Procedure

Candidates for surgery were housed in the laboratory animal facility for a period of 2 days and given *Tenebrio* larvae, cat food, and water ad libitum. Shrews were then anesthetized by using Methoxyflurane (Pitman-Moore, Inc.) inhalation therapy. A radio-transmitter-battery package (AVM Instrument Company) encapsulated in "Elvax" paraffin coating material (Mini-Mitter Company) was surgically implanted within the peritoneal cavity by access through the ventrolateral abdominal wall. Each encapsulated radio-transmitter-battery package ranged in weight from 2.6 to 3.0 g and was pretuned to a specific frequency that ranged between 150–151 MHz. To insure that frequencies did not drift during the study, temperature-sensitive transmitters were calibrated before and after use by immersion in a water bath of known temperature (ranging from 22 to 42°C) as recorded by a YSI Model 42SC telethermometer and a standard laboratory mercury thermometer. Following surgical implantation, the peritoneum and outer skin were closed using 4-0 Ethicon silk. The shrew was then retained in the animal facility for 2 days, fed *Tenebrio* larvae, cat food, and water ad libitum and released in the specific study regime the following day. Upon release, the body mass was recorded. Since the battery life (two 1.5 volt silver oxide batteries) of the radio-transmitter package was a maximum of 45 days, shrews were recaptured during the study period and implanted with new transmitter-battery packages.

Experimental Regimes

Outdoor Enclosure

Following surgical implantation of radio transmitters, shrews were released into an outdoor enclosure. The purpose of this enclosure was to restrict the movements of shrews in order to facilitate radiotelemetry measurements and also to minimize loss of transmittered shrews due to dispersal or predation. The outdoor enclosure measured 4.8 by 2.5 by 1.4 m and was constructed of 0.25 inch clear plexiglass framed by 2 by 4 inch outdoor lumber (Fig. 1). The interior of the enclosure consisted of a layer of soil 1.5

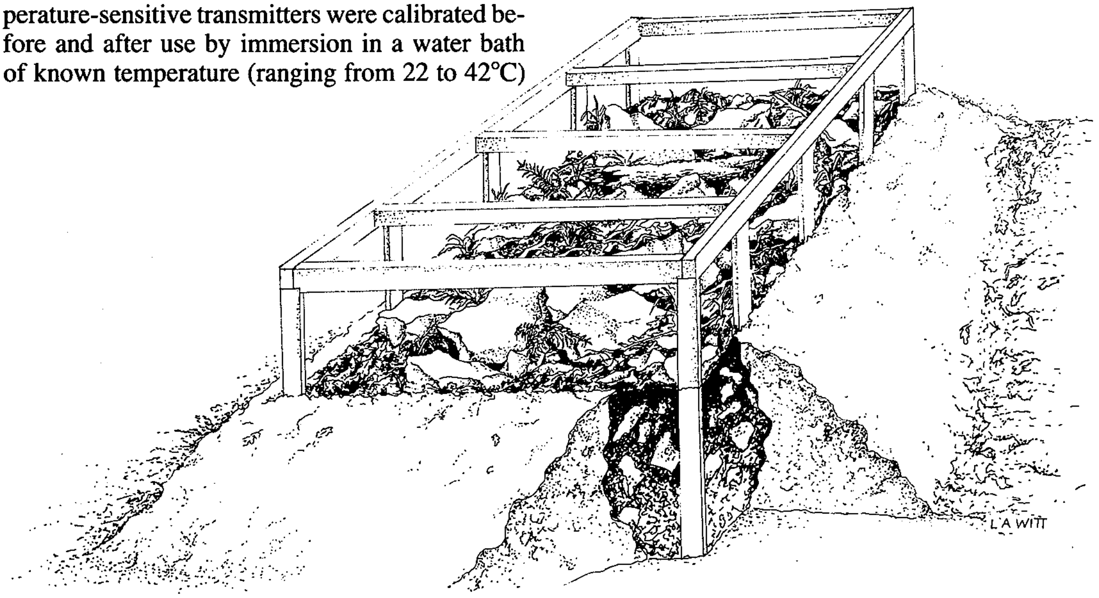


Figure 1. Schematic diagram of outdoor enclosure measuring 4.8 by 2.5 by 1.4m.

m deep provided with rocks, logs, sticks, ferns, and herbs, simulating the natural environment. The enclosure was covered with a 2 cm^2 polypropylene net to restrict predators while permitting normal precipitation to reach the inside environment. The bottom of the enclosure consisted of small gauge fiberglass screening, set upon a 40 cm deep base of no. 2B gravel, to permit drainage and prohibit burrowing activities of shrews and other small mammals. A soil embankment was graded from the surrounding ground to the side of the enclosure in order to maintain a soil temperature inside the enclosure that approximated that of the outside soil. Within the enclosure, three wooden nest boxes (25 by 15 by 15 cm) were positioned along three walls of the enclosure and supplied with grasses and leaves. Nest boxes were buried slightly below ground level, and a feeding station sheltered within a plastic canister was positioned adjacent to each box.

The outdoor enclosure was placed in a maple-cherry-locust forest in close proximity to the live-trapping area mentioned earlier. Ambient temperature (1.0 m above ground) was recorded continuously on a remote one-point thermograph (Qualimetrics, Inc.) housed in a standard weather station. Subsurface temperature (25 cm below ground) was recorded four to six times daily by employing a YSI Model 42SC telethermometer. Shrews residing in the outdoor enclosure were each provided with 5.0 g of *Tenebrio* larvae equivalent to approximately 31.5 kcal per day (Cummins and Wuycheck 1971). This ration slightly exceeded the mean daily food eaten by individual *B. brevicauda* during winter (3°C) of 30.0 kcal reported by Randolph (1973). In addition, each shrew residing in the outdoor enclosure was also provided with a daily ration of 13.0 g of canned cat food (9 Lives, "Hearty Meaty Meal") to insure adequate moisture in their diet. The above daily feeding plus the presence of natural foods in the soil of the outdoor enclosure probably represented a surplus of food for the shrews during the 3–month study.

Shrews were tracked within the outdoor enclosure from four to six times daily during the 3–month study period. Conventional radiotelemetry equipment was used and the location of a transmittered shrew was detected with a multichannel CE-12 radio receiver and handheld Yagi antenna (Custom Electronics, Inc.). Radio transmitters included both directional and temperature sensing circuitry. Therefore, it was possible to locate the position of the shrew by line of sight with the antenna based on the maximum audible tone of the signal received and to record its body temperature. Upon locating the shrew within the enclosure, its signal was decoded using an AVM Pulse Interval Timer. This timer measured the interval between transmitter pulses to an accuracy of 1 millisecond (0.001 second). Used in conjunction with the calibration curve for each individual transmitter it was possible to determine the body temperature of a given shrew to within an accuracy of 0.5°C.

Observation Chamber

Body temperature fluctuations, nest design, and distribution and food- hoarding behavior of *B. brevicauda* were evaluated by employing an observation chamber coupled with radiotelemetry techniques. The chamber was constructed of 0.25 inch clear plexiglass framed by 2 by 4 inch outdoor lumber and housed within a wooden shelter (Fig. 2). The plexiglass panels permitted observation of the underground activities of shrews. The chamber measured 130 by 23 by 100 cm and was filled with soil to a depth of 60 cm and covered with a thin layer of leaf litter to simulate the natural environment. A YSI general purpose thermistor probe was placed at a depth of 25 cm below the surface in order to monitor soil temperature. A nest of grasses and leaves was situated slightly below the litter layer, and a feeding station housed within a plastic canister on the surface of the ground was placed in one corner of the chamber. Fiberglass insulation panels enclosed the sides of the chamber in order to maintain the soil temperature at a similar level as that of the natural environment. Further, during extreme cold periods, it was necessary to insulate the shelter with hay bales augmented by two infrared heat lamps in order to maintain the soil temperature of the chamber within "natural" levels. The chamber was covered by a sheet of 0.25 inch clear plexiglass perforated with ventilation holes. The observation chamber was employed to test only one transmittered shrew provided with a daily ration of 5.0 g of *Tenebrio* larvae and 13.0 g of canned cat food. A similar surgical and telemetry monitoring protocol was followed for the chamber as outlined above for the outdoor enclosure.

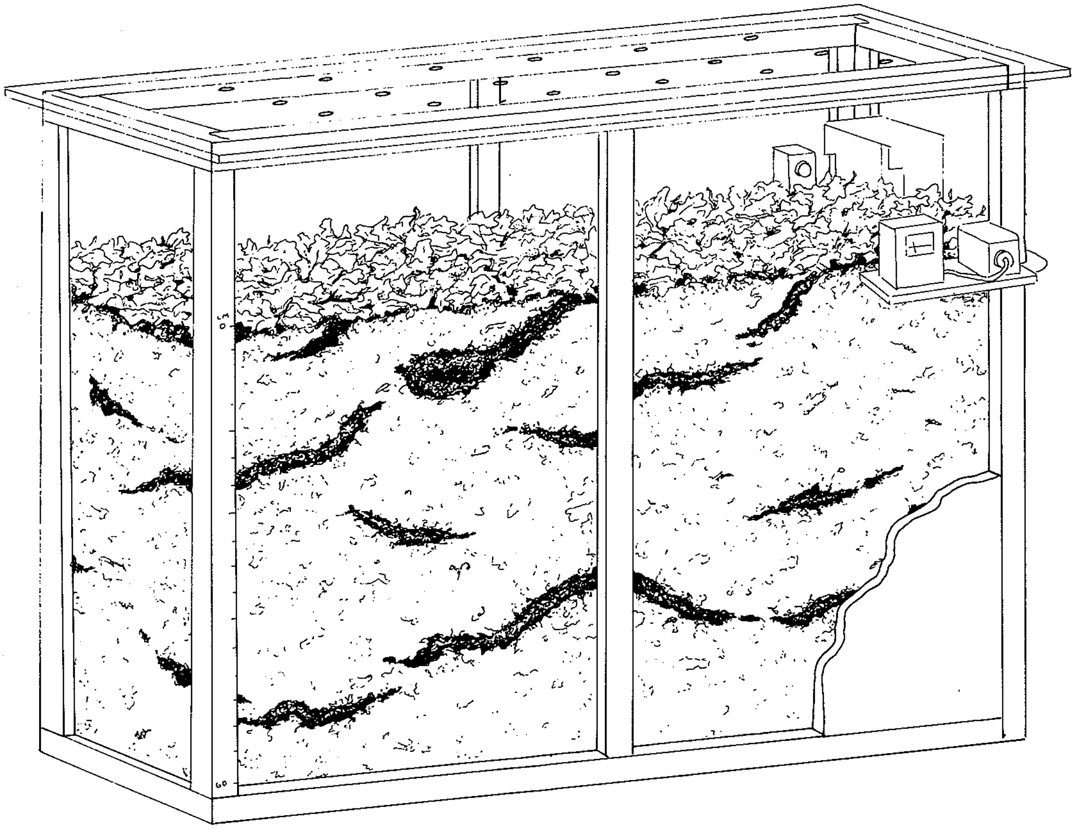


Figure 2. Schematic diagram of the observation chamber measuring 130 by 23 by 100 cm.

Minihabitat

The influence of decreasing food supply on body temperature of *B. brevicauda* was examined for shrews housed in a minihabitat within a controlled environment. Shrews implanted with radio transmitters were placed singly in a rectangular 0.25 inch plywood box (57 by 35 by 19 cm) filled to 12 cm with soil and placed in a Precision Dual Control Incubator (Model 818, uniformity ±0.5°C). A thin layer of leaf litter covered the soil and a nest composed of grasses and leaves was placed slightly below the litter in one corner of the minihabitat. YSI general purpose thermistor probes placed 6.0 cm below the surface of the soil, within the nest, and in the incubator provided measurements of the temperatures of three different thermal regimes. The minihabitat was covered by a sheet of 0.25 inch clear plexiglass perforated with ventilation holes. The minihabitat served as the site for the food deprivation study outlined below.

Following capture and implantation, shrews were housed in the laboratory animal facility for an acclimation period of 2 days, during which time they were fed 6.0 g of *Tenebrio* larvae, cat food, and water ad libitum. Following this adjustment period, shrews were weighed on a triple beam balance to the nearest 0.1 g and placed in the minihabitat housed in the incubator at a simulated winter photoperiod (10L:14D) and temperature regime (3°C). On day 1, shrews were provided with 5.5 g *Tenebrio* larvae. The food ration was maintained at this level for 3 days and then reduced by 0.5 g for the next 3 days. This food deprivation sequence was continued until shrews exhibited a 40% reduction in their body mass at which time the experiment was terminated. For one animal, death resulted before loss of 40% of its body mass. Each day at 0800 hours, shrews were captured and weighed; and upon return to the minihabitat, they were given their daily ration. Water was provided ad libitum throughout the duration of the food deprivation study. Body temperature was measured four to six times daily by employing radiotelemetry techniques outlined earlier.

RESULTS

Body Temperature Dynamics

Mean daily body temperatures of two shrews (animal nos. FR2 and FR5) recorded from 18 December 1986 to 18 March 1987 in the outdoor enclosure are shown in Fig. 3. Maximum and minimum ambient and subsurface temperatures of the enclosure are cast below mean daily body temperature for comparative purposes. Ambient temperature for the enclosure ranged from a low of −21.5°C to a high of 21.0°C (25 January and 6 March 1987, respectively). Subsurface temperatures showed minimal fluctuation ranging from 0.5 to 2.0°C throughout the study. Snow depth was intermittent ranging from 1.0 to 23.0 cm with the maximum length of continuous snow cover lasting only 15 days (19 January to 3 February 1987).

For both animals combined, the overall average daily body temperature during the winter study period was 38.3°C (SE = 0.04). The average daily body temperature for animal no. FR2 ranged from a low of 37.8°C on 18 January to a high of 39.1°C on 20 January. Although average daily body temperature fluctuated slightly during the course of the study, there seemed to be no relationship with either ambient or subsurface temperatures occurring in the enclosure. The average daily body temperature for animal no. FR5 ranged from a low of 36.8°C on February 11 to a high of 39.7°C on 17 and 18 March. The monitoring sequence of animal no. FR5 was marked by two brief interruptions occurring on 24 December and 11 February, due to failing transmitter batteries. At such time, the shrew was removed from the enclosure, implanted with a new transmitter-battery package and returned to the original capture site within the enclosure. During the months of January and February, the average daily body temperature of animal no. FR5 fluctuated a maximum of only about 2°C. However, beginning on 2 March, a stepped increase in average daily body temperature occurred. This trend may have resulted from the gradual increase seen in both ambient and subsurface temperatures during this time period. It is important to note, however, that shrews foraged in a complex system of underground tunnels, rarely venturing to the surface. Thus, the influence of ambient temperature on the thermoregulatory budget of *B. brevicauda* is probably minimal. The interpretation of the stepped trend seen for animal no. FR5 is complicated by the fact that the seasonal accumulation of underground food caches may have influenced this animal's energy budget and resultant body temperature. Further, an additional factor complicated interpretation of this trend. During the second implantation surgery of animal no. FR5 (12 February 1987) several fetuses in early stages of development were present within the right horn of the uterus. However, subsequent live-trapping of animal no. FR5 in mid-March 1987 indicated that lactation did not occur. Further, no juveniles were captured within the enclosure. Both of these factors indicated that the embryos were probably resorbed or aborted following return to the enclosure after surgery in mid- February. It is also possible that the temperature inflection beginning in early March represented a physiological response to embryo resorption.

Body temperatures of *B. brevicauda* (animal nos. FR2 and FR5) recorded four to six times daily from 31 December 1986 to 5 February 1987 (FR2) and from 18 December 1986 to 18 March 1987 (FR5) in the outdoor enclosure are shown in Figs. 4 and 5, respectively. Average daily body temperature for the above animals during the duration of this study was presented in Fig. 3.

Body temperature for animal no. FR2 (Fig. 4) showed a slightly more conservative amplitude in hourly body temperature than animal no. FR5. Body temperatures ranged from a low of 37.4°C on 17, 18, and 19 January at 1800, 2200, and 0800 hours, respectively to a high of 39.7°C on 21 and 25 January at 2200, 2100, and 2300 hours respectively. Average body temperature for the 36–day study period was 38.4°C (SE = 0.04). As was seen in Fig. 3, a slightly elevated plateau was apparent for animal FR2 beginning on 19 January and lasting the duration of the study. One-way ANOVA revealed that no significant corre-

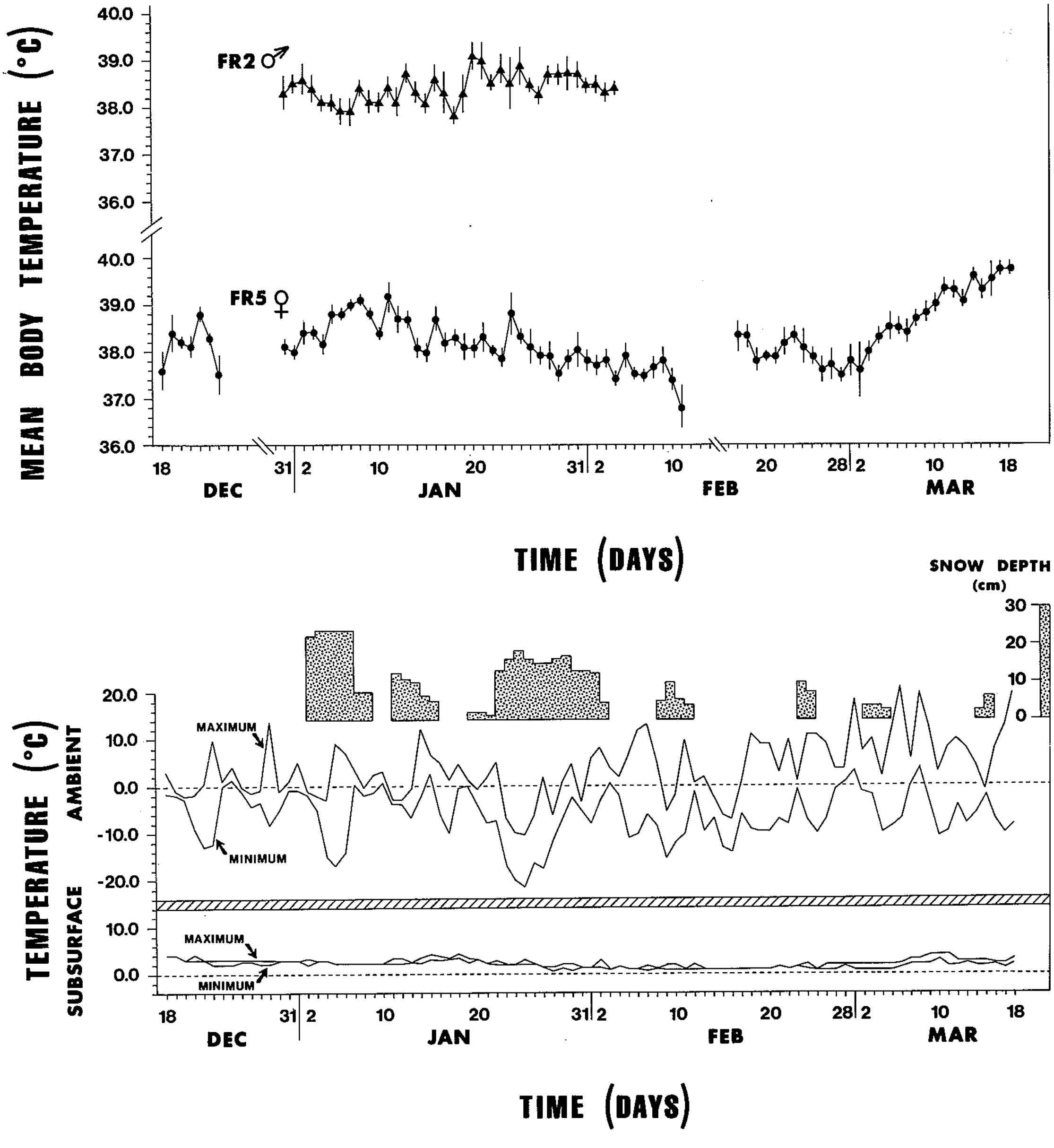


Figure 3. Mean daily body temperature of *Blarina brevicauda* (animal nos. FR2 and FR5) recorded from 18 December 1986 to 18 March 1987 in the outdoor enclosure. Vertical lines represent ± 1 SE of the mean. Breaks between readings of animal no. FR5 on 25 December 1986 and 11 February 1987 indicate replacement of radio transmitter. Maximum and minimum ambient and subsurface temperatures recorded from the enclosure are cast below mean daily body temperature. Snow depths within the enclosure are shown by stipled bars.

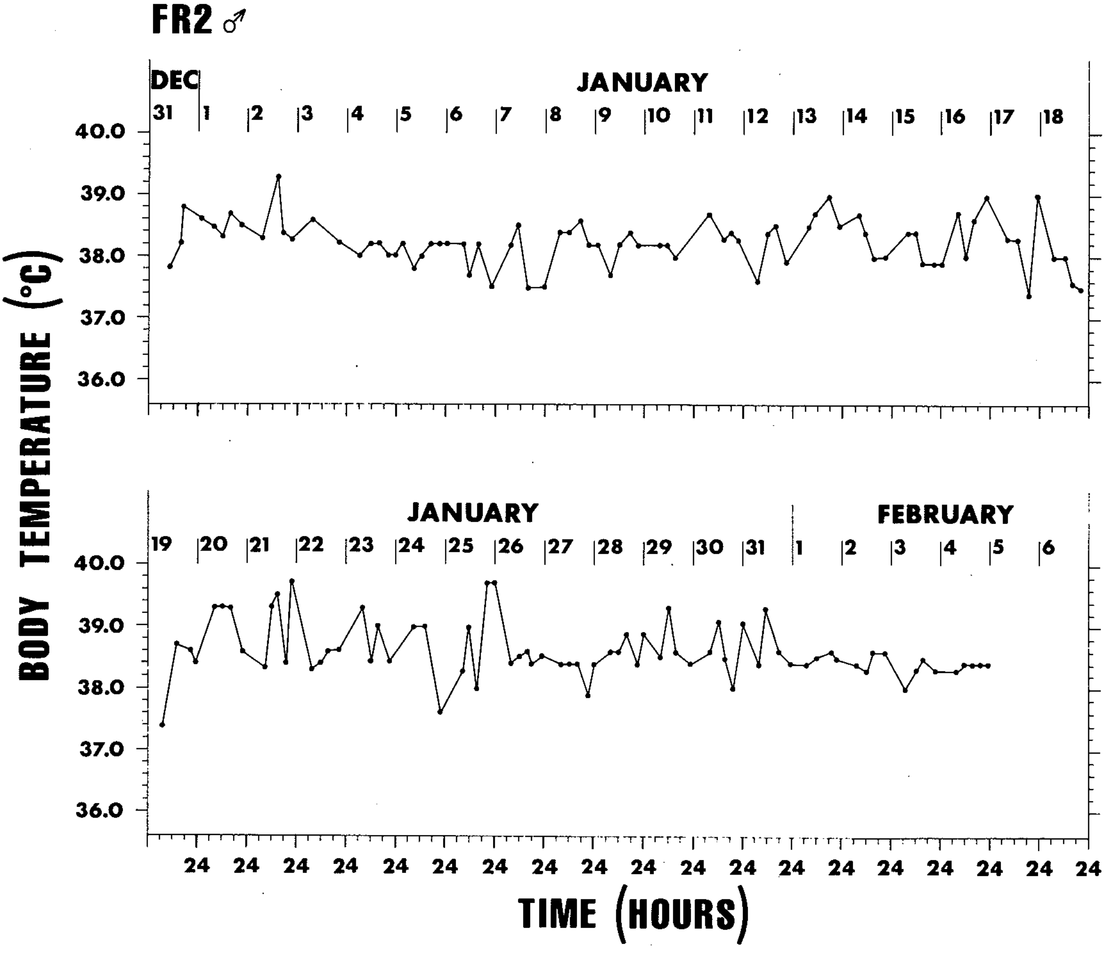


Figure 4. Body temperature of *Blarina brevicauda* (animal no. FR2) recorded from four to six times daily in the outdoor enclosure from 31 December 1986 to 5 February 1987.

lation existed between body temperature and time of day (F = 1.84, d.f. = 4, P = 0.12).

Body temperatures for animal no. FR5 (Fig. 5) ranged from a low of 35.8°C at 2100 hours on 2 March to a high of 40.0°C occurring at 1200 hours on 16 March. Although these extremes did occur, most body temperatures were within a narrow range between 37.4 and 39.0°C. The average body temperature for the 90–day study period was 38.3°C (SE = 0.04). An exception to this narrow amplitude was noted during 10 to 18 March when most temperatures were above 39.0°C for animal no. FR5. When analyzed for the entire 90–day period, animal no. FR5 exhibited seemingly random shifts in body temperature. As was the case with animal no. FR2, one-way ANOVA revealed that no significant correlation existed between body temperature and time of day (F = 0.31, d.f. = 5, P = 0.50).

Mean daily body temperature of *B. brevicauda* (no. FR1) recorded for a period of 68 days in the observation chamber is shown in Fig. 6. Daily maximum and minimum soil temperature is cast below mean body temperature for comparative purposes. The break between body temperature readings at day 23 indicates failing transmitter batteries, at which time the shrew was removed from the chamber, implanted with a new transmitter-battery package, and then returned to the original capture site within the chamber. Dur-

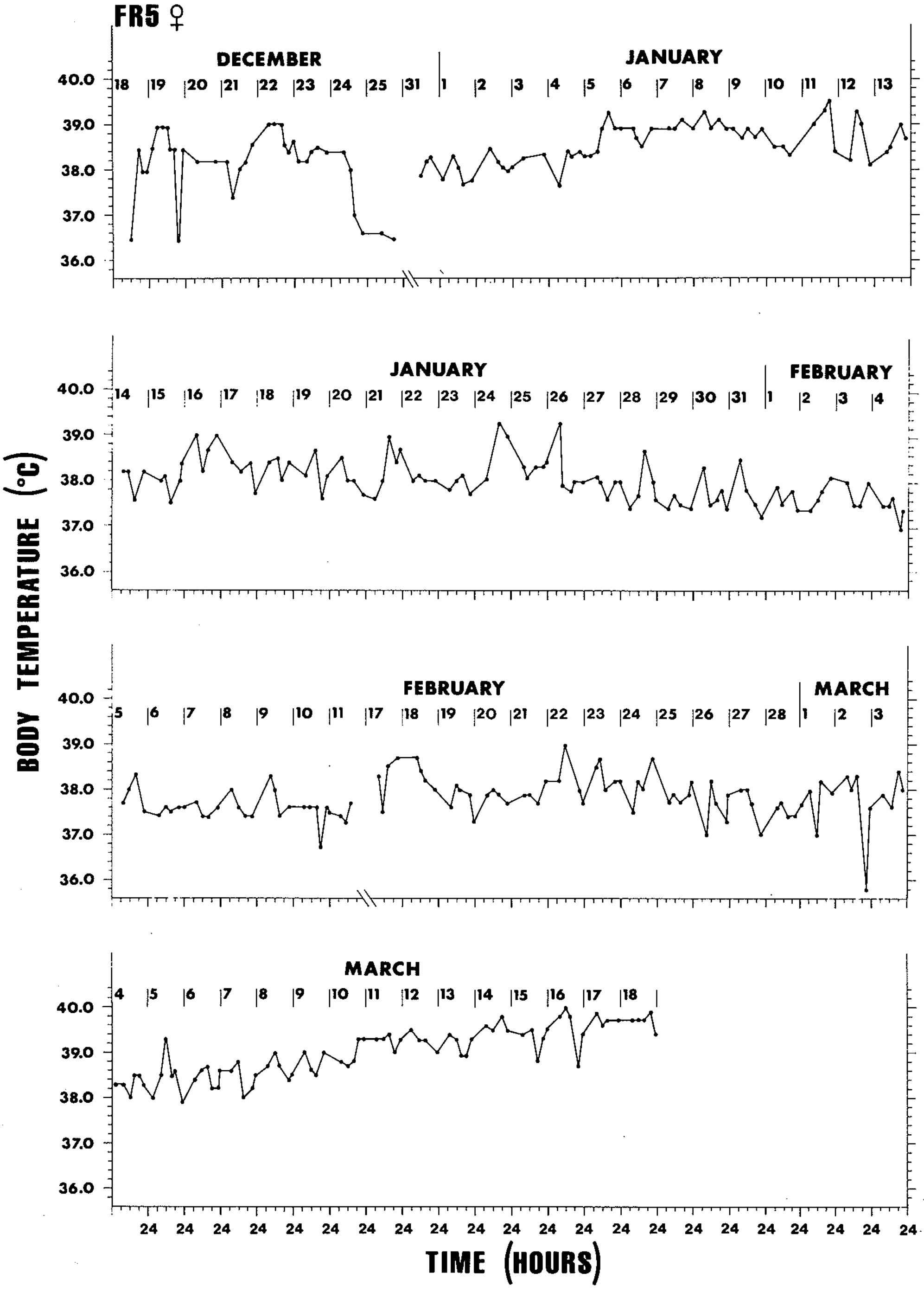


Figure 5. Body temperature of *Blarina brevicauda* (animal no. FR5) recorded four to six times daily in the outdoor enclosure from 18 December 1986 to 18 March 1987. Breaks between readings on 25 December 1986 and on 11 February 1987 indicate replacement of radio transmitter.

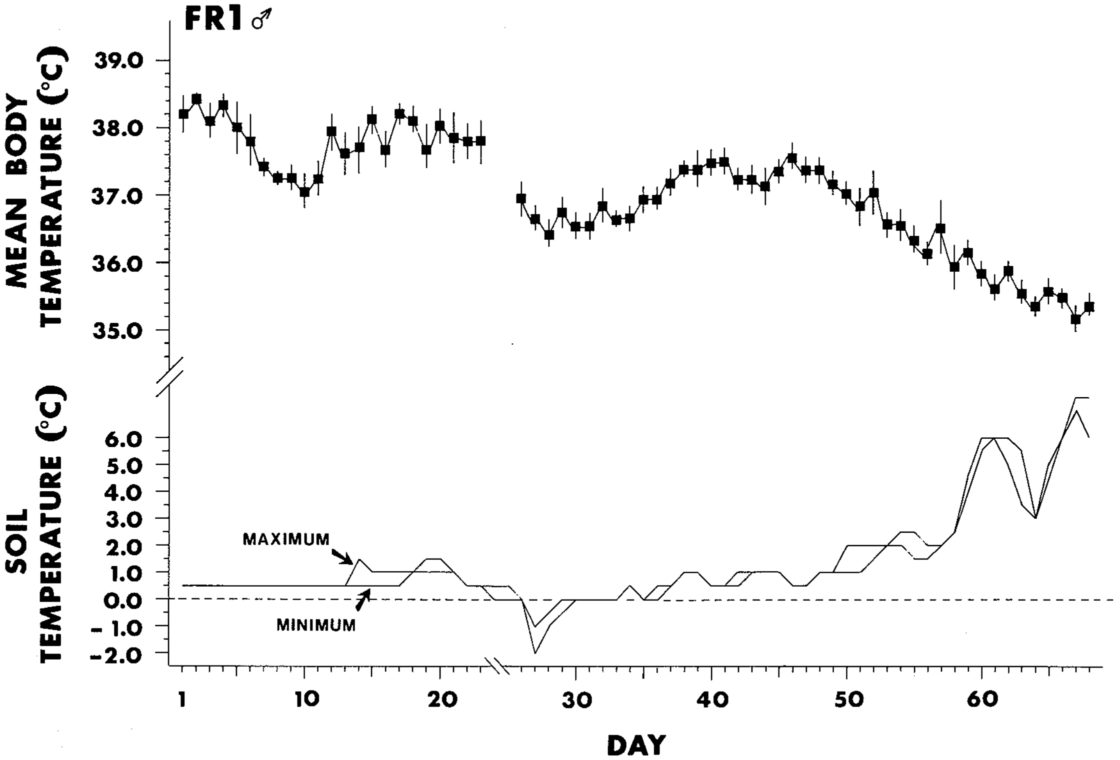


Figure 6. Mean body temperature of *Blarina brevicauda* (animal no. FR1) recorded daily in the observation chamber. Vertical lines represent ± 1 SE of the mean. The break between readings at day 23 indicates replacement of radio transmitter. Maximum and minimum soil temperatures are cast below mean daily body temperature.

ing the experimental period, body temperature averaged 37.0°C (SE = 0.05), ranging from 35.2 to 38.2°C.

Soil temperature ranged in the observation chamber from a low of −2.0°C on day 27 to a high of 7.5°C on days 67 and 68. This great variation in soil temperature was an artifact of experimental design. Because the chamber measured a width of only 23 cm (Fig. 2) it was not possible to insulate the soil sufficiently to prohibit the influence of fluctuations in the "outside" temperatures. Insulation against cold extremes was reasonably successful, achieved by employing tactics outlined under the Methods section. However, it was difficult to cool the soil within the chamber when "outside" temperatures increased during the latter part of the study (19 February to 10 March; see Fig. 3).

During the initial stages of the monitoring period, mean body temperatures of animal no. FR1 fluctuated between 37.1 and 38.4°C while soil temperatures remained stable ranging from 0.5 to 1.5°C. At this time, soil temperatures approximated subsurface temperatures of the outdoor enclosure (Fig. 3). On day 27 (28 January), however, ambient temperatures outside the chamber plummeted to −21.5°C at which time a minimum soil temperature of −2.0°C occurred within the chamber. At this time, a slight decline in mean daily body temperature occurred. Next, mean daily body temperature exhibited a gradual stepped increase paralleling an increase in soil temperature. Average daily body temperature reached a peak of 37.6°C on day 46 followed by a pronounced yet gradual decline culminating in a low of 35.2°C on day 67—a drop in mean daily body temperature of approximately 0.11°C per day. During this time, an opposite trend occurred in soil temperature, ranging from a low of 0.5°C on day 49 to a high of 7.5°C on days 67 and 68—an increase in soil temperature of approximately 0.32°C per day. The significance of this inverse relationship between mean daily body temperature and daily soil temperature could not be evaluated statistically due to insufficient sample size.

It is difficult to attribute the stepped decline in average daily body temperature solely to an increase in soil temperature in that other factors must be considered. As mentioned in the Methods section, shrew no. FR1 was provided with a daily food ration of 5.0 g *Tenebrio* larvae, equivalent to approximately 31.5 kcal per day, and supplemented by 13.0 g of canned cat food. Throughout the study period, the shrew had established a minimum of eight underground caches of larvae. The positions of many of these caches (each possessing from 3 to 10 larvae) were assessed by viewing through the plexiglass enclosing the soil of the chamber. Food caches were distributed in small chambers commonly radiating from the major burrow system which reached a depth of 55 cm below the surface.

The shrew occupying the observation chamber was presented a food ration at 0800 hours each day and within a period of 15 minutes had procured and cached all larvae placed within the feeder. Beginning on day 46, this feeding behavior become less stereotyped, with visitation of the shrew to the feeder spanning the entire day. This decreased foraging behavior was believed to be due to satiation attributable to a large accumulation of food caches and possibly coupled with decreased thermoregulatory demands as a result of the increased soil temperatures. Further, due to the small size of the observation chamber the animal would require a minimum of activity in order to secure food. The influence of specific dynamic action (SDA) is also likely to have contributed to the above body temperature decline. As soil temperature increased, foraging activity decreased and a depressed food intake resulted. This reduction in food ingestion logically resulted in a decreased calorigenic heat production and resting metabolic rate (Merritt 1986) as evidenced by a decrease in body temperature. It was clear that excess food was available to the shrew within the chamber. During the study, body mass dynamics of shrew no. FR1 clearly indicated a significant increase in body mass ranging from 16.6 g recorded on day 1 to the terminal mass of 26.5 g recorded on day 68. Total body mass gained during the study period was 9.9 g representing a rate of 0.15 g increase in mass per day.

Results of the food deprivation study for *B. brevicauda* (nos. FL1, FL2, FL3, FL4) maintained in the incubator-housed minihabitats are shown in Fig. 7. Mean daily body temperature of animal no. FL1 was 37.9°C (SE = 0.04) during the study period ranging from a low of 37.6°C to a high of 38.4°C. Body mass ranged from an initial 20.0 g to an ending mass of 13.6 g on day 15. Because body mass was not recorded on a daily basis, it can only be presumed that a gradual daily decline occurred during the 15-day experimental period in which food quantity was reduced. Body temperature remained stable during the course of the experiment.

Animal no. FL2 exhibited an average daily body temperature of 37.4°C (SE = 0.07), ranging from a low of 36.9°C to a high of 38.1°C. During the period of decreasing food rations, body mass exhibited a gradual stepped decline from an initial mass of 17.4 g on day 1 to an ending mass of 12.5 g on day 13. This mass decline represented a rate of 0.38 g per day. Although body mass showed a decline corresponding to decreased increments of food, body temperature remained stable except during the last 3 days in which a sudden increase in temperature was noted.

Animal no. FL3 exhibited an average daily body temperature of 38.8°C (SE = 0.05) during the experimental procedure ranging from a low of 37.0°C on day 1 to a peak of 38.6°C on day 10. As with animals nos. FL1 and FL2, body mass declined as the food ration declined. Animal no. FL3 exhibited the most rapid rate of mass loss of all the experimental animals. Body mass ranged from 18.8 g on day 1 to a low of 13.0 g on day 11—a rapid decrease in body mass of 0.53 g per day.

Animal no. FL4 displayed an average daily body temperature of 37.2°C (SE = 0.02) during the 22-day study period. Following a low of 37.0°C on day 1, the body temperature exhibited a sharp increase to 38.8°C on day 2 and then remained at this elevated level. On day 10, the average daily body temperature showed a drop ending in a low of 37.2°C on day ll. From day 11 to day 21, mean daily body temperature remained at a stable level. Body mass of animal no. FL4 exhibited a slight decline during the first 6 days of the study followed by a slight increase and a 13–

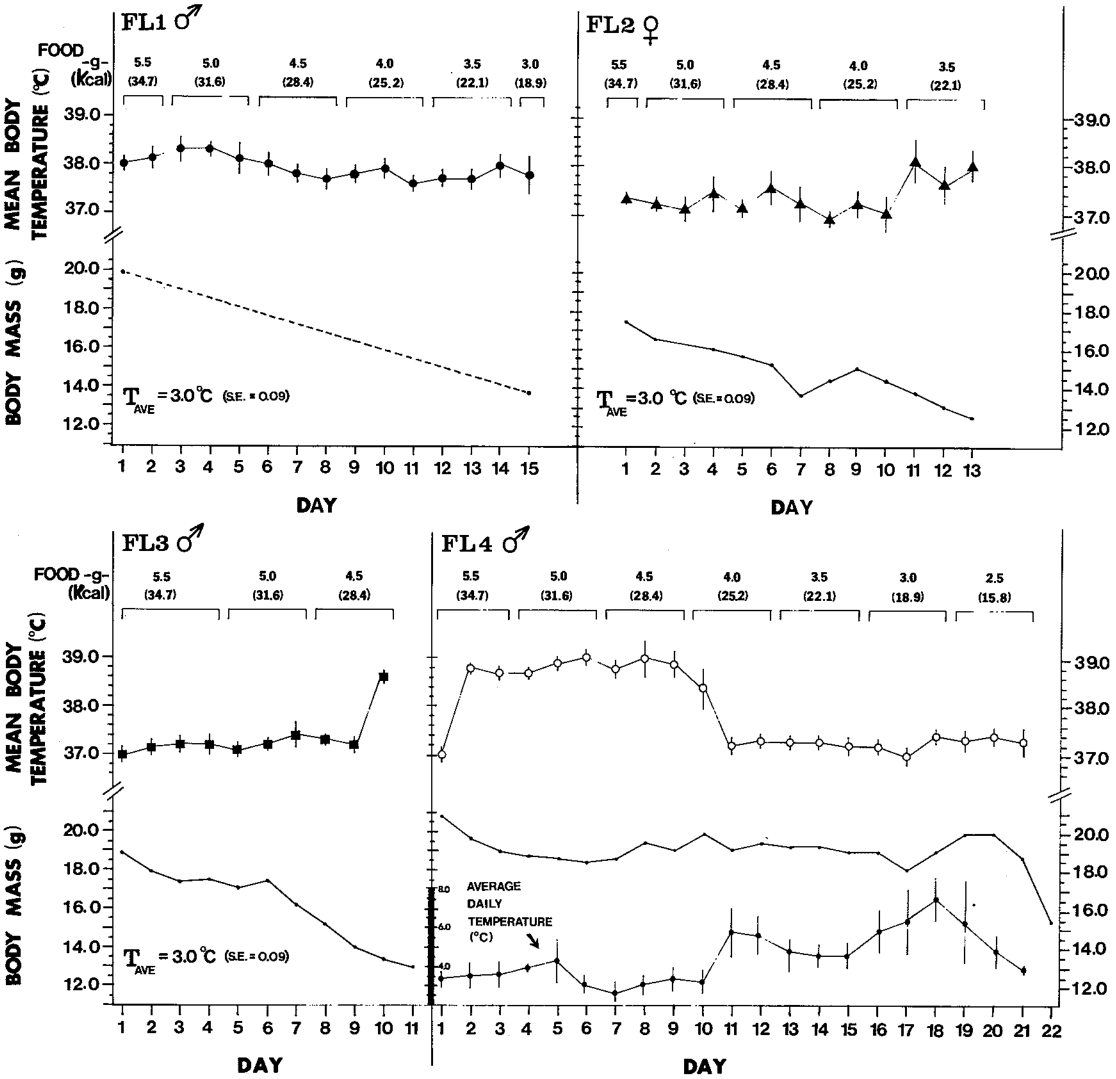


Figure 7. Food deprivation experiment of *Blarina brevicauda* (animal nos. FL1, FL2, FL3, FL4) maintained in the incubator-housed minihabitats. Mean body temperature is presented for each day as is body mass (except for animal no. FL1). Daily feeding ration for each 3–day interval is represented by food mass (g) and energy content (kcal, ash free dry weight) along upper horizontal axis. Average daily incubator temperature (± 1 SE) for duration of study is shown for each shrew except animal no. FL4 for which average daily temperature was depicted for reasons described under Results.

day plateau at the level of about 19.5 g. On day 21 a precipitous drop occurred in body mass resulting in the death of animal no. FL4 on day 22. Unlike other shrews tested in the food deprivation study, animal no. FL4 exhibited a sharp decline in average daily body temperature at day 10—the same day in which the incubator experienced "freeze up." This malfunction resulted in a rapid increase in the temperature of the minihabitat from an average daily temperature of 3.2°C to a peak of 5.8°C. Efforts to reduce the incubator temperature to a level of 3°C were unsuccessful and the temperature climbed to a maximum of 7.5°C on day 18 followed by a slight decline until the study ended on day 21. It is noteworthy that mean body temperature of animal no. FL4 showed a decline on day 10 which corresponded to an increase in average daily temperature on the same day. This inverse relationship also occurred in the experiments held in the observation chamber (Fig. 6). Although a decrease in body temperature did correspond to an increase in ambient temperature in both the observation chamber and food deprivation experiments, the explanations for these trends are not identical. Within the observation chamber a decrease in body temperature was attributed to reduced activity, excess food, and resultant decrease in the calorigenic effect of food (SDA). In contrast, in the food deprivation experiment, food was not in excess, and activity was maintained at normal levels. In order to explain this phenomenon, additional research under controlled laboratory conditions is needed in order to isolate the specific factor(s) responsible for triggering the abrupt decline in body temperature in both the observation chamber and food deprivation experiments.

Communal Nesting

Figure 8 presents data concerning the position of each transmittered shrew within the outdoor enclosure from 18 December 1986 to 18 March 1987. Circles, squares, and diamonds signify animals nos. FR5, FR2, and FR3, respectively. Numbers within each symbol represent each monitoring period performed four to six times daily within the enclosure. For purposes of clarity, the enclosure is represented in six time frames with dates of monitoring periods listed along the horizontal axis of each.

Animal no. FR5 was monitored in the enclosure for the entire duration of the study, whereas animal no. FR2 resided in the enclosure from 31 December 1986 to 4 February 1987. Animal no. FR3 resided in the enclosure throughout the entire study; however, its position during the period from 2 January to 16 January was not known due to technical problems.

Study of Fig. 8 shows that *B. brevicauda* exhibited nonoverlapping home ranges within the outdoor enclosure and that no group nesting occurred. For example, throughout the study, animal no. FR5 remained principally in the vicinity of nest box "A" and "B" with periodic forays to nest box "C." Although animal no. FR2 showed a period of residence in the vicinity of nest box "B" from 2 January to 31 January, during this time animal no. FR5 shifted its range to nest box "A" and "C." During the last half of the study (1 February to 18 March) animal no. FR5 occupied principally nest box "B" with short visits to nest box "A." During this time, animal no. FR2 resided at nest box "C," later to be found dead at this location. The cause of death of animal no. FR2 was presumed to be due to predation by either animal nos. FR5 or FR3 as evidenced by wounds on the body of the deceased shrew. From 1 February to 18 March, animal no. FR5 confined much of its activity to the nest box "B" possibly due to pregnancy. As mentioned earlier, pregnancy was noted in animal no. FR5 by the presence of several fetuses observed during implantation surgery on 12 February 1987. This pregnancy occurred about 2 weeks earlier than expected in the natural environment and may have been attributable to confinement of shrews in the outdoor enclosure.

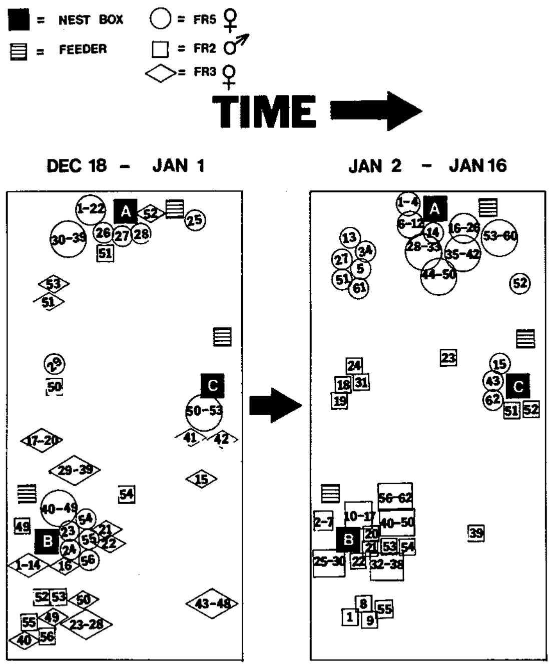
During the study, animal no. FR3 occupied primarily the lower half of the outdoor enclosure. Here, it established a nest located below a log in the lower corner of the enclosure and showed strong site tenacity to this nest throughout the study. This animal was equipped with a directional radio transmitter only, therefore no body temperature measurements were conducted.

DISCUSSION

Body Temperature Dynamics

The winter period in north temperate and boreal regions of the world is characterized by climatic instability in the form of extreme cold and scarcity of food and water. Small endotherms equipped with the ability to exhibit physiological heterothermy surely gain an adaptive edge in coping with harsh climatic perturbations. The ability to abandon homeothermy for torpor or hibernation is well-known for insectivorous bats, ground squirrels, heteromyid rodents, hummingbirds, swifts, and goatsuckers (Bartholomew 1972, Hudson 1978, Lyman et al. 1982, McNab 1983). Shrews, the smallest of all land mammals, characterized by their high mass-specific energy demands and high thermal conductance are excellent "evolutionary" candidates to exhibit temporal heterothermy as an escape tactic from maintenance of high body temperature during periods of food scarcity. However, physiological heterothermy within the Soricidae is rare (Dawson 1973, Webster 1974, Lindstedt 1980, Lyman et al. 1982).

Vogel (1976, 1980) proposed two distinct "metabolic levels" among soricids. The subfamily Crocidurinae (white-toothed shrews) is characterized by comparatively low metabolic rates and low body temperatures. Further, members of this subfamily possess the ability to exhibit torpidity (Vogel 1974, 1976, 1980; Hutterer 1977; Nagel 1977; Genoud 1985). In contrast, members of the subfamily Soricinae (red-toothed shrews) tend to exhibit high metabolic rates and elevated body temperatures; and they lack the ability to exhibit torpidity (Morrison et al. 1959, Calder 1969, Gebczynski 1977, Deavers and Hudson 1981, Tomasi 1985, Merritt 1986). Explanations for these different metabolic profiles of Crocidurinae and Soricinae are presented by Vogel (1976, 1980) and more recently by Genoud (1985). The lower metabolic levels of Crocidurinae are re-



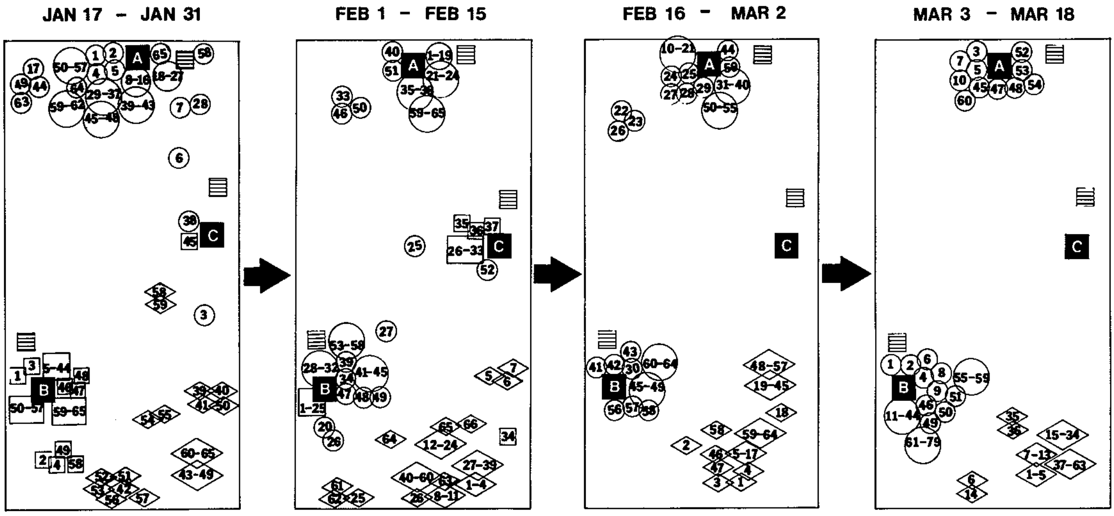


Figure 8. Diagram of outdoor enclosure showing position of transmittered *Blarina brevicauda* (animal nos. FR5, FR2, FR3) in relation to nest boxes and feeders recorded from 18 December 1986 to 18 March 1987. For purposes of clarity, the enclosure is represented in six time frames with dates of monitoring periods listed along the horizontal axes of each. Circles, squares, and diamonds represent animal nos. FR5, FR2, and FR3, respectively. Numbers within a given symbol represent a specific time interval of a monitoring sequence. Ranges in numbers (e.g., 30–39) signify no change in position of a given shrew during a specific time period.

portedly attributable to physiological adaptation in response to their origin in the Palaeotropical Region; whereas the higher metabolic levels of Soricinae are thought to reflect an adaptation to colder climates encountered in the Holarctic Region, the site of their origin (Vogel 1976, 1980). However, these subfamilial thermoregulatory profiles are not without exceptions. Both the desert shrew (*Notiosorex crawfordi*) and the Suisun shrew (*Sorex sinuosus*), members of Soricinae, are reported to exhibit temporal heterothermy (Lindstedt 1977, Newman and Rudd 1978, respectively). It is interesting to note that unlike many members of the Soricinae, *N. crawfordi* and *S. sinuosus* inhabit geographic regions marked by seasonally mild temperatures—the former commonly residing in semidesert scrub associations of southwestern United States and Mexico (Armstrong and Jones 1972) and the latter restricted to tidal marshes of northern California (Hall 1981). The low rate of metabolic heat production typified by *N. crawfordi* may aid this desert soricid in tolerating high ambient temperatures (Lindstedt 1977, 1980). Metabolic trials conducted at 20°C by Newman and Rudd (1978) found *S. sinuosus* to exhibit inactivity, slowed breathing rates, and a drop of 63 to 88% from resting metabolic rates. However, torpor patterns were unpredictable and could not be induced under fasting conditions.

The northern short-tailed shrew occurs throughout much of the north-central and northeastern United States and southern areas of adjacent Canada. It reaches its northernmost limit in central Manitoba, Canada. Here, this shrew must combat winter temperatures that commonly reach −40°C (Buckner 1966). It seems likely that *B. brevicauda* could indeed enhance overwinter survival by gaining a degree of independence from the perturbations imposed by northern winters—the ability to enter a state of temporal hypothermia would certainly optimize survival. However, research aimed at defining the thermoregulatory budget of *B. brevicauda* has demonstrated that this shrew maintains a high body temperature ranging from 37 to 38.5°C and does not exhibit temporal hypothermia (Doremus 1965, Neal and Lustick 1973, Platt 1974, Deavers and Hudson 1981). Results of the present study employing implantation of temperature-sensitive radio transmitters concur with the above research. Our research revealed an average daily body temperature of 38.3°C ranging from 36.8 to 39.7°C for *B. brevicauda* residing in an outdoor enclosure during winter months. Further, results derived from our field studies coupled with laboratory food deprivation experiments indicate that, like the majority of members of the subfamily Soricinae, *B. brevicauda* does not possess the physiological capability to enter a temporal state of adaptive hypothermia. Thus, the ability of *B. brevicauda* to successfully combat vicissitudes of winter must depend on a combination of other behavioral, anatomical, and physiological adaptations (Table 1).

Social Thermoregulation

In boreal and montane areas the ability of nonhibernators to exhibit social thermoregulation in the form of communal nesting confers a distinct energetic advantage by reducing thermal conductance. This behavioral tactic is especially important during winter when food supply is limited and cold air temperatures encountered within foraging and nesting zones stress thermoregulatory budgets. For small endotherms, such as shrews, conservation of energy by communal nesting would indeed confer an adaptive premium during winter months. However, winter aggregations are rare among temperate and arctic soricids (Sealander 1952, Crowcroft 1957, Eisenberg 1966, Hawes 1977, Churchfield 1984, West and Dublin 1984). Soricids tend to be "winter-solitary" species (West and Dublin 1984); because they exhibit pronounced intra- and interspecific territoriality even during the nonbreeding season, the establishment of well-defined territories during winter may prevent depletion of food resources and/or regulate population density (Hawes 1977, West and Dublin 1984). Several examples of social thermoregulation in soricids do, however, exist. The least shrew (*Cryptotis parva*) is well-known to exhibit tolerance of conspecifics during winter when they are not reproductively active. Hamilton (1934) reported finding two nests with three and five occupants each during winter in New York. Further, Davis and Joeris (1945) discovered 12 *C. parva* within a single nest in mid-December in eastern Texas. In addition, evidence of the social nature of *C. parva* is reported by McCarley (1959) who uncovered a nest in eastern Texas that housed 31 adult shrews! It is possible that *C. parva* formed this unusually large colony to counteract the effect of unseasonably cool prevailing temperatures occurring in early January. More recently, Vogel and Genoud (1981) and Genoud (1985) reported communal nesting of the greater white-toothed shrew (*C. russula*) in a montane region of western Switzerland. Aggregations of two or more individuals were common during winter and communal nesting may be typical during all seasons.

Many experimental methods have been employed to elucidate the nesting habits and tolerance of conspecifics of *B. brevicauda*. The early works of Shull (1907) and Eadie (1944) described the nests and burrow systems. The elaborate nests of *Blarina,* composed of grasses, sedges, and leaves and arranged in the form of a hollow ball, served as important food caches, but occupants of these nests were not found. Except for the laboratory work of Rood (1958) who observed mutual tolerance and sociality of *B.brevicauda,* all other field and laboratory studies attest to the solitary and highly territorial nature of this large shrew (Pearson 1944, Platt 1976, Martin 1981b, Merritt 1986). Research efforts of the present study employing radiotelemetry techniques within an outdoor enclosure clearly demonstrate that *B. brevicauda* is a winter-solitary species (Fig. 8). During the course of our study, apparently unrelated individuals did not employ communal nesting and exhibited nonoverlapping home ranges. The possibility of communal nesting between siblings and/or other related individuals of *B. brevicauda* during winter has yet to be tested and represents an important direction for future research.

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Speciation in the *Sorex cinereus* Group

C.G. VAN ZYLL DE JONG

Abstract

Morphometric relationships among 15 taxa of the *Sorex cinereus* group were analyzed by canonical variates analysis using 13 cranial measurements and by Wagner analysis using morphometric data and qualitative character scores. The results of the analyses were used to determine the taxonomic status of the populations studied and to reconstruct, in light of known vicariance events, the pattern and mode of speciation leading to present diversity. The analyses revealed two main divisions within the *cinereus* group, a northern one of apparent Beringian origin and a southern one. The former comprises seven taxa: *haydeni* Baird 1958, *pribilofensis* Merriam 1895, *jacksoni* Hall and Gilmore 1932, *leucogaster* Kuroda 1933, *ugyunak* Anderson and Rand 1945, *portenkoi* Stroganov 1956, and *camtschatica* Yudin 1972. The latter includes *cinereus* Kerr 1792 (with subspecies), *lesueurii* Duvernoy 1842, *streatori* Merriam 1895, *hollisteri* Jackson 1900, *lyelli* Merriam 1902, *fontinalis* Hollister 1911, *preblei* Jackson 1922, and *milleri* Jackson 1947. Based on evidence from morphology, and sympatry or parapatry, the specific status of *S. cinereus* (including *fontinalis, lesueurii, streatori*, and *hollisteri* among others), *S. haydeni*, and *S. preblei* is assured. The status of allopatric taxa is more difficult to evaluate. In the Beringian subgroup the tundra dwelling *ugyunak, jacksoni*, and *portenkoi* may represent a single species, while the island forms *pribilofensis* and *leucogaster* and the woodland form *camtschatica* probably represent three separate species. The southern allopatric *lyelli* and *milleri* are morphologically close to the southern subspecies of *S. cinereus*. Karyological and biochemical studies may further clarify the taxonomic status of allopatric forms. Speciation leading to present diversity conforms to the allopatric or allo-parapatric model.

INTRODUCTION

In his revision of the American long-tailed shrews (*Sorex*), Jackson (1928) established the *Sorex cinereus* group for four closely related taxa in the subgenus *Otisorex: S. cinereus, S. fontinalis, S. lyelli*, and *S. preblei*. Since that time the validity of the group has withstood the test of time, while the number of taxa comprised in it has more than doubled. Findley (1955a, 1955b) concluded that the Mexican *S. milleri* belonged in this group. Shortly after, Stroganov (1956) reported shrews belonging to this group from eastern Siberia. Hoffmann and Peterson (1967) examined the shrews of the Bering Strait area and decided that the insular taxa *S. jacksoni* and *S. pribilofensis* from St. Lawrence and St. Paul Island, respectively, should be placed in the *cinereus* group and not in the *araneus-arcticus* group as had been the practice till then. A considerable amount of systematic information relating to the group in northeastern Siberia and neighboring parts of North America has since been published (e.g., Reimers et al. 1968, Dolgov and Krivosheyev 1973, Okhotina 1977, van Zyll de Jong 1982). In the center of the group's distributional range *S. c. haydeni* was found to constitute a distinct species (van Zyll de Jong 1980, van Zyll de Jong and Kirkland 1989), while in the east the idea that *fontinalis* might represent a separate sibling species was revived (Kirkland 1977).

As a result of these and other studies Junge and Hoffmann (1981) listed eight species of the *cinereus* group in North America. With the addition of the three Siberian taxa, the *cinereus* group constitutes the most numerous and most widely distributed group of North American *Sorex*.

The contributions to our understanding of the systematics of the group have been piecemeal, limited in scope to a few taxa at the time or focussing on part of the group's distributional range. The analyses to date have relied almost exclusively on morphology, cytogenetic (Meylan 1967, Ivanitskaya and Kozlovsky 1985) and biochemical data (George 1988) being available for only a few taxa.

The present study reviews the phylogenetic

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relationships within the *Sorex cinereus* group based on morphological data and presents a hypothesis of the pattern and mode of speciation of the group.

MATERIALS AND METHODS

The number of specimens of the 15 terminal taxa examined in this study are: 394 *cinereus* Kerr 1792 from the Northwest Territories, Yukon, Alberta, Michigan, and Wyoming; 268 *lesueurii* Duvernoy 1842 from Indiana, Illinois, and Iowa; 227 *haydeni* Baird 1858 from the Canadian prairie provinces; 13 *pribilofensis* Merriam 1895; 18 *streatori* Merriam 1895 from British Columbia; 18 *hollisteri* Jackson 1900 from Alaska; 3 *lyelli* Merriam 1902; 164 *fontinalis* Hollister 1911 from Maryland and Pennsylvania; 21 *preblei* Jackson 1922 from Montana, Oregon, Nevada, Utah, and Wyoming; 12 *jacksoni* Hall and Gilmore 1932; 20 *leucogaster* Kuroda 1933; 30 *ugyunak* Anderson and Rand 1945; 21 *milleri* Jackson 1947; 31 *portenkoi* Stroganov 1956; and 34 *camtschatica* Yudin 1972. Smaller subsamples of each taxon or geographic population (N = 30, except where available specimens were less) were used in the craniometric analysis. The material used in the present analysis has been listed in detail elsewhere (van Zyll de Jong 1980, 1982; van Zyll de Jong and Kirkland 1989), except for the samples of *S. preblei* (2 KU, 12 OSUFW, 4 USNM, 3 UU) and *S. lyelli* (3 MVZ) (acronyms follow Yates et al. 1987). All taxa were represented by skulls and skins.

The morphological characters used in the following analyses consist of mensural data complemented by a small number of qualitative characters. The former were employed in an ordination procedure, using canonical variates analysis (CVA; Biostat). The technique was used to describe and ordinate multivariate observations, and conformity of the data to the assumptions of multivariate normality and equal variance-covariance structure were not tested (Albrecht 1980). The distance data (Mahalanobis D) were used in a cluster analysis (UPGMA, Sneath and Sokal 1973).

The morphometric analysis is based on the following measurements of the skull and mandible (for definitions see van Zyll de Jong 1980): 1) greatest length of skull; 2) width of cranium; 3) least interorbital width; 4) width across I1–I1; 5) width across M2–M2; 6) length of the upper unicuspid toothrow; 7) P4–M3 length; 8) length of mandible; 9) height of coronoid process; 10) coronoid process condyle length; 11) greatest condylar depth; 12) width of lower condylar facet; and 13) length of mandibular toothrow.

The qualitative characters examined include the degree of pigmentation of the lower incisor, the position of the infraorbital and lacrimal foramina relative to the mesostyle of M1 (van Zyll de Jong 1980), and pelage coloration. Incisor pigmentation was scored on the basis of the number of clearly defined areas of pigmentation (three, two, or one). The relative position of the infraorbital and lacrimal foramina was recorded as posterior, even, or anterior to the mesostyle of M1. A character matrix consisting of the first two canonical variate scores for the craniometric data and scores for the qualitative characters examined (scored from 0 to 1) were used in constructing a Wagner tree (Farris 1970).

RESULTS

Canonical Variates Analysis

The results of the CVA are presented in a three-dimensional scattergram (Fig. 1) showing the centroid for each taxon and a minimum spanning tree linking nearest neighbors in canonical variate space. *Sorex c. cinereus* is represented by three geographic subsamples (northwestern Canada, northern Michigan, and Wyoming), as is *lesueurii* (Indiana, southern Michigan, and Iowa).

The canonical variate scores differentiate the taxa and reveal several subgroups indicating differences in shape of the cranium and mandible. Canonical variable I represents primarily differences in length of upper unicuspids, width across I1–I1, coronoid process-condyle length, and width across M2–M2 (Table 1). Canonical variable II represents primarily variation in width across I1–I1, P4–M3 length, height of the coronoid process, and width across M2–M2. Canonical variable III discriminates among the taxa on a similar combination of characters (character 4, 9, 5, 6, see Table 1). The first three canonical axes account for 76% of the variation.

Shrews with relatively long and narrow skulls, possessing long unicuspid toothrows are thus situated above those with broad skulls and short unicuspid toothrows, while larger forms are toward the right along a descending axis.

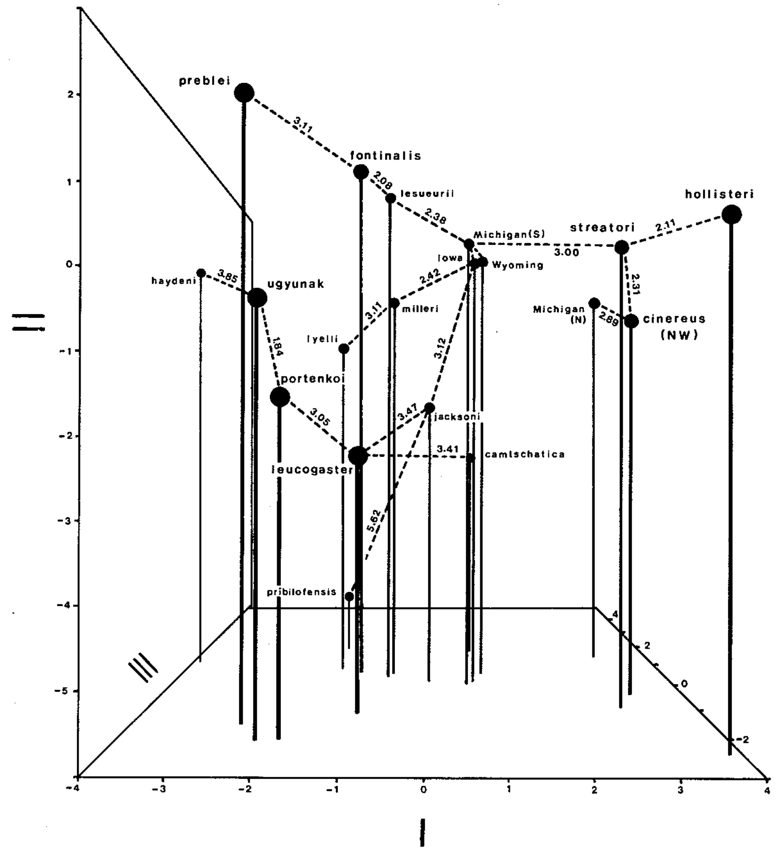

Figure 1. Three-dimensional projection of the centroids representing 19 samples of shrews of the *S. cinereus* group onto the first three canonical variables with minimum spanning tree showing distances (D) between nearest neighbors. *S. c. cinereus* and *S. c. lesueurii* are represented by three geographic samples each (northwestern Canada, northern Michigan, and Wyoming; and Indiana, Iowa, and southern Michigan; respectively). Graduations on the axes are in D units.

Table 1. Normalized Canonical Vectors for interpreting contribution to discrimination along the first three canonical variate axes of 13 variables.

Measurement	I	II	III
01. Greatest length of skull	0.110	−0.116	0.099
02. Width of cranium	0.000	0.001	0.003
03. Least interorbital width	0.099	−0.138	0.015
04. Width across I1-I1	−0.611	−0.665	−0.598
05. Width across M2-M2	−0.201	−0.295	0.446
06. Length of upper unicuspids	0.686	0.157	−0.241
07. P4-M3 length	−0.154	0.504	0.217
08. Length of mandible	0.022	−0.188	−0.128
09. Height of coronoid process	0.069	0.332	0.490
10. Coronoid process-condyle length	−0.222	−0.027	0.127
11. Greatest condylar depth	−0.116	0.098	0.234
12. Width of lower condylar facet	0.008	0.011	−0.014
13. Length of mandibular toothrow	0.039	0.051	−0.026

The centroids are arranged in two main tiers. The upper one comprises the geographic forms of *S. cinereus*, with the larger northern long rostrum morphs to the right and the smaller southern short rostrum morphs with *preblei* to the left. The lower tier consists of Beringian forms and *haydeni*, with *pribilofensis* off by itself near the bottom. Somewhat intermediate to the two principal tiers, but linked to southern forms of *cinereus*, are *S. milleri* and *S. lyelli*.

The Beringian taxa (*camtschatica, jacksoni, leucogaster, ugyunak, portenkoi,* and *pribilofensis*—as well as *haydeni*) differ from the other taxa primarily in having relatively broader widths across I1–I1 and M2–M2, and shorter P4–M3 and unicuspid lengths.

The generalized distances among the taxa are further summarized in a phenogram obtained by UPGMA cluster analysis (Fig. 2). It shows two approximately equivalent clusters, joined at the 4.96 D level, representing the Beringian taxa including *lyelli* and the forms of *S. cinereus*. These clusters are linked to *haydeni* and *preblei* more distantly (D = 5.46) and finally to *pribilofensis* (D = 7.69).

In the first two clusters only *lyelli* appears out of place being paired with *camtschatica*. In canonical variate space *lyelli* is nearest *milleri* (D = 3.11) and *cinereus* from Wyoming (D = 3.39; Fig. 1). The morphometric relationships of the more distant clusters are obscured by the increasing distortion at lower levels of the phenogram. Thus, as we have seen before (Fig. 1), the closest morphometric affinity of *preblei* is to *fontinalis* (D = 3.11) and that of *haydeni* to *ugyunak* (D = 3.86), while *pribilofensis* is closest to *jacksoni* (D = 5.62).

Comparison of Qualitative Characters

The southern taxa *fontinalis, lesueurii,* and *milleri* agree with the northern subspecies of *S. cinereus* in the mode of the relative position of the infraorbital and lacrimal foramina, the degree of pigmentation of the lower incisor (Table 2), and in having a bicolored pelage, while *preblei* differs from all aforementioned forms with respect to the position of the foramina and coloration of the pelage.

The Beringian taxa *ugyunak, portenkoi, jacksoni, leucogaster,* and *pribilofensis* share the possession of a tricolored pelage. The first three taxa also share the anterior position of the infraorbital and lacrimal foramina; whereas *leucogaster, pribilofensis,* and *camtschatica* resemble *S. cinereus* in this respect. Of the Beringian taxa, *camtschatica* is most similar to *S. cinereus* with respect to the three qualitative characters compared.

Sorex haydeni shares the anterior position of the infraorbital and lacrimal foramina with *jacksoni, ugyunak,* and *portenkoi*. It also shows a tendency to tricoloration of the pelage, particularly in old adults, which links it to five of the Beringian taxa. However, *haydeni* differs from all other taxa in the heavier pigmentation of the incisor.

Results from the small sample of *S. lyelli* may not be conclusive.

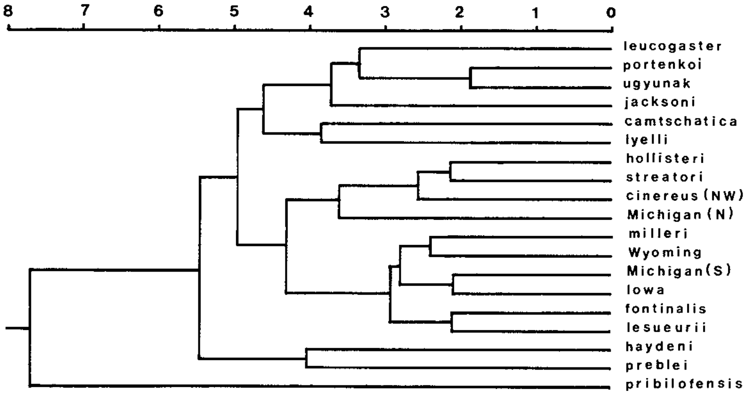

Figure 2. Distance phenogram derived by UPGMA clustering from the matrix of intercentroid generalized distances. Cophenetic correlation r = 0.75.

Table 2. Frequency of occurrence (%) of three states of two characters in 14 taxa of shrews.

		Position of intraorbital and lacrimal foramina relative to mesostyle of M1			Degree pigmentation of i1 (i.e., distinct areas of pigmentation)		
Taxon	N	Posterior	Even	Anterior	Three	Two	One
cinereus	312	89.1	9.9	0.9	98.2	1.8	—
hollisteri	18	94.4	5.6	—	46.2	53.8	—
streatori	18	100.0	—	—	100.0	—	—
lesueurii	170	67.6	31.8	0.6	82.8	11.2	6.0
fontinalis	138	66.7	32.6	0.7	96.9	3.1	—
milleri	21	85.7	14.3	—	100.0	—	—
preblei	17	29.0	64.7	5.8	57.1	42.8	—
camtschatica	34	76.5	23.5	—	77.8	18.5	3.7
leucogaster	19	94.7	5.3	—	100.0	—	—
jacksoni	11	—	—	100.0	90.9	9.1	—
ugyunak	21	—	9.5	90.5	100.0	—	—
portenkoi	28	10.7	28.6	60.7	86.3	13.6	—
haydeni	45	4.4	6.7	88.9	2.5	76.9	20.5
pribilofensis	13	100.0	—	—	8.3	83.3	8.3
lyelli	3	33.3	33.3	33.3		66.6	33.3

Wagner Analysis

The Wagner tree generated from the morphometric data and the qualitative character scores for all 15 taxa of the *cinereus* group is depicted in Fig. 3. The results of the cladistic analysis show a clear dichotomy between the Beringian and southern taxa (the former including *haydeni*) and are similar to those obtained in an earlier more restricted analysis using somewhat different characters (van Zyll de Jong 1982).

The patristic distances within each cluster are generally of similar magnitude, although that

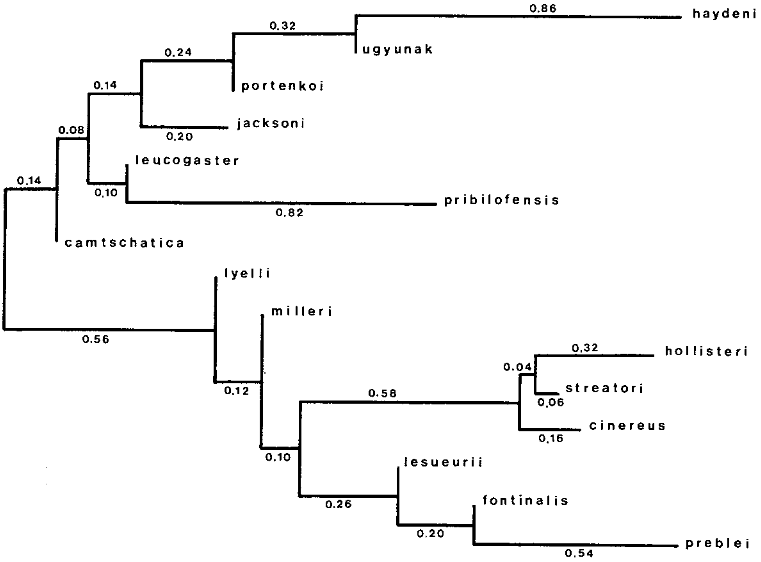

Figure 3. Wagner tree showing phylogenetic relationships of 15 taxa of the *S. cinereus* group. The tree was calculated by the Wagner distance procedure and the root estimated midway between the two most divergent taxa.

of the most divergent pair in the Beringian cluster, *haydeni* and *pribilofensis* (2.48), exceeds that of the most divergent pair of the southern taxa, *preblei* and *hollisteri* (1.94). If *haydeni* is excluded from the Beringian group, the within cluster divergence is closer (*pribilofensis-ugyunak* 1.62).

The taxon in the Beringian and southern cluster showing the smallest distance from the "ancestor" (i.e., the midpoint in our tree) are *camtschatica* and *lyelli*, respectively. They may thus represent the morphologically most primitive members of the group.

DISCUSSION

Taxonomic Considerations

The results of the present and previous morphological analyses allow us to draw conclusions regarding the specific status of the taxa studied. In considering first those taxa with sympatric or parapatric distributions, we find that populations of *cinereus, haydeni,* and *ugyunak* in their respective zones of contact are distinct epiphenotypes (sensu Wiley 1981). No evidence of intermediates between these neighboring populations was found, justifying the conclusion that they represent distinct species (van Zyll de Jong 1980, 1982). With respect to *cinereus* and *lesueurii* and *fontinalis,* the morphological evidence (van Zyll de Jong and Kirkland 1989) indicates that populations of each in allopatry are distinct epiphenotypes, but with apparent complete introgression throughout the zone of contact. In this case, the observations strongly suggest that we are dealing with distinct subspecies of one species. The specific status of *preblei* is well-founded as it occurs sympatrically with *cinereus* and *haydeni* (Hoffmann et al. 1969, Hoffmann and Fisher 1978, Tomasi and Hoffmann 1984). Morphologically, *preblei* has its closest affinity to the southern short-rostrum morphotypes of *S. cinereus* (*fontinalis* and *lesueurii*).

Turning now to those taxa with allopatric distributions, we will assume that a single species is probably present if a single epiphenotype is found in two or more disjunct areas. This situation pertains to the Beringian taxa *ugyunak, portenkoi, leucogaster,* and *jacksoni*. It is true that *jacksoni* is somewhat more divergent morphometrically from its nearest neighbors than these are from one another, yet each has essential characters in common. However, *leucogaster* and *portenkoi,* the only two Bergingian forms whose karyotypes have thus far been studied, differ in the number of their chromosomes (see below), which suggests that they may be specifically distinct. Some allopatric forms of similar epiphenotype may thus have differentiated into separate species. Only further study could clarify the status of such forms.

Biogeographic data may also be useful in assessing the specific status of allopatric forms, in particular that of insular forms. For example, of the six small mammals, other than shrews, that are found on St. Lawrence, St. Matthew, and the Pribilof Islands in the Bering Sea, only one, *Dicrostonyx exsul* of St. Lawrence Island, appears to have achieved reproductive isolation (Rausch and Rausch 1972). Another one, *Microtus abbreviatus* from St. Matthew Island, has diverged rather strongly phenotypically from the ancestral *M. miurus,* although it shares the same karyotype and is completely interfertile (Rausch and Rausch 1968). It should therefore be regarded as a distinct subspecies of *M. miurus*. The remaining four (*Lemmus sibiricus nigripes, Clethrionomys rutilus albiventer, Microtus oeconomus innuitus,* and *Spermophilus parryi lyratus*) have differentiated into distinct subspecies (Rausch and Rausch 1968, 1975a, 1975b). These observations underline the tentative nature of taxonomic decisions at the species level for allopatric populations based on morphological considerations alone.

The taxonomic position of *lyelli,* another allopatric taxon, is uncertain. Craniometrically, *lyelli* resembles *milleri* and the small forms of *S. cinereus* from Wyoming and southern Michigan, and in the three qualitative characters examined it resembles *S. cinereus* as well. The small number of specimens examined necessitates further study of a larger sample. Similarly, its nearest neighbor morphometrically, *milleri,* is close to the southern forms of *cinereus* although it is separated from them by a very long distance geographically. Clarification of the true relationship of these two taxa to *cinereus* must await study of biochemical and cytogenetic data; until then it would be best to maintain them as separate species.

The remaining allopatric taxa, *camtschatica* and *pribilofensis,* can be diagnosed without knowing their geographic origin and can on that basis be considered distinct species.

In summary, on the basis of the morphological evidence examined and the criteria outlined above, we may tentatively accept the following species in the *cinereus* group: *S. cinereus, preblei, lyelli, milleri,* in the southern subgroup, and *S. haydeni, S. pribilofensis, S. jacksoni* (including *portenkoi* and *ugyunak*), *S. leucogaster, S. camtschatica,* in the Beringian subgroup. The majority of these species are defined phenetically and confirmation of their validity must come from further study of different character sets, particularly cytogenetic and biochemical characters. As pointed out earlier, evidence from other sources is as yet quite meager. Basic karyotypes have been published for only three taxa, *S. c. cinereus* (Meylan 1967), *S. leucogaster,* and *S. j. portenkoi* (Ivanitskaya and Kozlovsky 1985). The first two share the same basic karyotype (2N = 66, 31 pairs of acrocentric and 1 pair of submetacentric autosomes; submetacentric heterosomes), whereas *portenkoi* differs substantially (2N = 60, 28 pairs of acrocentric and 1 pair of submetacentric autosomes, submetacentric heterosomes). Allozyme data for *haydeni, cinereus,* and *fontinalis* (George 1988) did not conclusively resolve the relationship of these forms. Comparisons of the morphology of the penis in a number of shrews of the *cinereus* group (J.A. Junge and R.S. Hoffmann, pers. comm.) provided support for the specific independence of *haydeni* and *preblei,* and showed *milleri* to be similar to *cinereus.* Information on penile morphology of other forms (Yudin 1969, van Zyll de Jong 1976, Okhotina 1977) is equivocal and therefore of limited use.

Origin and Speciation

The origin of the *cinereus* group can be traced back to the late Kansan and perhaps to the late Blancan (Kurtén and Anderson 1980). Fossil occurrence suggests a distribution extending much farther south than the recent one in the Irvingtonian and Rancholabrean. These southern extensions probably occurred during periods of glaciation.

A broad outline of the pattern and mode of speciation of the *cinereus* group can be constructed on the basis of morphological evidence and historical biogeographic data. A possible scenario is as follows. During the Wisconsinan, a period spanning approximately 70,000 years and as many shrew generations, the ancestral population of the *cinereus* group became separated into two major allopatric segments, one in Beringia the other south of the ice sheet, when the Cordilleran and Laurentide ice sheets merged between 24,000 and 13,000 years B.P. (Hopkins 1967). This constituted the first and major vicariance event in the biogeographical history of the group. Beringia had a cold and dry climate and large areas supported xeric vegetation comprising cold steppe and steppe tundra (Hopkins 1967, Hopkins et al. 1982). Taiga became restricted to relatively small isolated areas in the Yukon and Tanana River valleys in eastern Beringia and a more extensive area in the Kolyma and Omolon River valleys in western Beringia. Environments south of the ice sheet during the height of glaciation consisted of a narrow zone of tundra-like grasslands with scattered clumps of spruce along the margin of the ice. Next to the tundra zone, boreal forest extended far southward where it gradually merged with the deciduous and warm coniferous forests.

The shrew populations isolated in Beringia were exposed to a very different environment and selective pressures than their presumably forest-adapted ancestors. Selection leading to the cold steppe-tundra phenotype ensued producing the tundra forms of the *cinereus* group we know today. Parenthetically, parallel evolution in shrews of the *S. araneus-arcticus* complex (subgenus *Sorex*) in the same area produced strikingly similar results. Populations isolated in major forest refugia experienced a less drastic change and could be expected to have diverged relatively little from their forest-adapted ancestors. This could account for the origin of *S. camtschatica,* which, aside from its large feet with well-developed hair fringe (Okhotina 1977, van Zyll de Jong 1982), is morphologically the most primitive of the Beringian taxa as suggested by results of the Wagner analysis.

During deglaciation subsequent vicariance events occurred, which in turn subdivided the newly evolved tundra form into a number of allopatric populations. Rising sea levels first isolated the Pribilof Islands about 16,000 years ago (Hopkins 1967), separating the lineage leading to *S. pribilofensis.* About 10,000 years ago the sea flooded the land bridge connecting Alaska and Siberia, and somewhat later it isolated St. Lawrence and Paramushir Islands from their respective mainlands, thereby separating the lineages leading to the Recent taxa *ugyunak, protenkoi, jacksoni,* and *leucogaster.*

The fact that *haydeni* is morphometrically similar to the tundra forms (particularly to *ugyunak* and *portenkoi*) and has a number of cranial characters in common with them, points to a possible northern (Beringian) origin. Southward migration of tundra or cold steppe-adapted forms could have taken place during the middle or late Wisconsinan, when an ice-free corridor between the Cordilleran and Laurentide ice caps existed (Rutter 1980). South of the ice sheet the situation was quite different. Unlike Beringia, the southern area experienced less drastic environmental change. The main effect of glaciation was a major southward shift and compression of existing vegetation zones. We may assume that the boreal long-rostrum morphotype of *S. cinereus* was distributed throughout the boreal forest zone as it is today. The austral short-rostrum morphotype similarly was distributed parapatrically in the adjacent temperate forest zone. In the course of deglaciation a gradual northward shift of these biotic zones took place, with the southern morphotype dispersing east (leading to *fontinalis*) and west (leading to *lesueurii*) of the Appalachians where the northern morphotype could maintain itself. In the extreme south, a population of the southern type became marooned in the Sierra Madre Oriental in northern Mexico giving rise to *milleri*. A similar event in California gave rise to *lyelli*. The beginning of these developments may have coincided with a significant warming of the climate between 11,000 and 9,500 years B.P. (Mott et al. 1981) and stabilized to the present pattern by approximately 9,340–1,000 years B.P., when the fauna in Pennsylvania was essentially modern (Guilday 1971).

The origin of *preblei* is more obscure. The morphological evidence suggests close affinity to the southern morphotypes of *S. cinereus* and a possible common origin. However, the possibility of an independent origin in a western refugium cannot be ruled out at the moment.

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Inter- and Intraspecific Variation among Coastal and Island Populations of *Sorex monticolus* and *Sorex vagrans* in the Pacific Northwest

SARAH B. GEORGE AND JAMES DALE SMITH

Abstract

Where *Sorex monticolus* and *Sorex vagrans* overlap in their distributions, especially in southwestern British Columbia, the two can be difficult to identify. Twenty-seven samples from Vancouver Island, the mainland, and adjacent coastal islands were examined using univariate and multivariate analyses of 14 cranial measurements. We attempted to distinguish between the two species and assess the amount of intraspecific variability within each of them. The two species unequivocally discriminate; and based on the analysis of population variability, we recognize two subspecies of *Sorex monticolus* within the study area: *Sorex monticolus setosus* Elliot, 1899 (including *Sorex monticolus mixtus* Hall, 1938, previously recognized from Texada Island) and *Sorex monticolus isolatus* Jackson, 1922. *Sorex vagrans vancouverensis* Merriam, 1895 is not distinct from the mainland subspecies, *Sorex vagrans vagrans* Baird, 1858. Populations of *S. vagrans* from the Gulf and San Juan Islands approach the size of S. monticolus (the larger shrew). Hypotheses regarding the different distributions of *S. vagrans* and *S. monticolus* are discussed.

INTRODUCTION

Distinguishing between *Sorex monticolus* and *S. vagrans* has been difficult where the ranges of the two species overlap, and some authors have regarded the taxa as conspecific (Findley 1955). In southwestern British Columbia, where *S. vagrans* reaches the northwestern limit of its distribution, the two taxa are found sympatrically on the southeast coast of Vancouver Island and on the mainland south of Jervis Inlet (Cowan and Guiguet 1956). Furthermore, specimens from Vancouver Island and coastal islands to the southeast are sometimes intermediate in size and in relative pigmentation of the incisors, characteristics frequently used to distinguish the species (Findley 1955, Hennings and Hoffmann 1977, van Zyll de Jong 1982a).

In the geographic area encompassed by this study, *Sorex vagrans* is classified into two subspecies: *S. v. vagrans* Baird, 1858, on the mainland and *S. v. vancouverensis* Merriam, 1895, on Vancouver Island. Regarding *vancouverensis,* Findley (1955:60) commented: "This is a poorly differentiated subspecies which is closely related to *S. v. vagrans*. The differences in color noted are average ones. Some individuals of this shrew might be difficult to separate from *S. v. isolatus* [= *S. monticolus isolatus*]." In his comparisons, he used "more brownish" ventral parts and winter pelage to distinguish *S. v. vancouverensis* from *S. v. vagrans*. Shorter tail and hind foot, narrower skull, and smaller teeth were used to separate *S. v. vancouverensis* from sympatric *S. m. isolatus*. Considerable confusion has prevailed in the identity of shrews from the Gulf and San Juan Islands, located southeast of Vancouver Island. Dalquest (1948) and Findley (1955) relegated specimens from Whidbey Island and the San Juan Islands, Washington, to *S. v. vagrans,* whereas Cowan and Guiguet (1956) classified shrews taken on the Canadian Gulf Islands as *S. v. vancouverensis*.

On the other hand, three subspecies of *Sorex monticolus* are recognized within the area of study: *S. m. setosus* Elliot, 1899, from the mainland, *S. m. mixtus* Hall, 1938, from Texada Island off the eastern coast of Vancouver Island, and *S. m. isolatus* Jackson, 1922, from Vancouver Island. *Sorex monticolus* is not known to occur on the San Juan Islands. Hennings and Hoffmann (1977) listed *S. monticolus* as occurring on only one of the Gulf Islands, Saturna Island. Findley (1955) commented that *S. m. isolatus* was smaller in size than *S. m. setosus* and morphologically close to *S. v. vancouverensis* (see above). He described

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S. m. mixtus as similar in color to *S. m. setosus* and *S. m. isolatus* but with a longer palate and shorter hind foot than either of these races.

The goals of this study were to: 1) analyze cranial variability of the two species with the aim of assessing morphometric discrimination, 2) describe patterns of intraspecific cranial variation in the two species, and 3) evaluate the taxonomic status of the five total subspecies recognized for *S. monticolus* and *S. vagrans* in the study area. In particular, we wished to resolve the confusion concerning the taxonomic status of the generally large-sized shrews (*S. vagrans*) from the Gulf Islands and to clarify the distinction of the sympatric or near sympatric populations of the two species on Vancouver Island.

METHODS

Two hundred eighteen specimens of *Sorex vagrans* and 184 *Sorex monticolus* (total N = 402) from 27 (13 *S. vagrans* and 14 *S. monticolus*) localities on Vancouver Island, adjacent islands, and mainland British Columbia were examined. Identification to species was based on the degree of pigmentation of the medial tine of the upper incisor (Hennings and Hoffmann 1977). In addition, the study included 83 specimens, which were either from localities of insufficient sample size to be included in the overall analysis or were of uncertain species identity (possessing intermediate tine pigmentation or having incisors worn past the pigmentation). With the diagnosis, we hope to better delineate the distributions of the two species in the study area. These specimens were linked to the overall analysis by an a posteriori diagnosis (see below). Seventeen cranial measurements were recorded: greatest length of skull, cranial breadth, least interorbital width, length of nasals, P^4–M^3 length, U^1–U^5 length, width across I^1–I^1, width across U^4–U^4, width across M^2–M^2, palatal length, post-palatal length, length of mandible, height of coronoid process, width of upper condylar facet, width of lower condylar facet, greatest condylar depth, and length of mandibular toothrow; for descriptions of these measurements, see Kirkland (1977) and van Zyll de Jong (1980).

BIOSTAT II MDA (multigroup discriminant function analysis; Pimentel and Smith 1986a) was used for discrimination among the 27 groups as well as for diagnosing the 83 unclassified individuals. MDA was used rather than principal component analysis because the latter method is more affected by sample size and is less powerful a discriminatory technique. Univariate statistics for all groups and variables as well as tests for normality and randomness were obtained by using BIOSTAT I STATS (basic descriptive statistics; Pimentel and Smith 1986b).

RESULTS

An initial run of MDA resulted in a within-dispersion determinant near zero, suggesting singularity or ill-conditioning of the data. We used the method outlined in Pimentel and Smith (1986b) to detect possible sources of linear or near linear dependence. Although no serious linear dependence was found, three variables (cranial and interorbital breadths, and width of upper condylar facet) were eliminated from the study because they had little, if any, effect on the overall discrimination of groups or species. However, the extremely small variances of the 14 variables used in the study appeared to be causing the ill-conditioning of the within-dispersion matrix. To alleviate this problem, we recoded the data by moving the decimal one place to the right. This is a means of converting very small numbers into larger numbers without altering the fundamental structure of the data. As a result, the decimal was moved one place to the right in the mean and two places in the variances. There was considerable improvement in the resulting within-dispersion determinant (0.0579748). An analysis using the MDA option for log transformation did not produce results markedly different from the untransformed data. Thus, aside from the recoding, the original data were analyzed and are discussed herein.

The means ± one standard deviation and the ranges for the 14 cranial measurements used in the study are shown in Table 1 for each of the 27 samples examined. The nature of the inter- and intraspecific variation is noteworthy. For the most part, cranial dimensions for *Sorex monticolus* average larger than those of *S. vagrans*. However, the most striking feature of the variation of these shrews is the extremely narrow ranges of variation for all cranial variables. The standard deviations shown in Table 1 are comparable to

Table 1. Means ± standard deviations and ranges (in parentheses) of the 14 cranial variables used in the study. See Specimens Examined for explanations of sample numbers; "V" refers to *S. vagrans* and "M" to *S. monitcolus*.

Sample #	N	Skull Length	Length of Nasals	P^4–M^3 Length	U^1–U^5 Length	I^1–I^1 Width	U^4–U^4 Width	M^2–M^2 Width
V-1	9	16.44±0.27 (16.1–16.9)	5.24±0.17 (5.0–5.6)	3.83±0.09 (3.7–3.9)	2.21±0.09 (2.1–2.4)	1.42±0.04 (1.4–1.5)	2.07±0.04 (2.0–2.1)	4.12±0.07 (4.0–4.2)
V-2	20	16.40±0.19 (16.1–16.8)	5.17±0.12 (5.0–5.4)	3.82±0.10 (3.6–4.0)	2.27±0.07 (2.2–2.4)	1.46±0.05 (1.4–1.5)	2.09±0.05 (2.0–2.2)	4.09±0.08 (4.0–4.2)
V-3	8	16.80±0.29 (16.3–17.2)	5.30±0.19 (5.1–5.7)	3.89±0.10 (3.8–4.0)	2.35±0.08 (2.2–2.4)	1.45±0.05 (1.4–1.5)	2.17±0.05 (2.1–2.2)	4.26±0.07 (4.2–4.4)
V-4	32	17.01±0.28 (16.3–17.6)	5.39±0.18 (5.0–5.9)	4.06±0.08 (3.9–4.2)	2.40±0.07 (2.2–2.5)	1.47±0.07 (1.3–1.6)	2.16±0.07 (2.0–2.3)	4.30±0.07 (4.2–4.4)
V-5	17	16.71±0.27 (16.2–17.2)	5.49±0.22 (5.0–5.8)	4.05±0.12 (3.8–4.3)	2.43±0.07 (2.3–2.5)	1.50±0.06 (1.4–1.6)	2.18±0.05 (2.1–2.3)	4.35±0.08 (4.2–4.5)
V-6	11	16.65±0.20 (16.2–16.9)	5.19±0.21 (4.8–5.5)	3.97±0.08 (3.8–4.1)	2.37±0.05 (2.3–2.4)	1.50±0.06 (1.4–1.6)	2.14±0.07 (2.0–2.2)	4.35±0.09 (4.1–4.4)
V-7	30	16.88±0.26 (16.3–17.6)	5.40±0.19 (4.9–5.7)	4.05±0.13 (3.9–4.6)	2.45±0.07 (2.3–2.6)	1.55±0.05 (1.5–1.6)	2.13±0.06 (2.0–2.2)	4.30±0.07 (4.2–4.4)
V-8	14	16.56±0.23 (16.2–16.9)	5.09±0.16 (4.8–5.3)	3.82±0.06 (3.7–3.9)	2.29±0.07 (2.2–2.4)	1.45±0.05 (1.4–1.5)	2.11±0.07 (2.0–2.2)	4.09±0.08 (4.0–4.2)
V-9	12	16.42±0.39 (16.0–17.2)	5.29±0.18 (5.0–5.7)	3.89±0.11 (3.7–4.1)	2.27±0.07 (2.2–2.4)	1.41±0.03 (1.4–1.5)	2.08±0.07 (2.0–2.2)	4.24±0.14 (4.1–4.5)
V-10	12	16.62±0.34 (16.0–17.1)	5.33±0.23 (5.0–5.7)	3.88±0.09 (3.8–4.0)	2.35±0.09 (2.2–2.5)	1.44±0.05 (1.4–1.5)	2.11±0.08 (1.9–2.2)	4.15±0.16 (4.0–4.5)
V-11	16	16.40±0.24 (16.0–17.0)	5.29±0.20 (4.8–5.7)	3.89±0.10 (3.7–4.1)	2.33±0.05 (2.3–2.4)	1.44±0.05 (1.4–1.5)	2.11±0.04 (2.0–2.2)	4.12±0.08 (4.0–4.2)
V-12	18	16.56±0.27 (16.1–17.1)	5.13±0.22 (4.9–5.7)	3.89±0.06 (3.8–4.0)	2.34±0.06 (2.3–2.5)	1.42±0.05 (1.4–1.6)	2.06±0.05 (2.0–2.1)	4.08±0.05 (4.0–4.2)
V-13	19	16.40±0.32 (16.0–17.0)	5.24±0.15 (5.0–5.5)	3.79±0.07 (3.7–3.9)	2.17±0.08 (2.0–2.3)	1.38±0.06 (1.2–1.5)	2.05±0.08 (1.9–2.2)	4.07±0.09 (3.9–4.3)

Table 1. (continued)

Sample #	Palatal Length	Post-pal. Length	Mandible Length	Coronoid Height	Lower cond. Width	Condylar Depth	Mandible Toothrow
V-1	6.56±0.17 (6.3–6.8)	7.65±0.17 (7.3–7.8)	8.30±0.19 (8.1–8.7)	3.51±0.11 (3.4–3.7)	1.15±0.05 (1.1–1.2)	2.01±0.08 (1.9–2.1)	4.65±0.11 (4.5–4.9)
V-2	6.57±0.11 (6.4–6.8)	7.54±0.14 (7.2–7.8)	8.20±0.18 (7.8–8.5)	3.51±0.06 (3.4–3.6)	1.20±0.06 (1.1–1.3)	2.02±0.09 (1.8–2.2)	4.58±0.08 (4.4–4.7)
V-3	6.72±0.13 (6.5–6.9)	7.86±0.20 (7.5–8.2)	8.39±0.16 (8.1–8.5)	3.60±0.11 (3.4–3.7)	1.26±0.05 (1.2–1.3)	2.07±0.05 (2.0–2.1)	4.64±0.11 (4.5–4.8)
V-4	6.98±0.15 (6.6–7.3)	7.61±0.18 (7.3–8.0)	8.54±0.18 (8.3–8.9)	3.63±0.09 (3.4–3.8)	1.15±0.06 (1.0–1.2)	2.02±0.06 (1.9–2.1)	4.77±0.10 (4.5–4.9)
V-5	6.82±0.20 (6.4–7.3)	7.62±0.11 (7.5–7.8)	8.60±0.19 (8.3–9.0)	3.63±0.08 (3.5–3.8)	1.21±0.02 (1.2–1.3)	2.05±0.07 (1.9–2.2)	4.77±0.11 (4.6–5.0)
V-6	6.67±0.10 (6.5–6.8)	7.65±0.12 (7.5–7.8)	8.34±0.11 (8.1–8.5)	3.60±0.09 (3.4–3.7)	1.24±0.05 (1.2–1.3)	2.05±0.07 (2.0–2.2)	4.68±0.09 (4.5–4.8)
V-7	6.83±0.18 (6.4–7.2)	7.74±0.19 (7.4–8.2)	8.55±0.18 (8.3–8.9)	3.61±0.08 (3.5–3.7)	1.19±0.04 (1.1–1.3)	2.01±0.07 (1.9–2.1)	4.82±0.09 (4.6–5.0)
V-8	6.66±0.13 (6.4–6.9)	7.51±0.18 (7.2–7.8)	8.30±0.14 (8.0–8.5)	3.47±0.08 (3.3–3.6)	1.16±0.05 (1.1–1.2)	1.97±0.05 (1.9–2.0)	4.61±0.07 (4.5–4.7)
V-9	6.62±0.25 (6.3–7.1)	7.49±0.16 (7.4–7.9)	8.33±0.29 (8.1–9.0)	3.53±0.17 (3.4–3.9)	1.17±0.07 (1.1–1.3)	1.97±0.08 (1.9–2.1)	4.63±0.12 (4.5–4.9)
V-10	6.72±0.20 (6.4–7.1)	7.65±0.17 (7.4–8.0)	8.30±0.18 (8.0–8.6)	3.55±0.11 (3.4–3.7)	1.17±0.05 (1.1–1.2)	1.97±0.10 (1.8–2.1)	4.66±0.11 (4.5–4.8)
V-11	6.57±0.13 (6.3–6.8)	7.54±0.17 (7.2–7.9)	8.27±0.15 (8.0–8.6)	3.47±0.08 (3.3–3.6)	1.16±0.05 (1.1–1.2)	2.01±0.07 (1.9–2.1)	4.64±0.09 (4.5–4.8)
V-12	6.62±0.12 (6.4–6.8)	7.53±0.21 (7.2–7.9)	8.31±0.14 (7.9–8.5)	3.44±0.11 (3.3–3.7)	1.14±0.07 (1.0–1.3)	1.98±0.06 (1.9–2.1)	4.71±0.07 (4.6–4.8)
V-13	6.47±0.14 (6.2–6.7)	7.39±0.25 (7.1–8.0)	8.27±0.16 (8.0–8.5)	3.46±0.10 (3.3–3.7)	1.12±0.07 (1.0–1.2)	1.93±0.12 (1.7–2.2)	4.52±0.11 (4.3–4.7)

Table 1. (continued)

Sample #	N	Skull Length	Length of Nasals	P^4–M^3 Length	U^1–U^5 Length	I^1–I^1 Width	U^4–U^4 Width	M^2–M^2 Width
M-14	7	16.91 ± 0.33 (16.5–17.4)	5.60 ± 0.16 (5.3–5.8)	4.04 ± 0.10 (3.9–4.2)	2.40 ± 0.06 (2.3–2.5)	1.50 ± 0.06 (1.4–1.6)	2.29 ± 0.04 (2.2–2.3)	4.47 ± 0.10 (4.4–4.6)
M-15	23	17.53 ± 0.34 (17.2–18.5)	5.68 ± 0.25 (5.3–6.2)	4.11 ± 0.14 (3.8–4.4)	2.48 ± 0.06 (2.4–2.6)	1.54 ± 0.06 (1.4–1.6)	2.33 ± 0.06 (2.2–2.4)	4.56 ± 0.12 (4.4–4.8)
M-16	19	17.46 ± 0.27 (16.9–17.9)	5.72 ± 0.22 (5.4–6.2)	4.19 ± 0.09 (4.0–4.3)	2.53 ± 0.07 (2.4–2.6)	1.57 ± 0.04 (1.5–1.6)	2.32 ± 0.06 (2.2–2.4)	4.50 ± 0.07 (4.4–4.6)
M-17	6	17.48 ± 0.17 (17.3–17.7)	5.87 ± 0.08 (5.8–6.0)	4.25 ± 0.05 (4.2–4.3)	2.53 ± 0.05 (2.5–2.6)	1.55 ± 0.05 (1.5–1.6)	2.30 ± 0.06 (2.2–2.4)	4.52 ± 0.12 (4.4–4.7)
M-18	16	17.51 ± 0.24 (17.0–17.8)	5.92 ± 0.20 (5.6–6.3)	4.23 ± 0.07 (4.1–4.4)	2.51 ± 0.08 (2.3–2.6)	1.59 ± 0.03 (1.5–1.6)	2.33 ± 0.06 (2.2–2.4)	4.48 ± 0.10 (4.3–4.7)
M-19	14	17.44 ± 0.28 (17.0–17.9)	5.83 ± 0.16 (5.6–6.0)	4.16 ± 0.06 (4.0–4.2)	2.58 ± 0.09 (2.4–2.7)	1.51 ± 0.05 (1.4–1.6)	2.33 ± 0.06 (2.2–2.4)	4.52 ± 0.11 (4.3–4.6)
M-20	10	17.55 ± 0.23 (17.3–17.9)	5.92 ± 0.13 (5.7–6.1)	4.17 ± 0.08 (4.1–4.3)	2.62 ± 0.04 (2.6–2.7)	1.57 ± 0.05 (1.5–1.6)	2.33 ± 0.05 (2.3–2.4)	4.52 ± 0.08 (4.4–4.6)
M-21	11	17.25 ± 0.27 (16.7–17.6)	5.71 ± 0.18 (5.4–5.9)	4.24 ± 0.05 (4.2–4.3)	2.43 ± 0.10 (2.2–2.5)	1.55 ± 0.07 (1.5–1.7)	2.32 ± 0.08 (2.2–2.5)	4.55 ± 0.05 (4.5–4.6)
M-22	14	17.08 ± 0.20 (16.7–17.4)	5.46 ± 0.19 (5.2–5.7)	4.15 ± 1.10 (4.0–4.4)	2.42 ± 0.07 (2.3–2.5)	1.59 ± 0.06 (1.5–1.7)	2.36 ± 0.08 (2.2–2.5)	4.57 ± 0.10 (4.4–4.8)
M-23	6	17.23 ± 0.15 (17.1–17.5)	5.87 ± 0.18 (5.6–6.0)	4.22 ± 0.18 (4.0–4.5)	2.47 ± 0.08 (2.4–2.6)	1.63 ± 0.05 (1.6–1.7)	2.38 ± 0.08 (2.2–2.4)	4.55 ± 0.05 (4.5–4.6)
M-24	10	17.21 ± 0.23 (17.0–17.7)	5.94 ± 0.21 (5.7–6.4)	4.35 ± 0.08 (4.2–4.5)	2.48 ± 0.08 (2.4–2.6)	1.60 ± 0.09 (1.4–1.7)	2.44 ± 0.08 (2.3–2.6)	4.72 ± 0.10 (4.5–4.9)
M-25	20	17.12 ± 0.19 (16.8–17.4)	5.77 ± 0.18 (5.4–6.1)	4.17 ± 0.09 (4.0–4.4)	2.46 ± 0.05 (2.4–2.5)	1.56 ± 0.05 (1.5–1.6)	2.34 ± 0.06 (2.2–2.4)	4.53 ± 0.06 (4.4–4.6)
M-26	9	17.33 ± 0.32 (16.9–17.8)	5.89 ± 0.22 (5.6–6.2)	4.32 ± 0.10 (4.2–4.5)	2.42 ± 0.07 (2.3–2.5)	1.59 ± 0.03 (1.5–1.6)	2.36 ± 0.05 (2.3–2.4)	4.67 ± 0.10 (4.5–4.8)
M-27	19	16.93 ± 0.23 (17.6–18.3)	6.10 ± 0.14 (5.9–6.4)	4.37 ± 0.08 (4.2–4.5)	2.59 ± 0.08 (2.5–2.7)	1.62 ± 0.06 (1.5–1.7)	2.35 ± 0.08 (2.2–2.5)	4.62 ± 0.09 (4.4–4.8)

Table 1. (continued)

Sample #	Palatal Length	Post-pal. Length	Mandible Length	Coronoid Height	Lower cond. Width	Condylar Depth	Mandible Toothrow
M-14	6.90±0.15 (6.7–7.2)	7.66±0.14 (7.4–7.8)	8.59±0.18 (8.4–8.9)	3.61±0.11 (3.5–3.8)	1.16±0.11 (1.0–1.3)	1.96±0.10 (1.8–2.1)	4.80±0.10 (4.7–4.9)
M-15	7.05±0.13 (6.9–7.3)	7.99±0.23 (7.6–8.5)	8.88±0.18 (8.5–9.3)	3.81±0.14 (3.6–4.1)	1.27±0.05 (1.2–1.4)	2.06±0.06 (2.0–2.2)	4.94±0.10 (4.7–5.1)
M-16	7.20±0.16 (6.8–7.4)	7.99±0.11 (7.7–8.2)	8.79±0.14 (8.5–9.0)	3.79±0.09 (3.6–3.9)	1.22±0.06 (1.1–1.3)	1.97±0.07 (1.9–2.1)	5.06±0.10 (4.9–5.2)
M-17	7.32±0.25 (7.1–7.8)	8.08±0.21 (7.9–8.4)	8.88±0.18 (8.7–9.2)	3.78±0.10 (3.7–3.9)	1.23±0.05 (1.2–1.3)	2.00±0.13 (1.8–2.1)	5.05±0.10 (4.9–5.2)
M-18	7.29±0.15 (7.0–7.6)	8.07±0.16 (7.8–8.4)	8.92±0.14 (8.7–9.2)	3.83±0.10 (3.6–4.0)	1.29±0.08 (1.2–1.5)	2.06±0.07 (1.9–2.2)	5.06±0.10 (4.9–5.3)
M-19	7.22±0.08 (7.1–7.3)	7.93±0.19 (7.7–8.2)	8.90±0.09 (8.8–9.1)	3.76±0.09 (3.6–3.9)	1.22±0.07 (1.1–1.3)	2.04±0.09 (1.9–2.2)	5.00±0.09 (4.9–5.2)
M-20	7.30±0.14 (7.1–7.5)	7.97±0.15 (7.7–8.2)	8.87±0.19 (8.5–9.1)	3.78±0.06 (3.7–3.9)	1.24±0.05 (1.2–1.3)	1.99±0.09 (1.8–2.1)	5.04±0.12 (4.9–5.2)
M-21	7.04±0.16 (6.7–7.3)	7.94±0.18 (7.6–8.2)	8.69±0.16 (8.5–8.9)	3.73±0.09 (3.6–3.9)	1.22±0.04 (1.2–1.3)	2.07±0.05 (2.0–2.1)	5.02±0.08 (4.9–5.1)
M-22	7.00±0.18 (6.7–7.0)	7.84±0.14 (7.6–8.0)	8.61±0.19 (8.3–8.9)	3.74±0.07 (3.6–3.9)	1.19±0.06 (1.1–1.3)	1.97±0.11 (1.8–2.2)	4.91±0.12 (4.7–5.2)
M-23	7.25±0.05 (7.2–7.3)	7.83±0.29 (7.6–8.3)	8.90±0.21 (8.6–9.1)	3.82±0.08 (3.7–3.9)	1.17±0.08 (1.1–1.3)	2.00±0.13 (1.9–2.2)	5.07±0.14 (4.9–5.3)
M-24	7.20±0.15 (6.9–7.4)	7.84±0.34 (6.9–8.1)	8.86±0.11 (8.6–9.0)	3.80±0.09 (3.6–3.9)	1.23±0.07 (1.1–1.3)	2.08±0.09 (1.9–2.2)	5.15±0.11 (5.0–5.3)
M-25	7.08±0.14 (6.7–7.3)	7.85±0.16 (7.6–8.1)	8.69±0.18 (8.4–9.1)	3.81±0.10 (3.7–4.0)	1.19±0.06 (1.1–1.3)	2.02±0.08 (1.9–2.2)	4.99±0.10 (4.8–5.2)
M-26	7.24±0.14 (7.1–7.5)	7.82±0.15 (7.6–8.0)	8.76±0.15 (8.5–9.0)	3.86±0.11 (3.7–4.0)	1.21±0.06 (1.1–1.3)	2.07±0.07 (1.9–2.1)	5.13±0.09 (5.0–5.3)
M-27	7.39±0.10 (7.2–7.5)	8.23±0.18 (7.9–8.5)	9.10±0.16 (8.8–9.4)	3.88±0.08 (3.8–4.0)	1.24±0.06 (1.1–1.3)	2.09±0.05 (2.0–2.2)	5.24±0.06 (5.2–5.4)

those reported by Diersing and Hoffmeister (1977) for *Sorex merriami* and *S. arizonae*, Diersing (1980) for *S. hoyi*, Kirkland and Van Deusen (1979) for the *S. dispar*-group, and van Zyll de Jong (1980, 1982b) for the *S. cinereus*-group.

The 95% and 99% confidence limits of g_1 (a measure of skewness) bracket zero for nearly all variables and samples, thereby indicating symmetry for these distributions. For those few cases where g_1 departed from symmetry, skewness to the right was indicated. Likewise the 95% and 99% confidence limits of g_2 (a measure of kurtosis) for most variables and samples bracketed zero, also indicating normal distributions. Leptokurtosis (narrow, high-peaked distribution) was indicated for all but one of the few cases where there was a non-normal distribution. The Kolmogorov-Smirnov D-statistic for goodness of fit to a normal distribution exceeded the critical value (adjusted for sample size) in many cases. This was not surprising given the narrow range of variation and highly peaked distributions outlined above.

The results of the a posteriori Student-Newman-Keuls multiple range tests generally reconfirm that *S. monticolus* is larger than *S. vagrans* (alpha = 0.05). Two variables (widths across U^4–U^4 and M^2–M^2) resulted in unambiguous, non-overlapping subsets of means that exactly correspond to species identity (Table 2). Width across U^4–U^4 further differentiated the Lund sample (group #24 in Fig. 1; $\bar{x}$ = 2.44) from all other *S. mon-*

Table 2. Results of Student-Newmann-Keuls test on four variables. See Specimens Examined for explanation of sample numbers.

	Greatest length of skull				U^4–U^4 width		
Sample #	Species	Mean	Subset	Sample #	Species	Mean	Subset
11	V	16.40		13	V	2.05	
2	V	16.40		12	V	2.06	
13	V	16.40		1	V	2.08	
9	V	16.42		9	V	2.08	
1	V	16.44		2	V	2.10	
8	V	16.56		11	V	2.11	
12	V	16.56		8	V	2.11	
10	V	16.62		10	V	2.11	
6	V	16.66		7	V	2.13	
5	V	16.71		6	V	2.14	
3	V	16.80		4	V	2.17	
7	V	16.88		3	V	2.18	
14	M	16.91		5	V	2.18	
4	V	17.01		19	M	2.26	
22	M	17.08		23	M	2.28	
25	M	17.12		14	M	2.29	
24	M	17.21		17	M	2.30	
23	M	17.23		21	M	2.32	
21	M	17.26		16	M	2.32	
26	M	17.33		15	M	2.33	
19	M	17.44		20	M	2.33	
16	M	17.46		18	M	2.33	
17	M	17.48		25	M	2.34	
18	M	17.51		27	M	2.35	
15	M	17.54		22	M	2.36	
20	M	17.55		26	M	2.37	
27	M	17.93		24	M	2.44	

Table 2. (continued)

	M^2–M^2 width							
Sample #	Species	Mean	Subset					
13	V	4.07	|					
12	V	4.08	|					
8	V	4.09	|					
2	V	4.10	|					
11	V	4.12	|					
1	V	4.12	|					
10	V	4.15	|					
9	V	4.24	|					
3	V	4.26	|	|				
4	V	4.30	|	|				
7	V	4.30	|	|				
6	V	4.32	|	|				
5	V	4.35		|				
19	M	4.43		|				
14	M	4.47		|	|			
18	M	4.48		|	|			
16	M	4.50		|	|			
17	M	4.52		|	|	|		
20	M	4.52		|	|	|		
25	M	4.53		|	|	|		
23	M	4.55		|	|	|	|	
21	M	4.56			|	|	|	
15	M	4.56			|	|	|	
22	M	4.57			|	|	|	
27	M	4.62				|	|	
26	M	4.67					|	|
24	M	4.72						|

	Length of mandibular toothrow							
Sample #	Species	Mean	Subset					
13	V	4.52	|					
2	V	4.58	|					
8	V	4.61	|	|				
9	V	4.63	|	|				
3	V	4.64	|	|	|			
11	V	4.64	|	|	|			
1	V	4.66	|	|	|			
10	V	4.66	|	|	|			
6	V	4.68	|	|	|			
12	V	4.71		|	|			
5	V	4.76			|	|		
4	V	4.77			|	|		
14	M	4.80			|	|		
7	V	4.82				|		
22	M	4.91				|		
15	M	4.94				|	|	
25	M	4.99				|	|	
19	M	5.00				|	|	
21	M	5.03				|	|	|
20	M	5.04				|	|	|
17	M	5.05				|	|	|
16	M	5.06					|	|
18	M	5.06					|	|
23	M	5.07					|	|
26	M	5.13						|
24	M	5.15						|
27	M	5.24						|

ticolus. Width across M^2–M^2 reached its maximum ($\bar{x}$ = 4.72) at Lund, which is distinct from all other *S. monticolus* except the Sumas sample (#26 in Fig. 1); this variable also divided the *S. vagrans* means into two significant, nonoverlapping subsets. With the exception of the *S. monticolus* sample from Alberni (group #14), mandible toothrow length separated *Sorex monticolus* from *S. vagrans*. In fact, when group 14 was removed from the data, that variable resulted in nonoverlapping subsets of means corresponding to species. Only a narrow range of overlap of means between species was seen for greatest length of skull, length of nasals, P^4–M^3 length, width across I^1–I^1, palatal length, mandible length, and height of coronoid process (Table 2).

Within species, there was considerable overlap between locality means. The River Inlet sample of *Sorex monticolus* (group #27 in Fig. 1) was the largest for nine of the 14 variables, and for two of these (greatest length of skull, $\bar{x}$ = 17.93; mandibular toothrow length, $\bar{x}$ = 5.24; Table 2), this sample was significantly larger than all other populations. The Vancouver Island populations of *S. monticolus* tended to average larger for several length measurements (greatest length of skull, length of upper unicuspid row, postpalatal length, and mandible length) and smaller for several width measurements (widths across I^1–I^1, U^4–U^4, and M^2–M^2). Within *S. vagrans*, samples from the mainland (groups #1 and #2 in Fig. 1), from Vancouver Island (groups #9–#13), and from Saltspring Island (group #8) tended to be smaller, whereas the remaining Gulf and San Juan Island populations (groups #3–#7 in Fig. 1 and Table 2) tended to be larger. For width

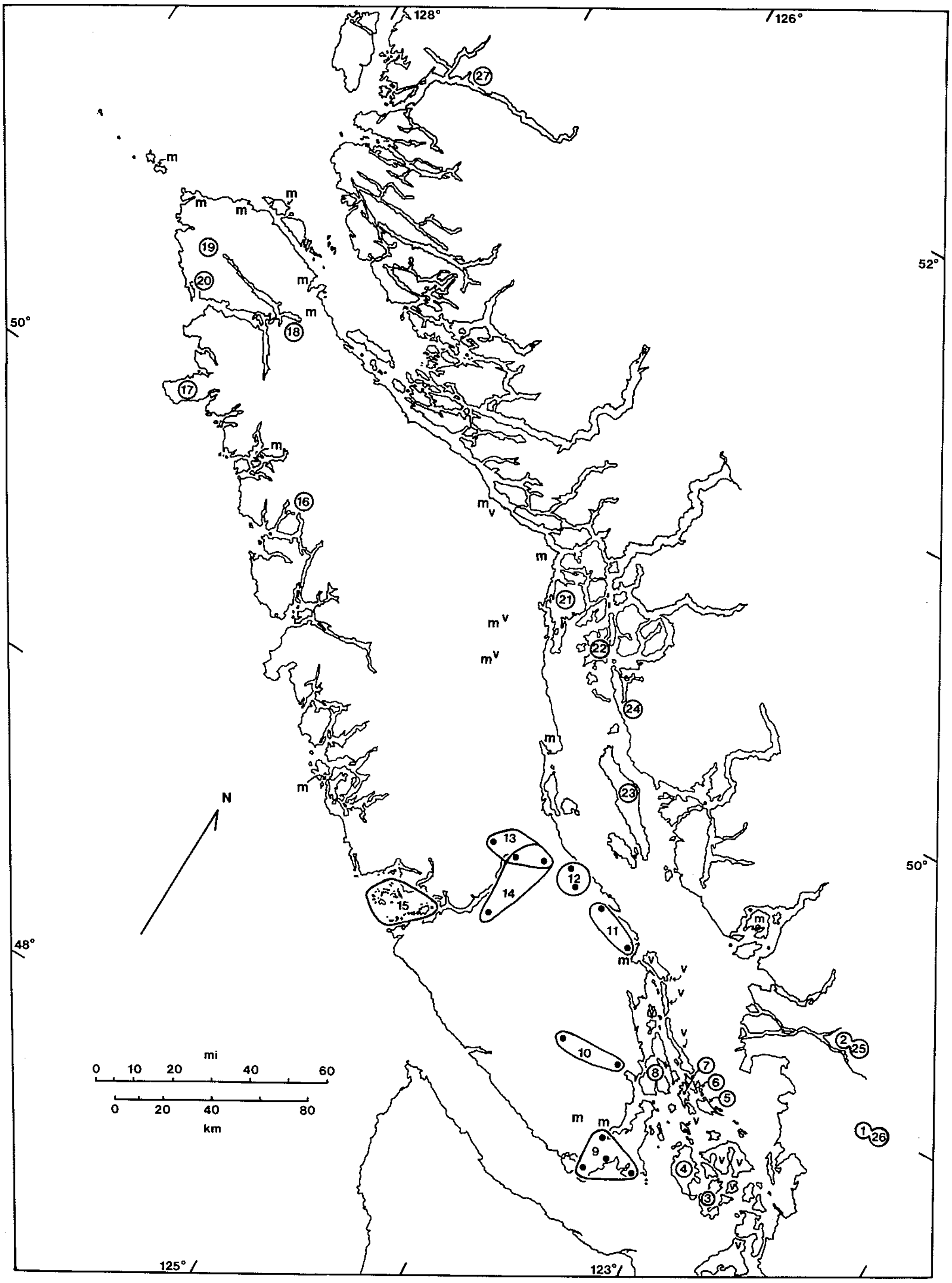

Figure 1. Map of the study area. See Specimens Examined section for definitions of sample numbers and detailed localities. Letters "m" and "v" refer to collection localities of diagnosed specimens; a single letter may represent more than one individual.

across M^2–M^2, the larger of the nonoverlapping subsets of *S. vagrans* samples included these five island populations.

Table 3 lists the first three standardized canonical vectors (Z-scores) and the percentage of the variance contributed by each variable to that respective canonical axis. Sixty-six percent of the cranial variation is explained by the first canonical axis, 8.23% is added by the second axis, 5.51% by the third for a cumulative total of 80.1%. Several cranial variables stand out as poor discriminators. Mandibular length hardly participates (3.6%) in the discrimination over the first three axes. Palatal and post-palatal length contribute only 35 and 22%, respectively, to the discrimination on these three axes. Interestingly, greatest length of skull (a widely used cranial dimension in mammalian morphometric studies) also contributes little to the multivariate discrimination of the two shrew species under study. This variable illustrates a paradox that often accompanies multivariate analyses. Viewed in the univariate context (e.g., SNK, Table 2), *Sorex vagrans* and *S. monticolus* are arrayed, respectively, from smallest to largest by their skull length. However, in the discriminant space of this study, *S. vagrans* are characterized as having relatively long skulls. This variable must be viewed with caution because only 35.7% of its variation is shown in the first three canonical axes.

The first canonical axis is clearly the most important for species discrimination. The second axis is one of intraspecific patterns of variability, especially for mainland and Vancouver Island populations of *Sorex monticolus*. The Gulf and San Juan Island samples of *S. vagrans* are affected by this second dimension as well. It is difficult to decipher the intraspecific variation in the third dimension of the MDA. There are no clear-cut groups beyond those portrayed by the first two axes. Indeed, the variation in this dimension appears to be random, with mainland and island samples intermixed. Width of the lower condylar facet is the "weightiest" variable (46.9%) in this canonical axis.

The "best" cranial variables for discriminating *Sorex vagrans* and *S. monticolus* are the widths of U^4–U^4 and M^2–M^2. Each contributed more than 90% of their respective variation to the discrimination of these shrews in the first three

Table 3. First three standardized canonical vectors (Z-scores) from discriminant function analysis for 14 cranial variables from *Sorex vagrans* and *S. monticolus*. The number in parentheses following each vector score indicates the percentage of the variance contributed by each variable to that respective canonical axis. The F-value for overall discriminance (test of equality of group centroids) is 7.482 with 364 and 4,535 degrees of freedom and is significant ($P > 0.01$).

	Standardized Canonical Vectors			Cumulative
Variable	1	2	3	Percent
Greatest length of skull	−0.084 (14.5)	−0.035 (0.1)	0.698 (21.1)	35.7
Length of nasals	0.259 (83.1)	0.048 (0.1)	−0.142 (0.5)	83.7
P^4–M^3 length	0.062 (21.0)	0.142 (3.7)	−0.465 (24.8)	49.5
U^1–U^5 length	0.125 (30.1)	−0.870 (49.9)	−0.104 (0.4)	80.4
I^1–I^1 width	0.067 (25.3)	−0.187 (6.8)	−0.389 (18.1)	50.2
U^4–U^4 width	0.303 (86.0)	0.241 (1.9)	0.447 (3.9)	91.8
M^2–M^2 width	0.374 (88.4)	0.355 (2.7)	0.265 (0.9)	92.0
Palatal length	0.106 (26.0)	−0.183 (2.6)	−0.362 (6.4)	35.0
Post-palatal length	0.016 (1.4)	−0.327 (20.3)	0.044 (0.2)	21.9
Length of mandible	0.018 (0.9)	−0.158 (2.5)	0.052 (0.2)	3.6
Height of coronoid process	0.149 (73.1)	0.153 (2.6)	0.031 (0.1)	75.8
Lower condylar facet width	−0.010 (0.7)	−0.310 (21.3)	0.585 (46.9)	68.9
Greatest condylar depth	−0.215 (75.8)	0.114 (0.7)	−0.246 (2.1)	80.9
Mandibular toothrow length	0.309 (74.3)	0.375 (3.7)	−0.306 (1.5)	79.5
Percent Trace	66.32	8.28	5.51	
Cumulative Percent	66.32	74.59	80.10	

dimensions of discriminant space. Recall that these two variables also reflect nonoverlapping subsets in the univariate SNK. Length of the mandibular toothrow is strongly linked with these two cranial variables in the first and second dimensions. Large size for these three variables are directly associated with the ordination of *S. monticolus* groups. Conversely, *S. vagrans* is characterized by small size of these variables. The Gulf and San Juan Island populations are intermediate, but are clearly aligned with *S. vagrans* centroids (Fig. 2). On the other hand, small size in greatest condylar depth (i.e., shallow) is associated with *S. vagrans,* whereas *S. monticolus* are deeper with respect to this measurement. These four variables also appear to account for the separation of the island and mainland populations of *S. monticolus.* They are joined in the second dimension by the length of the upper unicuspid toothrow, but negatively so.

MDA Geisser classification probabilities allow the evaluation of the relationships among groups by assigning each individual to the group it most closely resembles. These probabilities also may be used to assign individuals of uncertain identity to groups (i.e., diagnosis). Considering all groups (N = 402) irrespective of species, there were 266 (66.2%) hits and 136 (33.8%) misses (Table 4). A hit amounts to the correct assignment of an individual to its a priori group and a miss is an incorrect assignment. Given the overall sample size and number of groups, this is not an unreasonable result. Even more striking is the fidelity of individuals to their a priori species identity. For *Sorex vagrans* (N = 218), there were 211 (96.7%) hits and 7 (3.3%) misses. Likewise, for *Sorex monticolus* (N = 184), there were 182 (98.9%) hits and 2 (1.1%) misses. Of the seven misses for *S. vagrans,* six of these specimens occurred on the Gulf and San Juan Islands,

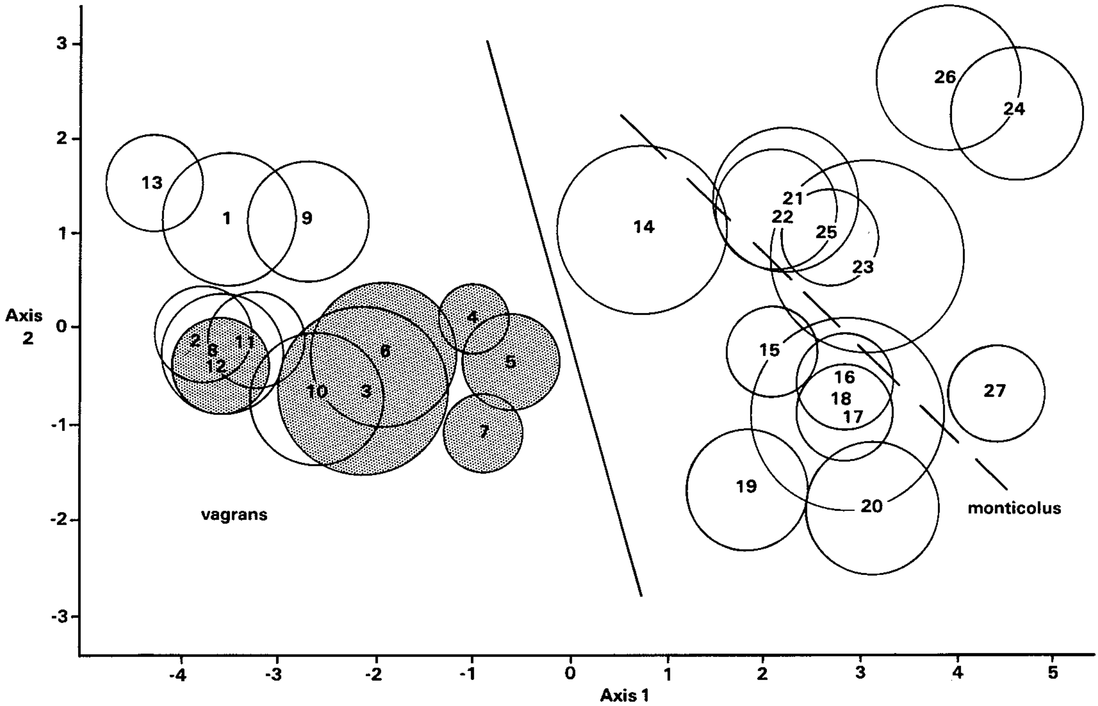

Figure 2. Canonical graphs from discriminant analyses (axes 1 by 2) for the 14 cranial variables examined. The 27 group centroids are plotted with their respective 95% confidence circles. Solid line denotes division between *Sorex vagrans* and *Sorex monticolus;* hatched line denotes separation of mainland and Vancouver Island samples of the latter species. Confidence circles of samples of *S. vagrans* from the Gulf Islands are stippled. See Specimens Examined section and legend to Fig. 1 for explanation of sample numbers.

Table 4. Classification table; rows are actual groups and columns are predicted groups. See Specimens Examined for explanation of sample numbers.

		S. vagrans													*S. monticolus*													
Sample #	N	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
V-1	9	6	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
V-2	20	1	12	1	0	0	0	0	1	1	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
V-3	8	0	0	6	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
V-4	32	0	1	0	24	2	0	1	0	1	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
V-5	17	0	0	0	1	9	2	1	0	0	0	1	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0
V-6	11	0	0	1	0	0	9	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
V-7	30	0	0	1	2	3	2	19	0	0	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
V-8	14	0	1	0	0	0	0	0	8	0	1	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
V-9	12	1	0	0	1	0	0	0	0	7	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
V-10	12	1	2	0	1	1	0	0	1	0	3	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
V-11	16	0	1	0	0	0	0	1	0	1	2	7	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
V-12	18	0	1	0	0	0	0	1	0	0	1	1	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
V-13	19	0	1	1	0	0	0	0	0	1	0	2	1	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0
M-14	7	0	0	0	0	1	0	0	0	0	0	0	0	0	5	0	0	0	0	1	0	0	0	0	0	0	0	0
M-15	23	0	0	0	0	0	0	0	0	0	0	0	0	0	1	18	0	1	1	1	0	0	0	0	0	0	1	0
M-16	19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	11	0	3	0	1	1	0	1	0	1	0	0
M-17	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	1	0	1	0	0	0	0	0	0
M-18	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	10	2	1	0	0	1	0	0	0	0
M-19	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	9	2	0	0	0	0	0	0	0
M-20	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	6	0	0	0	0	0	0	1
M-21	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	7	1	0	1	1	0	0
M-22	14	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	9	0	1	1	0	0
M-23	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1
M-24	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	1	0	1
M-25	20	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2	1	0	14	0	0
M-26	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	8	0
M-27	19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	17
Actual Size		9	20	8	32	17	11	30	14	12	12	16	18	19	7	23	20	6	16	14	10	11	14	6	10	20	9	19
Predicted		9	20	10	29	16	15	24	10	11	11	18	25	16	8	23	14	6	18	19	10	10	13	9	10	19	10	20

further supporting the univariate observation that these island populations approach *S. monticolus* in cranial size. The 83 specimens diagnosed by the MDA are listed in the Specimens Examined section under the appropriate taxon, and denoted in Fig. 1 as "m" or "v" at the collection locality. Since we obtained 97% and 99% correct assignments for *S. vagrans* and *S. monticolus*, respectively, in the original MDA, the confidence for the diagnosis also is high.

A plot of the centroids for the first and second canonical vectors is shown in Fig. 2; circles denote 95% confidence radii. *Sorex vagrans* (groups #1–#13) segregates from *Sorex monticolus* (groups #14–#27) along the first vector (separated by solid line in Fig. 2). The *S. monticolus* sample from Alberni (group #14) appears to be intermediate along the first axis and has the smallest crania of the *S. monticolus* populations (Table 1). Correspondingly, the sympatric population of *S. vagrans* (group #13) has the smallest cranial dimensions for that species as well. Within the *S. monticolus* groups in Fig. 2, the hatched line separates the Vancouver Island populations (groups #14–#20) from the remaining populations (groups #21–#27). There is no corresponding segregation of Vancouver Island and mainland populations of *S. vagrans*. However, most of the Gulf and San Juan Island populations (stippled in Fig. 2) segregate from the other *S. vagrans* centroids and ordinate toward the *S. monticolus* centroids. Consistent with past reports (Findley 1955, Cowan and Guiget 1956), this is an indication of their overall cranial size intermediate to *S. vagrans* and *S. monticolus*. The one exception to this is the centroid representing Saltspring Island (group #8), which ordinates with Vancouver Island and mainland samples.

DISCUSSION

Although *Sorex monticolus* and *Sorex vagrans* in southwestern British Columbia have been difficult to distinguish, the results of this morphometric study clearly show that they are quite distinct in discriminant space. *Sorex vagrans* is cranially the smaller of the two species. Widths of U^4–U^4 and M^2–M^2 are the best cranial variables to use in identification of the two species. Length of the mandibular toothrow and greatest condylar depth also are strong species discriminators. In the area under study, these variables may be more reliable than pigmentation of the upper incisors, which is useful in other regions where these two species overlap (Hennings and Hoffmann 1977, van Zyll de Jong 1982a).

At the intraspecific level, our results support the continued recognition of *Sorex monticolus isolatus* from Vancouver Island as distinct from *S. m. setosus* on the adjacent mainland. The Vancouver race has a longer skull and narrower palate than the mainland form. The shrews of this species from Texada Island were distinguished as *S. obscurus mixtus* by Hall (1938) and synonymized with *S. monticolus* by Hennings and Hoffmann (1977). Hall (1938) diagnosed these as being medium in size, dark colored, with a short hind foot (13 mm or less), and a long palate (7 mm or more). In his comparisons, he noted that the palate of *mixtus* is longer than that of either *isolatus* or *setosus*. Findley's (1955) characterization essentially followed Hall's. All of the Texada Island material (including the holotype) of this species was examined and included in this study. While the hind foot measurements are slightly shorter than those of *S. monticolus* from the surrounding areas, the palatal length is clearly intermediate between mainland and Vancouver Island samples. This is the case with all other cranial variables employed in this study except width across the incisors, which averaged widest ($\bar{x} = 1.63$) in the Texada shrews. Aside from this, the Texada Island sample ordinated with samples from the adjacent mainland. In view of this and in the absence of compelling evidence to the contrary, we hereby relegate *S. m. mixtus* to synonymy under *S. m. setosus*.

As with *Sorex monticolus*, the Vancouver Island and mainland populations of *S. vagrans* have been assigned to different geographic races, *S. v. vancouverensis* and *S. v. vagrans*, respectively. However, unlike *S. monticolus*, there appears to be little support of such a proposition for *S. vagrans*. How the somewhat larger shrews ("*monticolus*-like") from the Gulf and San Juan Islands fit into this picture was a primary concern of the study. Samples of shrews from San Juan, Lopez, Pender, Saturna, and Samuel Islands formed a loosely associated group which ordinated toward an intermediate position between *S. vagrans* and *S. monticolus* (Fig. 2). We have already shown that these shrews are clearly assignable to *S. va-*

grans although they tend to average larger in some cranial dimensions than either Vancouver Island or mainland samples of *S. vagrans*. This is especially true for the two "best" discriminators found in the study, widths of U^4–U^4 and M^2–M^2. These samples form an uninterrupted (no other samples interspersed among them) group at the large extreme for *S. vagrans* for these two variables (Table 2). They are also at the large extreme of *S. vagrans* for greatest length of skull, palatal length, mandibular length, height of the coronoid process, and length of mandibular toothrow, but they overlap with the *S. monticolus* sample from Alberni (Table 2). We do not believe that there is any particular relationship with the *S. monticolus* sample other than that it was usually at the small extreme for this species. As noted above, the sample from Saltspring Island was associated with Vancouver Island or mainland samples throughout. Again, in the absence of compelling evidence to the contrary, we herewith place *S. v. vancouverensis* in synonymy under *S. v. vagrans*. Although the Gulf and San Juan Island populations average somewhat larger in several cranial measurements, we feel that there is insufficient evidence at this time to support the recognition of these shrews as a separate and distinct subspecies of *S. vagrans*.

Of 10 individuals examined in the diagnosis from Whidbey Island, in the Puget Sound of Washington, nine were classified as *S. vagrans* (Specimens Examined). Variability for the tenth was apportioned among 19 samples, with 56% of the total assigned to *S. monticolus*. This, along with the fact that this individual possessed a *S. vagrans*-pattern of incisor pigmentation, suggests that the classification to *S. monticolus* is questionable, and more shrews from Whidbey Island must be examined before the presence of *S. monticolus* can be documented.

The results of this work raise some interesting biogeographic questions. On the one hand, we found that the Gulf and San Juan Island shrews are large *Sorex vagrans* rather than small *S. monticolus*. Hennings and Hoffmann (1977) list *Sorex monticolus* from Saturna Island (of the Gulf Islands) based on several specimens at the Museum of Comparative Zoology (MCZ). These individuals were excluded from the discrimination portion of our study, but were included in the diagnosis. The single intact specimen from MCZ is unquestionably *S. vagrans* (see Specimens Examined). The other specimens could also be identified as *S. vagrans* based either on incisor pigmentation, where possible, or on widths across U^4–U^4 and M^2–M^2. Therefore, we disagree with Hennings and Hoffmann (1977); our results suggest that *S. monticolus* apparently does not exist on any of the Gulf or San Juan Islands. Given its extensive distribution in the surrounding regions and western North America, this fact is unexpected. Of course, it is possible that this species simply has not yet been recorded from these islands. We are not inclined to accept this argument given the large number of shrews (all *S. vagrans*) that have been taken there.

Two additional explanations remain. First, *Sorex monticolus* simply did not have access to these insular regions. This species did not occur in the area at a time when it was possible to gain access to these islands either by dispersal or vicariance. Other possible deterrents to access might have involved ecological constraints in the form of physiographic barriers or microhabitat requirements (see below). Second, *S. monticolus* was formerly distributed on these islands and has since become extinct. Explanations for the extinction might include any or all of the arguments pertaining to competitive exclusion, changing resources, etc.

Hawes (1977) examined microhabitat affinities of the two species at Haney, British Columbia, on the mainland (samples #2 and #25 were made up entirely of her specimens). She found that *Sorex monticolus* was associated with stands of western hemlock (*Tsuga heterophylla*) on well-drained mor (raw humus) soils, whereas *Sorex vagrans* was associated with more mesic microhabitats, characterized by western red cedar (*Thuja plicata*), red alder (*Alnus rubra*), vine maple (*Acer circinatum*), and moder (partly decayed humus) soils. The distribution of *S. vagrans* on Vancouver Island, limited to the southern and eastern coasts and occasionally inland at low elevations [referred to as the Gulf Islands biotic area by Cowan and Guiguet (1956) and as the Georgia Depression physiographic subdivision by Armstrong et al. (1965)] might be explained by this affinity for warmer, more mesic sites. The physiography of much of the rest of Vancouver Island (inhabited by *S. monticolus*) is relatively steep, rugged, and cool, suggesting more well-drained soils and possibly excluding *S. vagrans*. Much of the west coast and central uplands of Vancouver Island are not represented by specimens of *Sorex* (Fig. 1) however. These areas must be sampled for shrews before definitive statements on the habitat preferences of the two species on the island can be made. Soils of several of the Gulf Islands have been characterized as being relatively mesic (Janszen 1977, 1981) and the climate as drier and warmer than surrounding regions (McKee 1972), which is more suggestive of the preferred habitat of *S. vagrans* (Hawes 1977).

The presence of *Sorex vagrans* on the Gulf and San Juan Islands is also interesting. Southwestern British Columbia (including Vancouver and adjacent islands) and adjacent Washington State were glaciated during the Pleistocene and have been ice-free only since 13,000 BP (Armstrong et al. 1965, Easterbrook 1969). Thus, *S. vagrans* can only have been present on the Gulf and San Juan Islands since that time. Data on sea levels in the area indicate that immediately following the retreat of the glaciers, water levels were considerably higher than today, receding to present levels around 9,000 yr BP. They continued to recede to approximately 35 ft below the present level between 9,000 and 5,000 yr BP, but since then, they have risen and been maintained very close to present levels (Easterbrook 1963, Mathews et al. 1970, Clague 1975). The depth of the waters surrounding the Gulf and San Juan Islands is considerably greater than 35 ft, and thus there are no data to suggest post-Pleistocene land connections.

The geologic data, thus, support a dispersal, not vicariant, mechanism for the post-glacial recolonization of the Gulf and San Juan Islands. This study, however, has only described the distribution and patterns of variation within *Sorex vagrans;* there is no phylogenetic component to the analysis, and thus we have not rigorously tested any historical biogeographic hypotheses.

It is not clear what the source population was for the recolonized islands; the area south of the Puget Lobe of the Cordillerian Glacier was unglaciated and certainly supported shrews. There is also evidence that the highest mountain ranges on Vancouver Island were ice-free, possibly acting as refugia for either or both *Sorex vagrans* and *Sorex monticolus* (Armstrong et al. 1965, Mathews et al. 1970). At this time it is not possible to reconstruct the biogeographic history of these species in the study area from the fossil record because no fossils of *Sorex* are known from the region (Kurtén and Anderson 1980; D. Nargosen, pers. comm.).

The final resolution of these questions requires more detailed phylogenetic information for both *Sorex vagrans* and *Sorex monticolus*. Also, information pertaining to the history of other faunal components and their evolution and distribution in this area, is needed. For example, do *S. vagrans* and *S. monticolus* belong to different faunal components that have had different biogeographic histories in this region? This and other similar questions are large time-scale considerations that have not yet been examined.

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SPECIMENS EXAMINED

Complete names for collections in which specimens are housed are given in the Acknowledgments; LACM refers to the Natural History Museum of Los Angeles County. Numbers designate samples to which the specimens were assigned (see Fig. 1).

Sorex monticolus setosus Elliott (samples #21–#27)
S. m. mixtus Hall

CANADA: *BRITISH COLUMBIA:* (#21): Quadra Island: (2 BCPM); 5.7 mi NE Heriot Bay (4 TCWC); 2.2 mi SE Heriot Bay (5 TCWC). (#22): Cortes Island: Smelt Bay Provincial Park (14 TCWC). (#23): Texada Island: 2 mi SSE Gillies, Harwood Point Park (3 TCWC); Vananda (3 MVZ). (#24): Lund, Malaspina Inlet (6 USNM); 3 mi E Lund, Okeover Arm Park (4 TCWC). (#25): Haney, UBC Research Forest (20 MVZ). (#26): Sumas (9 USNM). (#27): River Inlet, head (19 USNM).

Sorex monticolus isolatus Jackson (samples #14–#20)

CANADA: *BRITISH COLUMBIA:* (#14): Vancouver Island: Alberni Valley (1 MVZ); Cameron Lake, Cameron Land District (1 ROM); Golden Eagle Mine, 18 mi S Alberni (3 MVZ); Mt. Coakley, Cameron Land District, 4,200 ft (2 ROM). (#15): Southeast Brabant Island (3 BCPM); Dodd Island (1 BCPM); Haines Island (1 BCPM); Hand Island (1 BCPM); South Jaques Island (1 BCPM); Nantes Island (2 BCPM); South Nettle Island (1 BCPM); Onion Island (2 BCPM); North Turret Island (1 BCPM); Tzartus Island (5 BCPM); Turtle Island (5 BCPM). (#16): 4.4 mi N Zeballos (14 TCWC); 2.9 mi S Zeballos (5 TCWC). (#17): Vancouver Island: Brooks Peninsula, lagoon (2 BCPM); Brooks Peninsula, Pyrola Lake (2 BCPM); Brooks Peninsula, Orchard Point Beach (2 BCPM). (#18): Marble River Recreation Area (16 TCWC). (#19): Vancouver Island: 9 mi W Holberg, San Josef Campsite (14 TCWC). (#20): 0.7 mi N Winter Harbour (10 TCWC).

Diagnosed Specimens

CANADA: *BRITISH COLUMBIA:* Cox Island: Cape Scott (1 BCPM). Denman Island: 3 mi S, 2.5 mi E Post Office (3 TCWC). Gambier Island (1 UBC). Hohoae Island (2 BCPM). Hope Island (1 BCPM). Vancouver Island: Cache Creek (1 NMC); Cape Scott (1 NMC); Comox (4 NMC, 1 UBC); Goldstream (1 USNM); SE shore Gooseneck Lake (2 TCWC); Hardy Bay Flats (1 UBC); Keogh River (1 UBC); Long Beach (1 UBC); Nanaimo, mouth of Millstone Creek (2 USNM); Port Hardy (1 NMC); Rock Bay (2 NMC); Sayward (2 NMC); Shushartie (1 NMC); Snake Lake (1 NMC); Sooke (1 UBC); 1 mi S Thomas Pt (1 UBC); Tofino (3 UBC); Upper Campbell Lake (5 NMC).

Sorex vagrans vagrans Baird (samples #1–#13)
Sorex vagrans vancouverensis Merriam

CANADA: *BRITISH COLUMBIA:* (#1): Sumas (9 USNM). (#2): Haney, UBC Provincial Forest (20 MVZ). (#5): Saturna Island: (3 BCPM, 2 UBC); 0.2 mi W East Point Lighthouse (12 TCWC). (#6): Samuel Island (11 BCPM). (#7): North Pender Island: (5 UBC); Grimmer Road (10 BCPM); Hay Point (1 BCPM); Prior Centennial Provincial Park (11 TCWC). South Pender Island: (3 BCPM). (#8): Saltspring Island: Fulford Harbor (2 UBC); North End Road (12 BCPM). (#9): Vancouver Island: Colwood (2 BCPM); Goldstream (1 MVZ, 2 ROM, 2 USNM); Matheson Lake Provincial Park (1 TCWC); Victoria, Albert Head (4 BCPM). (#10): Vancouver Island: Duncan (1 BCPM); Duncan, Somenos Lake (9 BCPM); Lake Cowichan (1 UBC); Renfrew, Cowichan Lake (1 BCPM). (#11): Nanoose (10 BCPM); Nanaimo (6 NMC). (#12): Vancouver Island: Coombs, Dudley Marsh (8 BCPM); 1 mi N Englishman River Falls Provincial Park (10 TCWC). (#13): Vancouver Island: Alberni Valley (14 MVZ); Cameron Lake, Cameron Land District (2 ROM); 22.2 mi W Port Alberni, Lake Sproat (3 TCWC). UNITED STATES: *WASHINGTON:* (#3): San Juan Co.: Lopez Island: (2 PSMNH); Richardson (6 USNM). (#4): San Juan Co.: San Juan Island: (3 PSMNH, 14 UW); American Camp National Historic Park (3 UW); English Camp (2 UW); 18 km NW Friday Harbor, Roche Harbor (4 UW); 3 mi N, 3 mi W Friday Harbor, Lakedale Campground (3 TCWC, 1 UW); 19 km W Friday Harbor (2 UW).

Diagnosed Specimens

CANADA: *BRITISH COLUMBIA:* Breakwater Island (1 BCPM). Gabriola Island (2 BCPM). Galiano Island (1 BCPM). Mayne Island: 0.7 mi SW (by road) Mayne (6 TCWC). Saturna Island (1 MCZ). Thetis Island (5 BCPM). Valdez Island (2 BCPM). Vancouver Island: Departure Bay (1 USNM); SE shore Gooseneck Lake (1 TCWC); Sayward (1 NMC); Upper Campbell Lake (2 NMC). Westham Island (3 BCPM). UNITED STATES: *WASHINGTON:* Island Co.: Whidbey Island, Deception Pass State Park (4 TCWC); Whidbey Island, Greenbank (6 LACM). San Juan Co.: Blakely Island (1 PSMNH); Orcas Island: Eastsound (3 USNM); Westsound (1 PSMNH); E side Westsound Bay (1 PSMNH); Stuart Island (1 PSMNH).

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