CONTIGUOUS ALLOPATRY OF THE MASKED SHREW AND SOUTHEASTERN SHREW IN THE SOUTHERN APPALACHIANS: SEGREGATION ALONG AN ELEVATIONAL AND HABITAT GRADIENT

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Abstract: Southeastern shrew (Sorex longirostris) and masked shrew (Sorex cinereus) distributions converge in the southern Appalachians. A 306,454-pitfall-trapnight survey in Alabama, Georgia, North Carolina, and South Carolina documented the presence of southeastern shrews in the Cumberland Plateau, Ridge and Valley, Upper Piedmont, and Blue Ridge physiographic provinces. Southeastern shrews occur at low elevations (\(\bar{x} = 524.9\) m), primarily in xeric upland hardwood, mixed pine (Pinus spp.)-hardwood, and pine forests. Masked shrews only occur in the Blue Ridge at high elevations (\(\bar{x} = 1,069.6\) m), primarily in mesic cove hardwood, northern hardwood, and montane streamside forests. Upper elevation limits of southeastern shrew and lower elevational limits of masked shrew show an inverse relation with latitude relative to shrew collections from farther north along the Appalachians. Southeastern shrews and masked shrews are allopatric in the southern Appalachians except in the Blue Ridge where the species exhibit contiguous allopatry, based on elevation and habitat associations.

Key Words: Elevational segregation; Habitat segregation; Masked shrew; Southeastern shrew; Sorex cinereus; Sorex longirostris; Southern Appalachians.

¹ Deceased.
INTRODUCTION

The masked shrew (*Sorex cinereus*) and the southeastern shrew (*Sorex longirostris*) are largely allopatric in the eastern United States (French, 1980a, b; Junge and Hoffman, 1981; van Zyll de Jong, and Kirkland, 1989; Jones et al., 1991). However, the two species are sympatric in the Midwest (Mock and Kivett, 1980; Rose, 1980; Greer, 1989; Hoffmeister, 1989) and central and southern Appalachians from West Virginia to Georgia (Pagels and Handley, 1989; Jones et al., 1991; Ford et al., 1994; Laerm et al., 1999). The two species are segregated by habitat in the Midwest where the two species are rarely syntopic (French, 1980c; Greer, 1989; Hoffmeister, 1989). Similarly, in the Appalachians of western Virginia, southeastern shrews and masked shrews are contiguously allopatric, segregated by altitude (Pagels and Handley, 1989). Moreover, the distributional demarcation between the austral southeastern shrew and the boreal masked shrew indicates a general north to south gradient of increasing altitudinal separation in the central Appalachians of Virginia (Pagels and Handley, 1989) through the southern Appalachians of northern Georgia and western North Carolina (Laerm et al., 1999). Recent soricid surveys in the southern Appalachians have provided new insights into the habitat associations of both species (Ford et al., 1994; Laerm et al., 1995; Laerm et al., 1999). We present the results of an analysis of southeastern shrew and masked shrew distributional data across four physiographic provinces, seven major overstory vegetation types, and elevation in the southern Appalachians of Alabama, Georgia, North Carolina, and Tennessee.

METHODS AND MATERIALS

Pitfall trap surveys were conducted at 231 sites in the southern Appalachians from July 1993 to August 1997. We surveyed 166 sites in the Blue Ridge of Georgia, North Carolina, and South Carolina, 36 sites in the Upper Piedmont of Georgia and South Carolina, 11 sites in the Ridge and Valley of Georgia, and 18 sites in the Cumberland Plateau of Alabama and Georgia (Fig. 1). Pitfall trapping represents the best soricid collection technique (Prince, 1941; Wolfe and Esher, 1981; Handley and Kalko, 1993; Ford et al., 1994; Kirkland and Sheppard, 1994). At the majority of sites, 20 (0.95—1) containers were placed to serve as pitfalls at or below ground level adjacent to forest floor debris such as downed coarse woody debris or emergent rock. Pitfalls were spaced approximately 7—10 m apart in a transect design either parallel with an adjacent stream or directly along the contour (Ford et al., 1994). Pitfalls were placed at 22 sites along aluminum drift-fence arrays (Ford et al., 1997, 1999). Pitfall trapping along natural cover and drift-fences provide similar estimates of soricid relative abundance and community assemblage in the southern Appalachians (McCay et al., 1998). All pitfalls were 25% filled with 5% formalin to preserve specimens. Collection duration at each site was ≥30 days and pitfalls were checked weekly or biweekly basis. Specimens were removed and preserved in 70% alcohol. Skulls were examined on all soricids not readily identified by external morphology (Laerm et al., 1999). Shrews from this study were placed in the Georgia Museum of Natural History collections.

We recorded elevation and placed pitfall sites into one of seven general forest
community types. Elevations ranged from 1,600 m in the Blue Ridge to <275 m at sites in the Cumberland Plateau, Ridge and Valley, and Upper Piedmont. Forest community types were characterized as: cove hardwoods, northern hardwoods, montane streamside, upland hardwood, mixed pine (Pinus spp.)–hardwood, pine, and riverine. Most (225 of 231) survey sites were forest stands ≥50–60 yr old. Six cove hardwood stands surveyed were 15–25 yr old and one upland hardwood site had been clearcut a few months prior to our survey. Stand age at these sites appeared to have little influence on shrew abundance (Ford et al., 1994, 1997). Cove hardwood communities occurred in sheltered concave landforms and north-facing slopes to approximately 1,200 m throughout the southern Appalachians, although they were most abundant in the Blue Ridge and Upper Piedmont physiographic provinces. Cove hardwoods, floristically rich and mesic communities, were dominated by yellow-poplar (Liriodendron tulipifera), northern red oak (Quercus rubra), yellow buckeye (Aesculus octandra), and basswood (Tilia americana). Northern hardwoods occurred on north-facing slopes and sheltered headwater ravines above cove hardwood communities at mid- to high elevations (>1,200 m) and across a variety of aspects and landforms at the highest elevations in the Blue Ridge. These communities were dominated by yellow birch (Betula alleghaniensis), black birch (B. lenta), American beech (Fagus grandifolia), and northern red oak often with dense understories of rosebay rhododendron (Rhododendron maximum) on the most mesic sites and striped maple (Acer pensylvanicum) and flame azalea (R. calendulaceum) on the less mesic sites. Montane streamside communities characterized by eastern hemlock (Tsuga canadensis)-white pine (P. strobus) overstories and dense understories of rosebay rhododen-
dron occurred in the Blue Ridge and along some sheltered Upper Piedmont streams. Upland hardwood communities occurred throughout at all elevations on submesic to xeric sites. Dominant overstory species include: northern red oak, white oak (O. alba), black oak (O. velutina), hickories (Carya spp.), red maple (Acer rubrum), and blackgum (Nyssa sylvatica). Shrub layers of American chestnut (Castanea dentata), Fraser’s magnolia (Magnolia fraseri), and rosebay rhododendron often are present in mesic upland hardwood sites, whereas more xeric sites were dominated by mountain laurel (Kalmia latifolia). Mixed-pine hardwood communities occurred on exposed ridges and sideslopes with southern or southwestern aspects throughout. Although variable across site moisture regimes, aspect, elevation, and disturbance histories, these communities were dominated by chestnut oak (O. prinus), scarlet oak (O. cocinea), blackgum, red maple, white pine, pitch pine (P. rigida), Virginia pine (P. virginiana), shortleaf pine (P. echinata), and table mountain pine (P. pungens). Thick growth of mountain laurel, greenbrier (Smilax spp.), or blueberry (Vaccinium spp.) often occurs in the understory. Pine communities dominated by pure or mixed stands of Virginia pine, shortleaf pine, and loblolly pine (P. taeda) occurred at low elevations in the Cumberland Plateau, Ridge and Valley, and Upper Piedmont physiographic provinces. Riverine communities occurred at low elevations along larger streams and rivers and were characterized by black willow (Salix nigra), alder (Alnus serrulata), river birch (B. nigra), and sweetgum (Liquidambar styraciflua) overstories. Bare scoured cobble and well-drained sandy outwashes were common.

Southeastern shrew and masked shrew collections are reported per 100 trapnights by physiographic province and forest community type. Logistic regression analysis (Gore, 1988; Walker, 1990) was used to assess effect of elevation and forest type on southeastern shrew and masked shrew distributions in the southern Appalachians. Collection sites were characterized as having either southeastern shrews or masked shrews present or absent. Site elevation was divided by 300 so that logistic regression odds ratio values could be assessed in meaningful 300 m (approximately 1,000 ft) elevation intervals. Because site moisture is an important factor influencing soricid distribution and abundance (Getz, 1961), we ranked the seven forest community types surveyed into five site moisture classes. We assigned values, mesic to xeric, of five to cove hardwood and montane streamside communities, four to northern hardwood communities, three to upland hardwood and riverine communities, two to mixed pine-hardwood communities and one to pine communities.

RESULTS

Two hundred seventeen southeastern shrews were collected at 60 sites and 2,442 masked shrews were collected at 101 sites following 306,454-pitfall trapnights (Fig. 1). Masked shrews only were collected in the Blue Ridge (Table 1). Southeastern shrews were collected in each physiographic province surveyed (Table 1). Southeastern shrews and masked shrews were not syntopic within the Blue Ridge. Southeastern shrews were collected in all forest community types except northern hardwoods whereas masked shrews were collected in all forest community types except the pine and riverine communities (Table 2). Mean (±2 SE) site elevation where southeastern shrews were present was 524.9 ± 46.5 m, range = 200–923 m. Mean site elevation where masked shrews were present was 1,069.6 ± 49.7
Table 1. Presence of masked shrew (Sorex cinereus) and southeastern shrew (S. longirostris) across physiographic provinces in the southern Appalachian region of Alabama, Georgia, North Carolina, and South Carolina, 1993–1997.

<table>
<thead>
<tr>
<th>Province</th>
<th>Total Sites</th>
<th>Trapnights</th>
<th>Masked shrew</th>
<th>Southeastern shrew</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blue Ridge</td>
<td>166</td>
<td>230,970</td>
<td>101 sites (2,442)</td>
<td>19 sites (53)</td>
</tr>
<tr>
<td>Cumberland Plateau</td>
<td>18</td>
<td>36,212</td>
<td>0 sites (0)</td>
<td>7 sites (30)</td>
</tr>
<tr>
<td>Piedmont</td>
<td>36</td>
<td>33,901</td>
<td>0 sites (0)</td>
<td>26 sites (92)</td>
</tr>
<tr>
<td>Ridge and Valley</td>
<td>11</td>
<td>5,434</td>
<td>0 sites (0)</td>
<td>3 sites (42)</td>
</tr>
<tr>
<td>All</td>
<td>231</td>
<td>306,454</td>
<td>101 sites (2,442)</td>
<td>55 sites (217)</td>
</tr>
</tbody>
</table>

Total specimens collected.

Table 2. Presence of masked shrew (Sorex cinereus) and southeastern shrew (S. longirostris) across forest type in the southern Appalachian region of Alabama, Georgia, North Carolina, and South Carolina, 1993–1997. Forest type is arranged from most mesic to most xeric.

<table>
<thead>
<tr>
<th>Forest type</th>
<th>Total Sites</th>
<th>Trapnights</th>
<th>Masked shrew</th>
<th>Southeastern shrew</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cove hardwood</td>
<td>43</td>
<td>97,956</td>
<td>24 sites (341)</td>
<td>3 sites (5)</td>
</tr>
<tr>
<td>Montane streamside</td>
<td>32</td>
<td>32,611</td>
<td>19 sites (329)</td>
<td>5 sites (10)</td>
</tr>
<tr>
<td>Northern hardwood</td>
<td>28</td>
<td>30,790</td>
<td>25 sites (1,102)</td>
<td>0 sites (0)</td>
</tr>
<tr>
<td>Upland hardwood</td>
<td>69</td>
<td>81,654</td>
<td>23 sites (496)</td>
<td>22 sites (88)</td>
</tr>
<tr>
<td>Riverine</td>
<td>7</td>
<td>10,660</td>
<td>0 sites (0)</td>
<td>3 sites (16)</td>
</tr>
<tr>
<td>Mixed pine-hardwood</td>
<td>39</td>
<td>44,223</td>
<td>10 sites (174)</td>
<td>15 sites (36)</td>
</tr>
<tr>
<td>Pine</td>
<td>13</td>
<td>8,560</td>
<td>0 sites (0)</td>
<td>12 sites (62)</td>
</tr>
</tbody>
</table>

Total specimens collected.

m, range = 615–1,600 m. Southeastern shrew and masked shrew occurrences were significantly related to site elevation and site moisture class (Table 3). The likelihood of southeastern shrew presence increased nearly 5 fold and 2 fold with every 300 m decrease in elevation and one unit decrease in site moisture class, respectively (Table 3). Conversely, the likelihood of masked shrew presence increased over 6-fold and approximately 1.5 fold with every 300 m increase in elevation and 1 unit increase in site moisture class (Table 3).

DISCUSSION

Masked shrew and southeastern shrew distribution support the observation of Pagels and Handley (1989) that these shrews segregate along an elevational gradient in the Appalachians. Moreover, the masked shrew’s lower elevational dis-
Table 3. Effect of elevation and forest habitat moisture condition (mesic) on presence of masked shrews (*Sorex cinereus*) and southeastern shrews (*S. longirostris*) in the southern Appalachians of Alabama, Georgia, North Carolina, and South Carolina, 1993–1997 as determined by multiple logistic regression.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>df</th>
<th>Parameter est.</th>
<th>Wald Chi-square</th>
<th>p &gt; Chi-square</th>
<th>Odds ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Masked shrew</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>1</td>
<td>-6.6355</td>
<td>56.8866</td>
<td>0.0001</td>
<td></td>
</tr>
<tr>
<td>Elevation</td>
<td>1</td>
<td>1.8705</td>
<td>47.3846</td>
<td>0.0001</td>
<td>6.491</td>
</tr>
<tr>
<td>Mesic</td>
<td>1</td>
<td>0.3889</td>
<td>7.0876</td>
<td>0.0078</td>
<td>1.475</td>
</tr>
<tr>
<td>Southeastern shrew</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>1</td>
<td>3.999</td>
<td>38.0677</td>
<td>0.0001</td>
<td></td>
</tr>
<tr>
<td>Elevation</td>
<td>1</td>
<td>-1.5929</td>
<td>37.7332</td>
<td>0.0001</td>
<td>0.203</td>
</tr>
<tr>
<td>Mesic</td>
<td>1</td>
<td>-0.5830</td>
<td>11.7028</td>
<td>0.0006</td>
<td>0.558</td>
</tr>
</tbody>
</table>

The distribution limit (615 m) and the southeastern shrew’s higher elevational distribution limit (923 m) observed, shows the increasing north to south elevation cline demarcating segregation between these two species (Rhoads, 1896; Komarek and Komarek, 1938; Gentry et al., 1968; Wharton, 1968; Caldwell and Bryan, 1983; Pagels and Handley, 1989; Ford et al., 1994; Laerm et al., 1999). Although masked shrews occur in the Ridge and Valley in Virginia (Pagels and Handley, 1989) and in the highest elevations of the Cumberland Plateau in Kentucky (Bryan, 1991), the species appears to be restricted to the Blue Ridge in the southern Appalachians. Elevations, with few exceptions, in the Piedmont, Ridge and Valley and Cumberland Plateau in the southern Appalachians do not exceed 615 m, the lower limit of masked shrew distribution regionally.

Lower average elevations and less varied topography restrict the abundance of cool, mesic habitats, such as cove hardwood forests, and preclude the existence of northern hardwood forests outside the Blue Ridge within the southern Appalachians. Although both southeastern shrews and masked shrews are considered to be habitat generalists over their entire distributions (Kirkland and Snoddy, 1999), masked shrew abundance tends to be correlated with high soil moisture holding capacity, soil organic matter, understory vegetation, and abundant ground structure such as thick leaf litter, large coarse woody debris and emergent rock (Pagels et al., 1994). These conditions frequently are encountered in the Blue Ridge in cove hardwood, northern hardwood, and montane streamside forests and are rarely found in other physiographic provinces or forest types. Masked shrews collected within upland hardwood or mixed pine-hardwood forests in the Blue Ridge occurred at elevations above 1,000 m where survey transects contained dense shrub layers of mountain laurel or flame azalea that promoted moist substrate microhabitats. The southeastern shrew is known from a wide diversity of habitats from abandoned fields in early succession to older bottomland hardwood forests throughout its distribution. Highest abundances are reported from mesic habitats (French, 1980a, 1980b; Pagels et al., 1982; Jones et al., 1991; Laerm et al., 1999; Menzel et al., 2000). However, southeastern shrews are associated with
xeric forest types at low elevations where masked shrews do not occur within the Blue Ridge portion of the southern Appalachians.

Our survey clearly indicates that masked shrews and southeastern shrews are largely allopatric within the southern Appalachians, with a zone of contiguous allopatry in the Blue Ridge where the two species occur in close geographic proximity but never together. Multi species assemblages of shrews tend to include species that are different in size more than assemblages of similar sized shrews (Fox and Kirkland, 1992). Nonetheless, the mechanisms and environmental thresholds (elevation, habitat type or climate) for masked shrews and southeastern shrews in the southern Appalachians have not been clearly elucidated. Degradation of and decreases in areal extent of northern and boreal forests from global climate change, atmospheric deposition, and insect attack (SAMAB, 1996; Halpin, 1997; Iverson et al., 1999) could possibly raise the elevation demarcation between masked shrews and southeastern shrews in the Blue Ridge. However, based on high relative abundances where masked shrews currently occur, we believe that if habitat conditions are favorable, masked shrews are superior competitors to southeastern shrews, resulting in few, if any areas of syntopy. Relationships of masked shrews and southeastern shrews to the other small-bodied soricids, such as the pygmy shrew (Sorex hoyi) and the least shrew (Cryptotis parva) merit further examination. For example, pygmy shrews occurred at 27 of the 51 sites where southeastern shrews were collected and 69 of the 101 sites where masked shrews were collected.

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