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NICHE RELATIONSHIPS OF TWO SYNTOPIC SPECIES OF SHREWS, *SOREX FUMEUS* AND *S. CINEREUS,* IN THE SOUTHERN APPALACHIAN MOUNTAINS

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The smoky shrew (*Sorex fumeus*) and the masked shrew (*S. cinereus*) are common soricids in mature southern Appalachian hardwood forests. To better understand the role of body size and niche relationships in these syntopic species, 12 50- by 50-m plots were established in the Pisgah National Forest of western North Carolina. Trapping was conducted from August through November 1996 and from March through August 1997 using Y-shaped drift fences with associated pitfalls. Prey items and microhabitat components were measured to examine correlations with abundance of shrew species. Total shrew captures ($n = 176$) included 105 (59.7%) *Sorex fumeus* and 41 (23.3%) *S. cinereus.* Smoky shrews were significantly larger than masked shrews in both mass and body length. Stepwise multiple regression analyses determined that a combination of litter moisture, class 5 coarse woody debris (CWD), and number of invertebrates and mountain dusky salamanders (*Desmognathus ochrophaeus*) was the best predictor of *S. fumeus* abundance ($R^2 = 92.8\%$), whereas *S. cinereus* abundance was best explained by a combination of litter moisture, leaf-litter depth, class 3 CWD, and invertebrate size ($R^2 = 57.7\%$). Microhabitat niche breadth (MB) of *S. cinereus* (2.11) was narrower than that of *S. fumeus* (2.27). Linear discriminant function analysis revealed significant ecological separation between the 2 shrew species ($D^2 = 0.62$), despite high levels of microhabitat niche overlap (MO = 65.7%). The larger body size of smoky shrews may provide an advantage in that it can use parts of the microhabitat that are inaccessible to its smaller congener, thereby reducing interspecific competition.

Key words: Appalachian mountains, body size, niche, resource partitioning, shrews, *Sorex*

Body size is believed to be an important, organizing factor in the community structure of many closely related coexisting vertebrate species (Asplund 1974; Bowers and Brown 1982; Dickman 1988; Krzysik 1979). In multispecies communities of shrews (Insectivora: Soricidae), species sort into 3 general size classes: large (>10 g), medium (5–10 g), and small (<5 g). These communities are not random assemblages but rather appear to follow a species-assembly rule that predicts that each of the 3 size niches (Kirkland and Snoddy 1999) should be filled with a single common species be-

fore a 2nd less common species of the same size class is present (Fox and Kirkland 1992; Kirkland 1991). Interspecific competition is the most likely mechanism responsible for these nonrandom associations (Fox and Kirkland 1992). Ecological separation in shrews may be achieved through differential exploitation of common resources by species of different size classes (Churchfield and Sheftel 1994; Ellenbroek 1980; Hawes 1977; Terry 1981; Yashino and Abe 1984). Larger body size may convey a competitive advantage by facilitating use of a wider range of prey items and higher-quality microhabitats inaccessible to

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more diminutive congeners (Dickman 1988; Fox and Kirkland 1992), resulting in a broader niche breadth (Churchfield 1991; Churchfield and Sheftel 1994; Wilson 1975).

Although microhabitat selection by soricids is strongly influenced by environmental moisture and protection from predators (Getz 1961; Seagle 1985), differences can reflect foraging behavior and diet as determined by body size (Churchfield 1991). The most common difference in foraging activity among syntopic shrews is stratificational segregation of the forest floor (Churchfield and Sheftel 1994; Ellenbroek 1980; Terry 1981; Yashino and Abe 1984). Although shrews have generalized diets because of their high metabolic rate (Aitchison 1987; Hamilton 1930), the larger member of a species pair is often more fossorial and may consume a greater proportion of large hypogeal prey, such as earthworms (Churchfield 1991; Churchfield and Sheftel 1994; Kirkland 1991; Whitaker and Cudmore 1987; Whitaker and French 1984). Shrew diversity should therefore depend on availability of different foraging microhabitats (Dickman 1988; Fox and Kirkland 1992). An understanding of how forest-floor resources are partitioned among syntopic species pairs is important in determining niche relationships of shrews and structure of soricid assemblages.

My goal was to determine patterns of resource use in 2 congeneric species of shrews (*Sorex* sp.) that co-occur in the higher elevations of the southern Appalachians. Soricid assemblages in this region tend to consist of 4 species of decreasing size: the northern short-tailed shrew (*Blarina brevicauda*), smoky shrew (*Sorex fumeus*), masked shrew (*S. cinereus,*) and pygmy shrew (*S. hoyi*), although occasionally there are others (Ford et al. 1997; Laerm et al. 1999). The masked shrew and smoky shrew are closely related species that are abundant throughout their ranges and are broadly sympatric. The potential for interspecific intolerance (Cawthorn 1994; Jameson 1949) due to their coexistence in a variety of habitats and their relative similarity in body size and diet (Hamilton 1930; Huggins and Kennedy 1989; Whitaker and Cudmore 1987; Whitaker and French 1984) make these species interesting subjects for studies of niche relationships. I tested hypotheses that in commonly occurring, syntopic species pairs of *Sorex* members sort into 2 distinct body size classes, larger body size conveys an advantage in terms of resource accessibility, and ecological separation between species is determined by body size and differential use of foraging microhabitat.

MATERIALS AND METHODS

Research was conducted in the Gingercake Creek drainage of the Pisgah National Forest, Burke County, western North Carolina. This area was characterized by steep (20–38°) slopes with numerous streams and seepages. Vegetation consisted primarily of mixed hardwoods with an understory of *Rhododendron* and mountain laurel (*Kalmia latifolia*). Stand age is about 55 years old, according to a United States Forest Service CISC database, and elevations averaged about 787 m (757–818 m). A more detailed description of the habitat is available in Brannon (1997).

Twelve 50- by 50-m plots were established, positioned with boundary lines parallel and perpendicular to prevailing contours. In the center of each plot was a drift fence array consisting of 3 arms of 3.0-m-long by 61-cm-tall aluminum flashing arranged in a "Y" with one 20-l pitfall (5-gallon plastic bucket) located at each end and another at the central intersection. Each of the 4 pitfalls was partially filled with water to drown captures and thus prevent predation within traps. In addition to effectively capturing shrews (Kirkland and Sheppard 1994), that method of trapping was useful for sampling prey items such as surface-active macroinvertebrates (Dickman 1988; Ryan 1986) and salamanders (Gibbons and Semlitsch 1981). A 50- by 50-cm board, elevated about 10 cm with nails, was placed over each pitfall to prevent accumulation of rain and leaves. Pitfalls were closed with tight-fitting plastic lids when not in use.

Trapping was conducted for 6 consecutive days each month from August to November

TABLE 1.—Nine resource variables used for backwards-elimination, stepwise multiple regression and linear discriminant function analyses.

Resource variable	Description
INVERTN	Total number of invertebrates
INVERTG	Average invertebrate size (mass in grams)
DESMOG	Total number of *Desmognathus ochrophaeus*
HRBCVR	Percentage herbaceous cover
CWD3	Volume of decay class 3 coarse woody debris
CWD4	Volume of decay class 4 coarse woody debris
CWD5	Volume of decay class 5 coarse woody debris
LITDEPTH	Leaf-litter depth (cm)
LITMOIST	Percentage moisture content of leaf litter

1996 and from March to August 1997. No collecting was done from December 1996 to February 1997 because of site inaccessibility. On a daily basis during each trapping period, vertebrates were removed from traps and taken immediately back to the lab, where they were measured, identified to species, and fixed in 10% formalin. All vertebrate specimens were later transferred to 70% ethanol and deposited in the collections of Appalachian State University.

Because most shrews take whatever prey they encounter within the constraints imposed by their body dimensions (Churchfield 1991), all invertebrate taxa were considered potential food items. Invertebrates were strained from pitfalls on the last day of each trapping period. Total number of invertebrates for each plot was counted, and individuals were identified to order and weighed to obtain the average prey size (mass in grams). Although shrews are known to also consume salamanders (Hamilton 1930, 1940; Whitaker and Cudmore 1987), only the mountain dusky salamander (*Desmognathus ochrophaeus*) was considered as potential prey because it is small and terrestrial and lacks noxious skin secretions of other, less palatable species (Brodie et al. 1979). Stomach contents of shrews were not examined.

Microhabitat features (Table 1) to be measured were selected on the basis of their probable importance to shrews in providing environmental moisture, prey abundance, and protective cover. Those included volume of coarse woody debris (CWD; fallen logs), percentage herbaceous cover, and leaf-litter depth and moisture content (Doyle 1987; Dueser and Shugart 1978; Lee 1995; Seagle 1985; Yahner 1986). Three 50-m transects were established at 12.5-m intervals across contours within each plot. Those transects

were used to determine relative amounts of CWD within plots using a line-intercept method. Diameter and length of any fallen log ≥10 cm in diameter at the point of intersection along the transect were recorded. Any branches ≥10 cm in diameter were treated as separate logs. Stage of decomposition of each log also was ranked from class 1 CWD for recently fallen trees with support points intact and little evidence of decay to class 5 CWD for extremely decomposed, soft, moist logs that were partially buried by soil and forest litter (Maser et al. 1979; Petranka et al. 1994). Decomposition classes differ in their ecological function (Maser et al. 1979). Because classes 1 and 2 logs are suspended above ground, have not undergone significant decay, and are uncommon in mature forests, they were considered to be unimportant as foraging microhabitat (Petranka et al. 1994).

Herbaceous cover, leaf-litter depth, and litter moisture content were measured every trapping period because of seasonal variability. At 5-m intervals along the middle transect, a 1-m² quadrat was established for a total of 10 quadrats per plot. Percentage cover of herbaceous plants <0.5 m high was estimated visually for each quadrat and averaged to obtain percentage cover per plot. Leaf litter was defined as nonwoody material and woody stems <10 mm in diameter. Average litter depths for each plot were measured by simply pressing a metric ruler through the litter to the A-horizon of the soil at each of the 10 quadrats. To obtain measurements of litter moisture, a 0.25-m² sample was collected randomly from each plot on 3 days during each trapping period. Samples were weighed immediately on return to the lab (wet mass), dried at 100°C for 24 h, and reweighed (dry mass). Litter moisture content was calculated as wet mass mi-

nus dry mass and expressed as a percentage of wet mass.

Differences in mass and body length (excluding tail length) between shrew species were examined using a 1-way analysis of variance. Microhabitat niche breadth (MB) for each species was calculated as

$$MB = \sum_j - p_{ij} \ln p_{ij}$$

where p_{ij} was the proportion of the total number of captures for species i captured at plot j (Yahner 1986). Microhabitat niche overlap (MO) between species pairs was calculated as

$$MO = 1 - 0.5 \sum_j |p_{xj} - p_{yj}|$$

where p_{xj} and p_{yj} were the proportions of total captures of species x and species y in plot j, respectively (Schoener 1968).

Combinations of resource variables (Table 1) may explain variation in shrew species abundance more adequately than can an individual predictor. The importance of each combination was determined by regressing the number of individuals captured per plot (dependent variable) on subsets of predictors (independent variables), using backwards-elimination, stepwise multiple regression (Minitab, Inc. 1996). That method began with a model containing a combination of all predictors and systematically eliminated those variables that contributed least to the overall regression equation. At each step, an F-statistic for each predictor remaining in the model was calculated, and the variable with the greatest amount of error was removed. That was equivalent to excluding the variable with the smallest partial correlation. That procedure was continued until additional removal of a predictor resulted in a significant reduction in the percentage of variation explained by the overall equation (R^2).

To verify ecological separation between species, the original 9 predictor variables were entered into a linear discriminant function analysis (Minitab, Inc. 1996). That procedure predicted species membership based on a set of continuous variables, with g = number of groups (species) and p = number of predictors. Stepwise models sequentially extracted those orthogonal variables most capable of separating species by maximizing among- to within-groups sums of squares and provided the Mahalanobis distances (D^2) or sample-squared distances between group means. Mahalanobis distances were used to test if population means showed significant segregation along the resource gradient by referring the equation

$$\left(\frac{n_1 + n_2 - p - 1}{(n_1 + n_2 - 2)p} \right) \left(\frac{n_1 n_2}{n_1 + n_2} \right) D^2$$

to an F-distribution with $v_1 = p$ and $v_2 = n_1 + n_2 - p - 1$ degrees of freedom and with n_1 and n_2 representing the sample size of each of the 2 shrew species, respectively (Johnson and Wichern 1992).

RESULTS

During 2,544 trap-nights, 176 shrews were captured. Of that total, 105 (59.7%) were *Sorex fumeus,* and 41 (23.3%) were *S. cinereus.* The remaining soricids consisted of 15 (8.5%) *Sorex hoyi,* 14 (8.0%) *Blarina brevicauda,* and 1 (0.6%) rock shrew, *Sorex dispar.* Other small mammals collected included 192 white-footed mice (*Peromyscus leucopus*), 115 woodland jumping mice (*Napeozapus insignis*), 16 red-backed voles (*Clethrionomys gapperi*), 11 golden mice (*Ochrotomys nuttalli*), and 2 chipmunks (*Tamias striatus*). Pitfall traps also captured 259 salamanders (65 *Desmognathus ochrophaeus*), 4 frogs, and 1 snake. A total of 9,486 invertebrates were collected. The most abundant taxa in decreasing order were Orthoptera, Coleoptera, Hymenoptera, lepidopteran larvae, Thysanura, spiders, millipedes, centipedes, earthworms, and snails, with each plot yielding similar proportions of each taxon.

Sorex fumeus and *S. cinereus* differed in mass ($F = 675.01$, *d.f.* = 1, 144, $P < 0.01$) and body length ($F = 283.14$, *d.f.* = 1, 144, $P < 0.01$). Mean mass (± 1 *SE*) was 8.47 $\pm$ 0.77 g for *S. fumeus* and 4.32 $\pm$ 0.85 g for *S. cinereus.* Mean body length was 55.3 $\pm$ 3.8 mm for *S. fumeus* and 46.5 $\pm$ 2.5 mm for *S. cinereus.*

Microhabitat niche breadth of *S. cinereus* (MB = 2.11) was narrower than that of *S. fumeus* (MB = 2.27). Despite high microhabitat niche overlap (MO = 65.7%), some resource partitioning was determined to exist between the 2 species. A combination of

TABLE 2.—Results of backwards-elimination, stepwise multiple regression analysis for 2 shrew species.

Species	Resource variable (x)	F	Partial coefficient	Regression constant	R^2
Sorex fumeus	LITMOIST	25.50	1.04	−31.38	0.928
	CWD5	18.15	−2.02		
	INVERTN	27.67	−0.01		
	DESMOG	6.10	−0.27		
S. cinereus	LITMOIST	2.53	0.34	−64.43	0.577
	LITDEPTH	6.92	0.11		
	CWD3	0.48	1.61		
	INVERTG	2.53	4.51		

litter moisture, class 5 CWD, and number of invertebrates and mountain dusky salamanders was the best predictor of S. fumeus abundance ($R^2 = 92.8\%$), whereas abundance of S. cinereus was best predicted by a combination of litter moisture, leaf-litter depth, class 3 CWD, and invertebrate size ($R^2 = 57.7\%$; Table 2). Linear discriminant function analysis showed that means of the microhabitat niches for the 2 species were significantly separated ($D^2 = 0.62$, $F = 1.92$, d.f. $= 9, 136$, $P < 0.05$), with 69.2% of the original observations correctly classified.

DISCUSSION

Morphological and behavioral differences can act to reduce interspecific competition between syntopic congeners. There may be a limit on how similar in size 2 co-occurring species can be and still avoid competitive exclusion. A ratio of 1.3 for length and 2.0 for body mass has been suggested as an estimate of the degree of difference necessary for 2 species to coexist syntopically in high numbers (Hutchinson and MacArthur 1959). These values correspond almost exactly to the size difference ratios observed for S. fumeus and S. cinereus in this study (1.2 for body length and 2.0 for mass). Such differences in body sizes facilitate coexistence of syntopic shrew species by allowing differential exploitation of foraging microhabitat and associated prey items (Churchfield 1991; Churchfield

and Sheftel 1994; Fox and Kirkland 1992; Kirkland 1991).

In multispecies communities, partitioning of the forest-floor microhabitat occurs along a vertical gradient in relation to differences in shrew body size (Kirkland 1991). Although there is a tendency for small species to take smaller, epigeal (litter-dwelling) prey and for large species to take larger, more hypogeal (soil-dwelling) prey (Churchfield and Sheftel 1994; Kirkland 1991), diet of shrews is not correlated clearly with body size (Churchfield and Sheftel 1994). Shrews have very generalized diets because of their high energy demands and rates of food consumption (Aitchison 1987), which largely reflect variable availability of different prey types (Churchfield 1991; McCay and Storm 1997). Despite high levels of dietary overlap in terms of taxonomic categories, shrews differ in the proportions that they consume each category (Churchfield 1991; Hamilton 1930; Whitaker and Cudmore 1987; Whitaker and French 1984). Size and location of prey may be more important than taxonomic group in reducing interspecific competition (Churchfield 1991; Kirkland 1991).

Diminutive species such as S. cinereus are better equipped to feed on tiny, surface- and litter-active invertebrates, while larger, more robust shrew species may be semifossorial (Kirkland 1991; Ryan 1986; Whitaker and French 1984). While some dietary overlap exists between smoky shrews and

masked shrews (Hamilton 1930; Whitaker and French 1984), *S. fumeus* consumes considerably more large prey, such as earthworms and centipedes, than does *S. cinereus* (Whitaker and Cudmore 1987), which reflects a partially hypogeal foraging mode (Kirkland 1991). Smoky shrews also consume a greater proportion of salamanders (Hamilton 1930). Although small body size may preclude diminutive species from efficiently handling and consuming large prey (Getz 1961; McCay and Storm 1997), the reverse is much less true (Wilson 1975). Thus, the smaller *S. cinereus* is limited more greatly by prey size than the larger *S. fumeus*, whereas the latter may only be limited by prey abundance. Increased body size may provide an advantage over smaller species by allowing use of a wider range of foraging microhabitats and food items (Dickman 1988).

Although dietary analyses were not performed in this study, correlations with microhabitat suggest that differences in foraging modes do exist between smoky shrews and masked shrews based on body size. Shrews require microhabitats with high levels of environmental moisture because it affects their water balance and availability of prey (Getz 1961; Kirkland 1991; Wrigley et al. 1979). Species exploit the best foraging microhabitats available to minimize energy expenditure and risk of predation (Barnard and Brown 1987; Hanski 1989; Seagle 1985; Yahner 1986). Although both species of shrews actively forage on the forest floor and in leaf litter, especially during periods of moderate rainfall (Brannon 1997; Kirkland et al. 1998; Vickery and Bider 1978), in this study only *S. fumeus* abundance was associated with class 5 CWD. Similarly, McCay et al. (1998) found smoky shrews to selectively use microhabitat structures such as logs and rocks, and Yahner (1986) found a negative relationship between logs and masked shrews. Although other forms of CWD and a deep layer of leaf litter can provide moisture, abundant prey, and protective cover

(Ash 1995; Gist and Crossley 1975; Lee 1995), logs that are in the later stages of decay may be optimal microhabitats because they also can offer a stable microenvironment refuge during periods of prolonged drought (Jaeger 1980; Maser et al. 1979). The spongy texture of extremely decomposed logs may enable burrowing by larger shrews while serving as both a moisture reservoir and a source of a wide variety of soil-dwelling invertebrates (Maser et al. 1979; McComb and Rumsey 1982) and salamanders (Jaeger 1980; Petranka et al. 1994).

Because of their high levels of rainfall, moderate temperatures, and abundant leaf litter, southern Appalachian hardwood forests generally are more productive than many other forests in terms of invertebrate biomass (Gist and Crossley 1975). Larger species of shrews have greater per capita food requirements than smaller species. Numerical dominance of shrew species may therefore be determined in part by habitat productivity (Hanski 1994; Kirkland and Snoddy 1999). Assuming no difference in foraging efficiency between species of different sizes, larger species should dominate in higher-quality habitats and vice versa. Typically, more generalized species are numerically dominant in multispecies communities of soricids (Churchfield 1991; Laerm et al. 1999).

In this study, *S. fumeus* was more abundant than *S. cinereus* and had a broader niche breadth, which may be indicative of its larger size and ability to utilize a greater variety of microhabitats and prey types. Conversely, the diminutive size of *S. cinereus* restricts its use of optimal foraging microhabitats and prey items in this habitat type (Laerm et al. 1999) and may make it competitively inferior to its larger congener (Dickman 1988; Fox and Kirkland 1992; Hawes 1977), resulting in a more compressed niche breadth (Churchfield and Sheftel 1994). However, if moisture and invertebrate prey are generally abundant, species may share a large proportion of the

available resources without the danger of competitive exclusion. Considerable niche overlap between congeners, as in this study between *S. fumeus* and *S. cinereus,* may often be correlated with reduced competition. Maximum tolerable overlap in niches should be lower in intensely competitive situations than in environments with a surplus of resources or low demand:supply ratios (Pianka 1972). It should be remembered, however, that shrews are not the only abundant forest-floor predators to use these resources (Jaeger 1980; Petranka et al. 1994).

Results of this study are consistent with the idea that body size is an important factor in the structuring of soricid communities (Churchfield 1991; Fox and Kirkland 1992; Kirkland 1991). Larger size may facilitate use of some prey items and foraging microhabitats that are inaccessible to smaller congeners (Dickman 1988). Coexistence of syntopic shrews is therefore dependent on different-sized species exploiting measurably different parts of their common environment, or distinct microhabitat niches.

ACKNOWLEDGMENTS

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