INFLUENCE OF ELEVATION AND FOREST TYPE ON COMMUNITY ASSEMBLAGE AND SPECIES DISTRIBUTION OF SHREWS IN THE CENTRAL AND SOUTHERN APPALACHIAN MOUNTAINS

W. MARK FORD, TIMOTHY S. MCCAY, MICHAEL A. MENZEL, W. DAVID WEBSTER, CATHRYN H. GREENBERG, JOHN F. PAGELS, AND JOSEPH F. MERRITT

ABSTRACT

We analyzed shrew community data from 398,832 pitfall trapnights at 303 sites across the upper Piedmont, Blue Ridge, northern Ridge and Valley, southern Ridge and Valley, Cumberland Plateau and Allegheny Mountains and Plateau sections of the central and southern Appalachian Mountains from Alabama to Pennsylvania. The objectives of our research were to describe regional species distributions and to identify macro-environmental factors important to shrews at both the community and individual species scales. Our study documented the presence of nine species with a low of three in the southern Ridge and Valley section to a high of eight in the Blue Ridge section where the Appalachian, Austral and Boreomontane fauna elements converge. Region-wide, shrew species richness was related to increasing elevation and was higher in mesic forest types than in xeric types. Conformity to expected distribution of shrew body-size (small, medium and large) appropriate for the central and southern Appalachian species pool showed no relationship to elevation gradients. However, xeric forest types conformed to a balanced assemblage of size classes less than expected. Among individual species, presence of masked shrew (*Sorex cinereus*) and smoky shrew (*Sorex fumeus*) was associated strongly with increasing elevation and mesic forests, whereas presence of southeastern shrew (*Sorex longirostris*) and southern short-tailed shrew (*Blarina carolinensis*) showed an opposite trend with elevation and forest type. The strong relationships we documented between presence of these four species with elevation and forest type facilitated reliable predictive habitat modeling. Conversely, the presence of pygmy shrew (*Sorex hoyi*) and northern short-tailed shrew (*Blarina brevicauda*) was not linked to forest type and only weakly linked to increasing elevation. Our analyses failed to produce meaningful relationships about extreme habitat specialists documented by our survey, the rock shrew (*Sorex dispar*) associated with colluvial talus, the water shrew (*Sorex palustris*) associated with high-gradient streams, and the least shrew (*Cryptotis parva*) associated with oldfields and early sucessional habitats.

INTRODUCTION

Within the central and southern Appalachian Mountains of the southeastern and mid-Atlantic United States, the family Soricidae is represented by 9 species of shrews (Kirkland and Snoddy 1999; Laerm et al. 1999). The Appalachian Mountains provide an extension of the Boreomontane and Appalachian faunal elements into a region with Austral affinities (Choate et al. 1994). Superficially, varied topography that produces considerable habitat heterogeneity and the high elevations that provide cool and moist climatic regimes are two complementary factors that enable the central and southern Appalachians to support a rich shrew community within local landscapes (i.e., > 2,000 ha). However, many of these species with sympatric regional distributions often are not syntopic. Strong local segregation occurs between similar species, such as the masked shrew (*Sorex cinereus*) and the southeastern shrew (*Sorex longirostris*; Pagels and Handley 1989; Ford et al. 2001). In part, this is a function of the varied habitat preferences among shrew species (Laerm et al. 1999) as well as differences in body size that contribute to fairly predictable species assemblages and local distributions (Fox and Kirkland

1992; Shvarts and Demin 1994; Churchfield et al. 1999). Nonetheless, the factors that explain presence of individual shrew species at the micro- or macro-habitat or even landscape distribution scales in the central and southern Appalachian Mountains have not been quantified.

Seven of the nine shrew species that occur in the central and southern Appalachian Mountains are listed as sensitive or species of concern in one or more states in the region (Laerm et al. 2000a). Therefore, the ability to understand the environmental factors responsible for distributional patterns of presence and absence within a shrew species' distribution is critical from a conservation viewpoint. Because most shrews are cryptic animals that are difficult to survey without time- and labor-intensive pitfall trapping (Kirkland and Sheppard 1994; Ford et al. 1997), developing easily quantifiable habitat parameters to accurately predict species presence would be useful in conservation planning and biodiversity management. For example, knowledge of masked shrew distribution in the southernmost Blue Ridge section could provide insights in defining and conserving functioning montane boreal or northern hardwood forest communities that currently exist as isolated relicts (Ford et al. 1994). Presence of water shrews (*Sorex palustris*) may be indicative of high water quality that merits extraordinary riparian zone protection in the central and southern Appalachian Mountains (Pagels et al. 1998), whereas presence of the rock shrew (*Sorex dispar*) probably are indicative of talus and rock outcrop habitats that support two rodents of very high conservation concern, the Allegheny woodrat (*Neotoma magister*) and the rock vole (*Microtus chrotorrhinus*). Accordingly, the objectives of our study were to: 1) examine the influence of elevation and forest type on shrew species richness and distribution of shrew species in the central and southern Appalachian Mountains; 2) examine the influence of elevation and forest type on maintaining conformity to equitable function groups of shrews as delineated by current species-assembly rules for shrews in the eastern United States; and 3) explore the utility of modeling shrew species distribution across the central and southern Appalachian Mountains.

METHODS

We assembled survey data from pitfall collections from 303 sites over 398,832 trapnights in the central and southern Appalachian Mountains in the upper Piedmont, Blue Ridge, northern Ridge and Valley, southern Ridge and Valley, Allegheny Mountains and Plateau and Cumberland Plateau sections from northeastern Alabama to southwestern Pennsylvania (Figure 1). Our collection data emanated from several ecological studies and unpublished survey efforts that were undertaken by the University of Georgia, the USDA Forest Service, the University of North Carolina at Wilmington, Virginia Commonwealth University, Marshall University, Kentucky Nature Preserves Commission and Powdermill Biological Station from 1979-2000 (Caldwell 1980; Cawthorn 1994; Ford et al. 1994; Laerm et al. 1994; Pagels et al. 1994; Hajenga 1995; Laerm et al. 1995a; Laerm et al. 1995b; Laerm et al. 1995c; Laerm et al. 1996a; Laerm et al. 1996b; Ford et al. 1997; Laerm et al. 1997; Ford et al. 1999; Laerm et al. 1999; Menzel et al. 1999; Ford et al. 2000a; Laerm et al. 2000b; Ford et al. 2001; Ford and Rodrigue 2001; Merritt et al. 2001;Keyser et al. 2001). The majority of these collections were obtained from pitfall trapping using 943 cm^3 plastic cups or #10 tin cans set in transects along natural cover such as coarse woody debris or boulders or associated with aluminum drift-fences. Pitfall trapping methods are described in detail by Ford et al (1994), Pagels et al. (1994) and McCay et al. (1998).

For each pitfall collection site, we determined Appalachian physiographic section, elevation, forest type, species presence and richness. Collection site elevations ranged from 160 m in the upper Piedmont to approximately 1,600 m in the Blue Ridge. Most sites were located in mature, second-growth forest stands that originated from forest harvesting or farm abandonment during 1880-1930 (Ford et al. 1994; Ford et al. 2000b). However, some collections were from younger-aged forest stands (15-50 years-old) or unharvested old-growth (Ford et al. 1997). We characterized each collection site as mesic or xeric forest type. Mesic forest communities were located at either high elevations or in areas with favorable site conditions, such as sheltered north-facing slopes and ravines, whereas xeric forests usually were located at either low- to mid-elevations or in exposed aspects and unsheltered landforms. Mesic forests included red spruce (*Picea rubens*)-dominated forests or northern hardwood communities dominated by American beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccarhum*) and black cherry (*Prunus serotina*) at the highest elevations, cove hardwood forests dominated by yellow poplar (*Liriodendron tulipifera*), basswood (*Tilia americana*) and northern red oak (*Quercus rubra*) on north-facing slopes and ravines; and eastern hemlock (*Tsuga canadensis*)-white pine (*Pinus strobus*)-dominated montane riparian areas along very sheltered, high-gradient streams (Ford et al. 2000a; Ford et al 200b; Ford and Rodrigue 2001). Xeric forest communities included upland hardwood forests dominated by several oak (*Quercus*) and hickory (*Carya*) species, red maple (*Acer rubra*) and blackgum (*Nyssa sylvatica*); mixed pine (*Pinus*)-hardwood dominated by various yellow pines and white pine along with hardwood associates from the upland hardwood community; yellow pine communities at the lowest elevations or the most exposed in the region dominated by species such as shortleaf pine (*Pinus echinata*) and pitch pine (*Pinus rigida*); and riverine communities dominated by black willow (*Salix nigra*), alder (*Alnus serrulata*) and sweetgum (*Liquidambar styraciflua*) along well-drained riparian terraces or scoured cobble and sandy outwashes (Ford et al. 1994; Laerm et al. 1999).

We performed linear regression to assess the relationship between shrew species richness and elevation (Steel and Torrie 1980). We analyzed species richness using ANCOVA with elevation as a covariate to assess how shrew species richness varied between mesic or xeric forest types (Steel and Torrie 1980). We converted site richness to a categorical variable by assigning 0-1 species as low, 2-3 species as medium, and > 4 species as high. We used a two-sample *t*-test to examine elevation differences between collection sites that conformed to equitable function groups with those that did not (Steel and Torrie 1980). Equitable function groups followed Fox and Kirkland's (1993) species assembly rules using small, medium, and large species as groupings that cannot have an additional species member unless other groupings are occupied by at least one species member. We used Fisher's Exact test to test for independence between equitable function group outcome (favored versus non-favored) and forest type (Stokes et al. 1995). For all physiographic sections where an individual species occurred, we analyzed presence with elevation and forest type using multiple logistic regression (Goguen and Mathews 2001; Teixeira et al. 2001). We assessed the percent correct classification of observations within each regression model using a jackknife procedure on the original dataset and also using 97 other shrew pitfall collections from the region (Figure 1.) where elevation and forest type could be obtained (Pagels and Tate 1976; Harvey et al. 1991; Harvey et al. 1992;

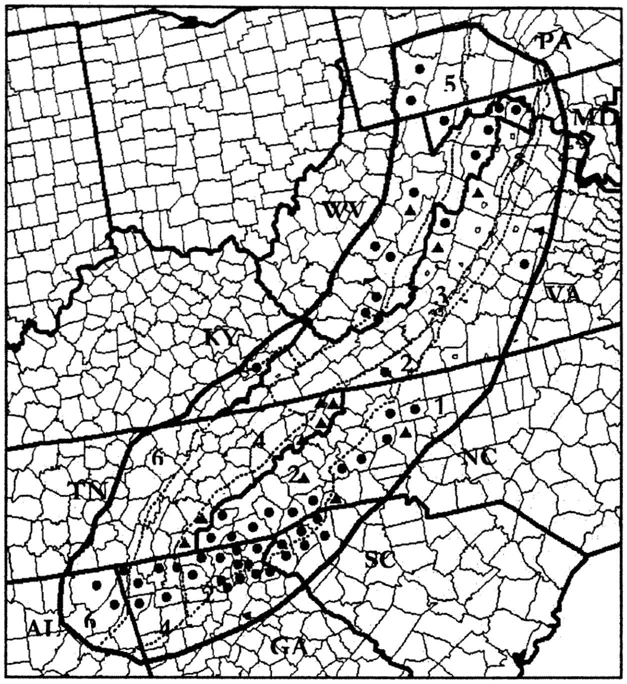


Fig. 1. – Shrew collection sites (n =303) in 6 physiographic sections in the central and southern Appalachian Mountains, 1979-2000 (circles). Within a county, circles may represent numerous collection sites and counties with two circles reflect sampling at different physiographic subsections. Triangles show the location of independently collected data (n = 97) used for logistic regression model validation. Appalachian physiographic sections are as follows: 1- Piedmont, 2 - Blue Ridge, 3- Northern Ridge and Valley, 4 - Southern Ridge and Valley, 5 - Allegheny Mountains and Plateau, and 6 – Cumberland Plateau.

Table 1. — Pitfall trapping effort and shrew captures across forest types, elevation, and physiographic subsections in the central and southern Appalachian Mountains, 1979-2000. Forest community types are as follows: SPR = red spruce, NHW = northern hardwood, CHW = cove hardwood, HWP = eastern hemlock-white pine-rhododendron riparian, UPH = upland hardwood, MPH = mixed pine-hardwood, YP = yellow pine, and RIV = low elevation riverine. Physiographic sections are as follows: P = Piedmont, BR = Blue Ridge, NRV = northern Ridge and Valley, SRV = southern Ridge and Valley, AP = Allegheny Plateau and Mountains, and CP = Cumberland Plateau. Sections where a species is known from other records but not collected in this study are noted in bold typeface. Three northern hardwood sites in Allegheny Plateau and Mountains had unknown pitfall trapping effort, hence totals are not reflected in the table.

	Sites	Trap-nights	Northern short-tailed shrew	Southern short-tailed shrew	Least shrew	Masked shrew	Rock shrew	Smoky shrew	Pygmy shrew	South-eastern shrew	Water shrew
SPR	45	37,928	16	0	1	442	10	29	8	0	0
NHW	41	39,211	176	0	0	1,372	9	571	46	0	1
CHW	54	111,758	368	0	3	787	16	1,337	148	5	0
HWP	37	36,793	113	0	0	364	2	724	27	10	5
UPH	90	99,077	195	96	5	538	12	585	86	131	2
MPH	40	45,191	55	6	8	180	4	230	48	36	2
YP	15	10,120	8	1	1	0	0	3	18	62	0
RIV	11	13,453	1	9	4	0	0	0	0	19	0
Elevations			246-1600	160-553	276-1524	507-1600	610-1524	246-1600	160-1600	160-923	795-1538
Sections			P, BR, NRV, AP, CP	P, SRV, CP	P, BR, NRV, SRV, AP, CP	P, BR, NRV, AP	BR, NRV, AP, CP	P, BR, NRV, AP, CP	P, BR, NRV, AP, CP	P, BR, NRV, SRV, CP	BR, NRV, AP

Mitchell et al. 1997; Dobony 2000; Greenberg 2001; D. Webster, University of North Carolina at Wilmington, unpubl. data) as validation datasets that were not used in the initial modeling (SAS Institute 1995). Statistical significance was indicated at $\alpha = 0.05$ for all tests. Finally, we used an exclusionary approach based on probability thresholds from logistic regression models as modified by Odom et al. (2001) to use spatial query tools in ArcView Spatial Analyst® to produce GIS coverages of predicted masked shrew distributional patterns at local scales.

RESULTS

Nine shrew species were present in the study region: northern short-tailed shrew (*Blarina brevicauda*), southern short-tailed shrew (*Blarina carolinensis*), least shrew (*Cryptotis parva*), masked shrew, rock shrew (*Sorex dispar*), smoky shrew (*Sorex fumeus*), pygmy shrew (*Sorex hoyi*), southeastern shrew (*Sorex longirostris*), and water shrew (*Sorex palustris*); Table 1). No individual species occurred in every physiographic section or forest community in the collection data (Table 1). Species richness varied from a low of three in the southern Ridge and Valley to a high of eight in the Blue Ridge (Table 1).

Shrew species richness was related positively to elevation ($r^2 = 0.306$, *d.f.* = 1, 299, $P < 0.001$) where richness = 1.14 + 0.002 (m). Mean elevation adjusted for the significant forest type covariate ($F = 60.53$, *d.f.* = 1, $P < 0.001$) was different among collection sites with high, medium, and low shrew species richness values ($F = 65.24$, *d.f.* = 3, 297, $P < 0.001$) with mean elevations (0 + SE) of high richness sites (1035.38 m + 30.57, $n = 89$) > medium richness sites (777.14 m + 22.88, $n = 170$) > low richness sites (487.80 m + 30.38, $n = 45$). Although mean elevation of collections sites that conformed to equitable function groups (825.30 m + 20.49, $n = 256$) and those that did not conform (743.83 m + 48.26, $n = 45$) did not differ ($t = 1.52$, *d.f.* = 299, $P = 0.12$), the collection sites not conforming to

Table 2. – Effect of elevation and generalized forest type (mesic or xeric) on presence of shrew species in the central and southern Appalachian Mountains, 1979-2000 as determined by multiple logistic regression. Presence and absence data by species were used only for physiographic sections within documented species distributions. Correct classification rates were based on internal jackknife procedures with data used for model formulation and also with independent validation datasets.

	R^2	Parameter estimate	Wald χ^2	$P > \chi^2$	Odds ratio	% Correct (jackknife)	% Correct (validation)
Northern short-tailed shrew	0.152					73	67
Intercept		-1.058	8.052	0.005			
Elevation		0.002	15.407	0.001	1.002		
Forest type		0.516	3.034	0.081	1.675		
Southern short-tailed shrew	0.358					77	80
Intercept		2.657	7.239	0.007			
Elevation		-0.008	12.497	0.001	0.992		
Forest type		-12.860	0.002	0.964	0.001		
Least shrew	0.041					47	89
Intercept		-1.919	8.382	0.004			
Elevation		-0.001	1.514	0.219	0.999		
Forest type		-0.480	0.480	0.484	0.619		
Masked shrew	0.509					79	67
Intercept		-4.854	67.721	0.0001			
Elevation		0.005	51.679	0.0001	1.005		
Forest type		1.084	12.217	0.005	2.956		
Rock shrew	0.060					92	87
Intercept		-4.372	24.967	0.0001			
Elevation		0.002	4.610	0.032	1.002		
Forest type		-0.222	0.167	0.683	1.249		
Smoky shrew	0.576					73	77
Intercept		-3.940	47.900	0.0001			
Elevation		0.006	54.078	0.0001	1.006		
Forest type		1.182	8.577	0.004	3.268		
Pygmy shrew	0.096					58	47
Intercept		-1.489	19.754	0.0001			
Elevation		0.002	18.929	0.0001	1.002		
Forest type		-0.264	0.933	0.334	0.768		
Southeastern shrew	0.495					83	77
Intercept		3.014	31.048	0.0001			
Elevation		-0.005	39.966	0.0001	0.995		
Forest type		-1.099	5.463	0.019	0.333		
Water shrew	0.220					96	97
Intercept		-8.295	20.238	0.0001			
Elevation		0.005	11.268	0.001	1.005		
Forest type		-1.290	2.482	0.115	0.287		

equitable function groups occurred more than expected in xeric forest types (Fisher's Exact test, $P = 0.002$).

Individually, presence of masked shrews and smoky shrews strongly was related to increasing elevation and forest type with elevational thresholds of presence lower in mesic forests than in xeric forests (Table 2; Figure 2). Conversely, southern short-tailed shrews and southeastern shrews showed the opposite relationship (Table 2; Figure 2). Elevation was related weakly to the presence of northern short-tailed and pygmy shrews (Table 2, Figure 2), as well as the rare water shrew that occurred at only 9 of 210 possible collection sites (Table 2). Similar to the water shrew, the skewed distribution and rarity of least shrews (present at 12 of 272 possible sites) and rock shrews (present at 20 of 250 possible sites) showed no relationship to elevation or forest type (Table 2). Percent correct classification rates of observed values using both the jackknife and validation procedures were high for northern short-

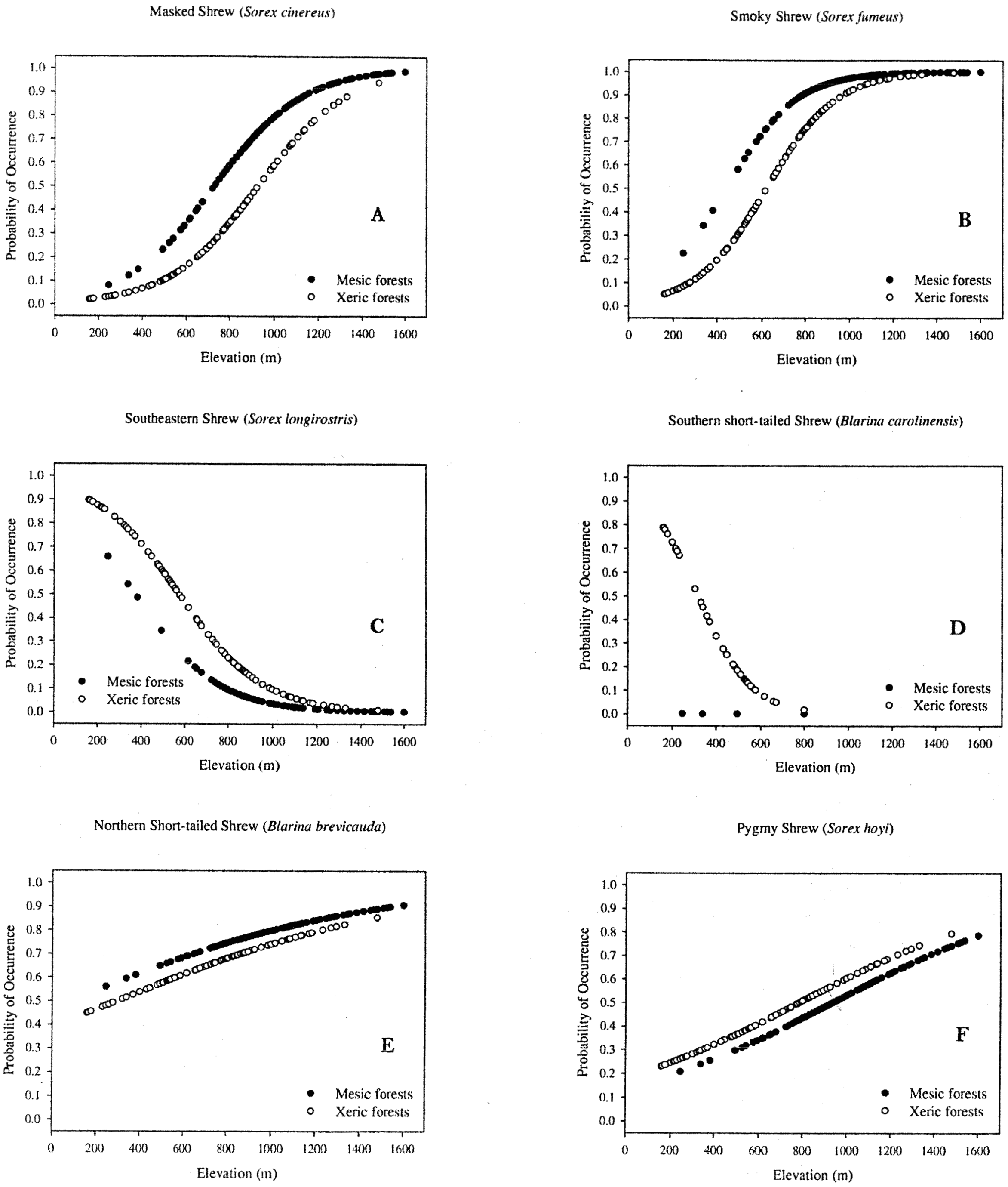
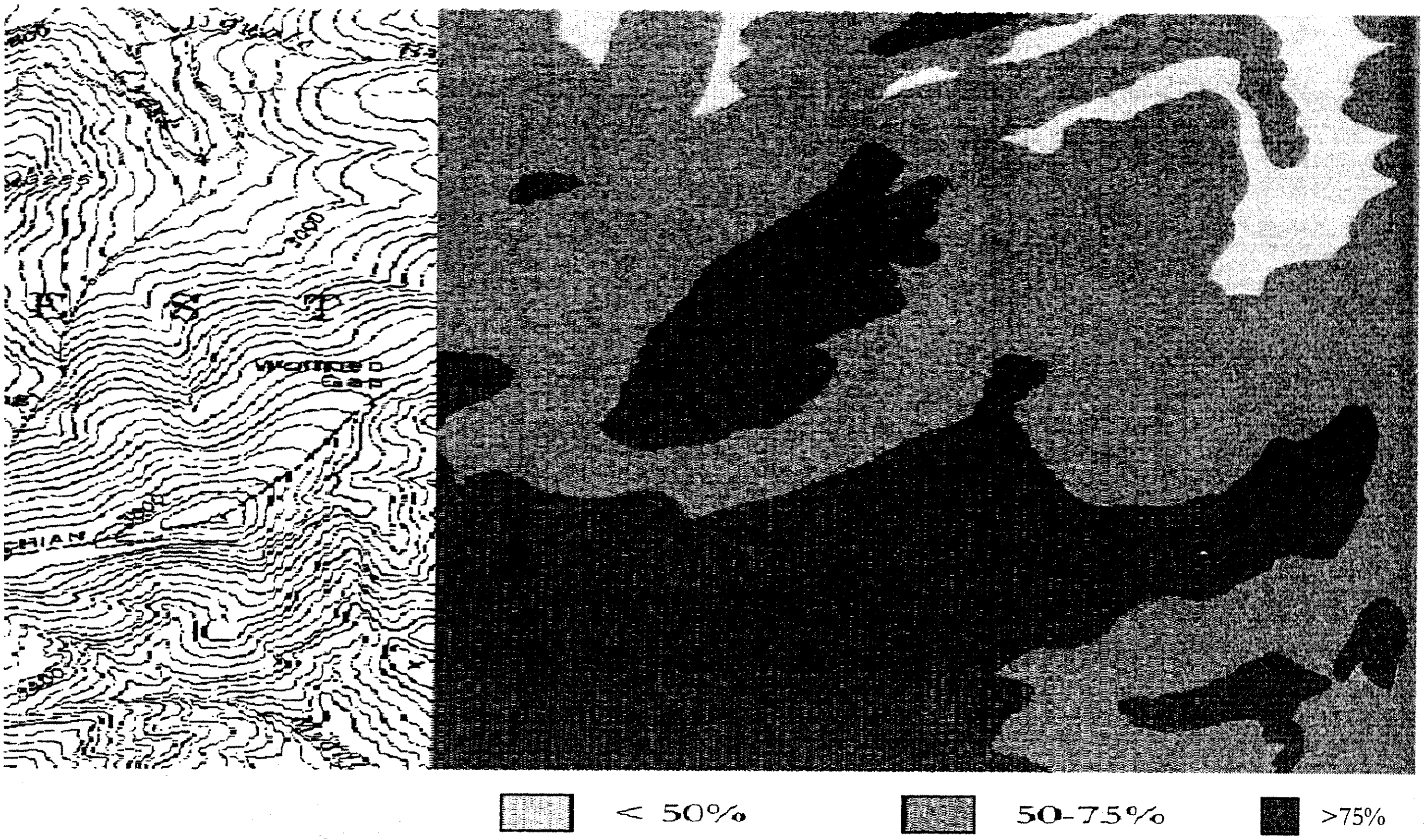


Fig. 2. – Predicted probabilities of occurrence of selected shrew species in the central and southern Appalachian Mountains based on logistic regression models, 1979-2000. Subfigures A and B show a greater probability of occurrence of masked shrews and smoky shrews in mesic forests and along an increasing elevational gradient. Subfigures C and D show the opposite trend with the southeastern shrew and southern short-tailed shrew as the greater probability of occurrence is higher in xeric forests at low elevations. Subfigures E and F show the weak, positive relationship between increasing elevation and a lack of relationship by forest type with the probability of occurrence of the northern short-tailed shrew and the pygmy shrew.



f occurrence of the masked shrew in a GIS based on logistic regression model incor-
pendent variables. The scene is a portion of the Tray Mountain USGS 7.5' quadran-
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threshold values of 0-50, >50-75, and >75 percent predicted probabilities of masked shrew occurrence for various combinations of elevation and forest type, we were able to construct a meaningful GIS coverage showing the distribution of the masked shrew over a regional portion of the Blue Ridge section in northern Georgia (Figure 3).

DISCUSSION

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; Rickart 2001).

The link between increased richness in groups such as birds, bats and rodents with increasing habitat diversity and rainfall and productivity has been demonstrated at both local and landscape scales (Nor 2001; Sanchez-Cordero 2001; Jetz and Rahbek 2002). Our data showing increased shrew species richness with elevation in the central and southern Appalachian Mountains conform to these patterns where elevational increases bring Austral faunal elements such as the southeastern shrew and least shrew in syntopy with Appalachian and Boreomontane species such as the smoky shrew, masked shrew, and northern short-tailed shrew.

For shrews in the central and southern Appalachian Mountains, especially species such as the northern short-tailed shrew, masked shrew, and smoky shrew, that are linked to cool and moist micro-habitats (Ford et al. 1994; Pagels et al. 1994; Laerm et al. 1999; Ford et al. 2000a; Merritt et al. 2001), increases in elevation result in more favorable micro-climates and increased invertebrate and woodland salamander food resources (Getz 1961; Ford et al. 2002a; Ford et al. 2002b), though McCoy (1990) cautioned that arthropod abundance and species richness in relation to elevation gradients in the southern Appalachian Mountains were a "complex interplay of local ecological interactions, latitude, disturbance and sampling regimes." Elevation and complex topography provide exposed aspects and xeric forests favorable to species such as the southeastern shrew and pygmy shrew in close proximity to mesic habitats that support other shrew species. This validates the increased "ecotone" effect hypothesis where high levels of habitat heterogeneity occur and species richness often is high (Lomolino 2001). In both tropical and continental montane systems, trends in small mammal species richness display a curvilinear mid-elevation peak in which climatic conditions begin to deteriorate and overall productivity declines (Heaney 2001; Rikart 2001). This pattern does not occur for shrews in the central and southern Appalachian Mountains because, save for the few peaks above 1,400 m in the Allegheny Mountains and Plateau in West Virginia and above 1,700 m in the Blue Ridge of western North Carolina and eastern Tennessee, elevations do not reach sufficient height to produce harsh alpine conditions occur (Fenneman 1938; Cogbill and White 1991).

Our data support observations that shrew assemblages in the eastern United States follow size-based assembly rules (Fox and Kirkland 1992; Kirkland and Snoddy 1999) because most sites conformed to an equitable distribution of size classes. Our inability to detect an elevational effect on conformity to equitable function groups at collection sites also may reflect the lack of sufficiently high elevations in the entire region where habitat conditions would deteriorate to the point that shrew community structure deviates from a favored state. Of the sites that did exhibit inequitable distributions of shrew size class composition, most occurred in xeric forests where two small shrews, the southeastern shrew and pygmy shrew, were syntopic in the absence of either a medium-sized smoky shrew or large-sized northern short-tailed shrew. This probably was a result of the lower availability of food resources in these xeric systems. It would be interesting to monitor favored state xeric sites over time to see if inclusion of species such as smoky shrew is not constant but rather a result of an ecotone tension periodically drawing from the adjacent mesic forests' species pool. Several of the collections from mesic forests that showed unfavored assemblages were places where the medium-size class was filled by smoky shrews and rock shrews, but the northern short-tailed shrew from the large-size class was absent. Because the rock shrew is closely tied to colluvial talus and rock outcrop habitats where soil development generally is poor (Pagels 1987; Laerm et al. 1999; Ford and Rodrigue 2001) and the northern short-tailed shrew is a semi-fossorial species often found where deeper, well-drained but moist soil conditions prevail (George et al. 1986), their mutual exclusion based on habitat preferences is expected.

Logistic regression models using elevation and forest type as predictive variables worked very well for the masked shrew and smoky shrew, two species associated with mid- to high-elevations within the more rugged sections of the southern and central Appalachian Mountains and for the southeastern and southern short-tailed shrew that occur in the foothills of the upper Piedmont and southern Ridge and Valley. From the standpoint of understanding species' habitat preferences, these models incorporating two easily defined habitat parameters are helpful because many studies have noted the difficulty of identifying specific micro- and macro-habitat important to shrews in the central and southern Appalachian Mountains (Pagels et al. 1994; Ford et al. 1997; McCay et al. 1998; Ford and Rodrigue 2001). Moreover, these analyses should provide ecological insights into how species such as masked shrews and southeastern shrews minimize direct contact across a wide area of sympatric distribution (Ford et al. 2001). These models can easily be converted to spatially explicit predictive coverages as we have demonstrated with the masked shrew for the Blue Ridge section in northern Georgia (Figure 3). Such efforts can aid conservation efforts by identifying areas where there is a high likelihood of encountering these species. For example, within the southernmost Blue Ridge in Georgia or South Carolina, areas with vegetative characteristics and faunal components of northern affinities, such as northern hardwood communities, are rare and restricted to either the highest elevations or the most sheltered north-facing landforms. Use of our predictive model for masked shrews along with established vegetation classification data will allow land managers in the southern Appalachians to quickly identify or rank northern hardwood patches in terms of quality and functionality and thereby assign a high protection priority without additional survey effort.

With some notable exceptions, such as habitats with abundant colluvial rock or low elevations of the upper Piedmont, southern Ridge and Valley and Cumberland Plateau sections, northern short-tailed shrews were widespread throughout much of the region. However, northern short-tailed shrews are less susceptible to pitfall trapping along natural cover than along drift-fences (McCay et al. 1998), and the majority of collections used the former method rather than the latter. Although it was once considered one of the most rare mammal species in North America (Laerm et al. 1994; Laerm et al. 2000b), widespread pitfall trapping efforts have shown the pygmy shrew to be widespread in occurrence and habitat utilization, but nowhere abundant (Pagels 1987; Laerm et al. 1999). Therefore, the lack of relationship with forest type and the weak relationship with elevation should be expected.

Although water shrews were linked to increases in elevation in our modeling effort, that species, along with least and rock shrews, was not specifically targeted by most of the collection data we analyzed. Water shrews are best collected using pitfall traps set at the water's edge along overhanging banks or snap-traps set in the stream channel (Pagels et al. 1998). These methods were not utilized at most of the 303 collection sites in our study. Regardless, we can infer that the water shrew's presence at higher elevations undoubtedly is linked to its affinity for undisturbed, high-gradient, first-order streams. At least 8 of the 20 collection sites where rock shrews occurred contained notable amounts of large emergent rock. No Blue Ridge, northern Ridge and Valley, Allegheny Mountain and Plateau, or Cumberland Plateau section collection site was far (> 1 km) from either that type of feature or colluvial talus or was below 600 m in elevation. Lastly, the presence of least shrews at most collection sites was a function of the site's close proximity to oldfields or other early successional habitats (e.g., newly regenerating timber harvests; Ford et al. 1994; Hajenga 1995). We are unable to explain the species' presence in a handful of locales in the Blue Ridge, including a high-elevation red spruce stand near the Mt. Rogers area in southwestern Virginia (Pagels 1991) and an area of older second-growth cove hardwoods with substantial old-growth legacy trees intermixed at Sosesbee Cove in northern Georgia (Ford et al. 1997). These individuals may have been captured in these older stands as they dispersed between early successional habitats.

CONCLUSION

The interplay of complex topography, forest type heterogeneity, and the geographic union of Austral, Appalachian and Boreomontane faunal groups join to render the central and southern Appalachian Mountains a biodiversity "hotspot" for soricids in North America. Despite this biocomplexity, we were able to effectively explain observed assemblage patterns of shrew communities as well as individual species presence using simple measures of elevation and forest type. Mesic forest types and increasing elevations tend to support the most speciose shrew communities in the central and southern Appalachians. Moreover, such sites also tend to display a greater frequency of equitably distributed membership in shrew size-classes. The opposite patterns are true for xeric forest types and lower elevations due in part that fewer of the whole region's species are adapted for these conditions, although some variation in size-class membership also was attributable to specialized habitat conditions such as emergent rock or high-gradient streams not directly measured in our study.

Whether or not the close adjacency of mesic and xeric forest types and high variation in local elevations produce a tension zone with a periodic expansion or contraction of individual species distributions at very localized scales to either create or disrupt balanced size-class distributions is unknown. These and the other underlying ecological mechanisms behind our observed patterns of shrew distribution in the central and southern Appalachian Mountains remain to be fully elucidated and should form the basis for future research.

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LITERATURE CITED

CALDWELL, R.S. 1980. First records of *Sorex dispar* and *Microsorex thompsoni* in Kentucky with distributional notes on associated species. Transactions of the Kentucky Academy of Science, 41:46-47.

CAWTHORN, J.M. 1994. Live-trapping study of two syntopic species of Sorex, *S.. cinereus* and *S. fumeus*, in southwestern Pennsylvania. Pp. 39-43 *in* Advances in the biology of shrews (J.F. Merritt, G.L. Kirkland, Jr., and R. K. Rose, eds.). Carnegie Museum of Natural History, Special Publication 18: 1-458.

CHOATE, J.R., J.K. JONES, and C. JONES. 1994. Handbook of mammals of the south-central states. Louisiana State University Press, Baton Rouge. 304 pp.

COGBILL, C.V. and P.S. WHITE. 1991. The latitude-elevation relationship for spruce-fir forest and treeline along the Appalachian mountain chain. Vegetation, 94:153-175.

CHURCHFIELD, S., V.A. NESTERENKO, and E.A. SHVARTS. 1999. Food niche overlap and ecological separation amongst six species of coexisting forest shrews (Insectivora: Soricidae) in the Russian Far East. Journal of Zoology, 249:349-359.

DOBONY, C.A. 2000. Factors influencing ruffed grouse productivity and chick survival in West Virginia. M.S. thesis, West Virginia University, Morgantown. 97 pp.

FENNEMAN, N.M. 1938. Physiography of the eastern United States. McGraw-Hill, New York. 714 pp.

FORD, W.M., B.R. CHAPMAN, M.A. MENZEL, and R.H. ODOM. 2002a. Stand age and habitat influences on salamanders in Appalachian cove hardwood forests. Forest Ecology and Management, 155:131-141.

FORD, W.M., J. LAERM, and K.G. BARKER. 1997. Soricid response to forest stand age in southern Appalachians cove hardwood communities. Forest Ecology and Management, 91:175-181.

FORD, W.M., J. LAERM, D.C. WEINAND and K.G. BARKER. 1994. Abundance and distribution of shrews and other small mammals in the Chattahoochee National Forest of Georgia. Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies, 48:310-320.

FORD, W.M., M.A. MENZEL, T.S. MCCAY, J.W. GASSETT, and J. LAERM. 2000a. Woodland salamander and small mammal responses to alternative silvicultural practices in the southern Appalachian of North Carolina. Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies, 54:241-250.

FORD, W.M., M.A. MENZEL, D.W. MCGILL, J. LAERM and T.S. MCCAY. 1999. Effects of a community restoration fire on small mammals and herpetofauna in the southern Appalachians. Forest Ecology and Management, 114:233-243.

FORD, W.M., M.A. MENZEL, T.S. MCCAY, and J. LAERM. 2001. Contiguous allopatry of the masked shrew and southeastern shrew in the southern Appalachians: segregation along an elevational and habitat gradient. The Journal of the Elisha Mitchell Scientific Society, 117:20-28.

FORD, W.M., M.A. MENZEL, and R.H. ODOM. 2002b. Elevation, aspect, and cove size effects on southern Appalachian salamanders. Southeastern Naturalist, 1:315-324.

FORD, W.M., R.H. ODOM, P.E. HALE, and B.R. CHAPMAN. 2000b. Stand-age, stand characteristics, and landform effects on understory herbaceous communities in southern Appalachian cove-hardwoods. Biological Conservation, 93:237-246.

FORD, W.M. and J.L. RODRIGUE. 2001. Sorcid abundance in partial overstory removal harvests and riparian areas in an industrial forest landscape of the central Appalachians. Forest Ecology and Management, 152:159-168.

FOX, B.J. and G.L. KIRKLAND, JR. 1992. North American soricid communities follow Australian small mammal assembly rule. Journal of Mammalogy, 73:491-503.

GETZ, L.L. 1961. Factors influencing the local distribution of shrews. The American Midland Naturalist, 65:67-88.

GEORGE, S.B., J.R. CHOATE, and H.H. GENOWAYS. 1986. *Blarina brevicauda.* Mammalian Species, 261:1-9.

GOGUEN, C.B. and N.E. MATHEWS. 2001. Brown-headed cowbird behavior and movements in relation to livestock grazing. Ecological Applications, 11:1533-1544.

GREENBERG, C.H. 2001. Response of reptile and amphibian communities to canopy gaps created by wind disturbance in the southern Appalachians. Forest Ecology and Management, 148:135-144.

HAJENGA, J.J. 1995. The distribution, ecology and natural history of shrews (Insectivora: Soricidae) in southern West Virginia. M.S. thesis, Marshall University, Huntington, West Virginia, 111 pp.

HARVEY, M.J., C.S. CHANEY, and M.D. MCGIMSEY. 1991. Distribution, status, and ecology of small mammals of the Cherokee National Forest, Tennessee (Southern Districts). Final Report USDA Forest Service. Tennessee Technological University Center for Management, Utilization and Protection of Water Resources, Cookeville. 65 pp.

HARVEY, M.J., M.D. MCGIMSEY, and C.S. CHANEY. 1992. Distribution, status, and ecology of small mammals of the Cherokee National Forest, Tennessee (Northern Districts). Final Report USDA Forest Service. Tennessee Technological University Center for Management, Utilization and Protection of Water Resources, Cookeville. 72 pp.

HEANEY, L.R. 2001. Small mammal diversity along elevational gradients in the Philippines: an assessment of patterns and hypotheses. Global Ecology and Biogeography, 10:15-39.

JETZ, W. and C. RAHBEK. 2002. Geographic range size and determinants of avian species richness. Science, 297:1548-1551.

KEYSER, P.D., D.M. SAUSVILLE, W.M. FORD, M.T. MENGAK, P. BROSE and D.H. VAN LEAR. 2001. Prescribed fire impacts to small mammals in an oak-shelterwood in the Virginia Piedmont. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies, 55:375-381.

KIRKLAND, G.L., JR., and P.K. SHEPPARD. 1994. Proposed standard protocol for sampling small mammal communities. Pp. 277-281 in Advances in the biology of shrews (J.F. Merritt, G.L. Kirkland, Jr, and R. K. Rose, eds.)., Carnegie Museum of Natural History, Special Publication 18: 1-458.

KIRKLAND, G.L., JR., and H.W. SNODDY. 1999. Biogeography and community ecology of shrews (Mammalia: Soricidae) in the northern Appalachian Mountains. Pp. 167-175, *in* Proceedings of the Appalachian Biogeography Symposium (R.P. Eckerlin, ed.). Virginia Museum of Natural History, 7:1-258.

LAERM, J., E. BROWN, L. LEPARDO, M.A. MENZEL, and W.M. FORD. 1996. Distributional occurrence and status of the least shrew (*Cryptotis parva*) in the southern Appalachians. Georgia Journal of Science, 53:153-158.

LAERM, J., E. BROWN, M.A. MENZEL, and W.M. FORD. 1995a. *Sorex fumeus* and *Sorex hoyi* on the Cumberland Plateau of Georgia. Georgia Journal of Science, 53:189-194.

LAERM, J., E. BROWN, M.A. MENZEL, A. WOJTALIK, W.M. FORD and M. STRAYER. 1995b. The masked shrew, *Sorex cinereus* (Insectivora: Soricidae) and the red-backed vole (Rodentia:Muridae) in the Blue Ridge Province of South Carolina. Brimleyana, 22:15-22.

LAERM, J., W.M. FORD and B.R. CHAPMAN. 2000a. Conservation status of terrestrial mammals of the southeastern United States. Pp. 4-16, in Fourth Colloquium on Conservation of Mammals in the Southeastern United States (B.R. Chapman and J. Laerm, eds.). Occasional Papers of the North Carolina Museum of

Natural Science and the North Carolina Biological Survey, 12:4-16.

LAERM, J., W.M. FORD, T.S. MCCAY, M.A. MENZEL, L.T. LEPARDO and J.L. BOONE. 1999. Soricid communities in the southern Appalachians. Pp. 177-193, *in* Proceedings of the Appalachian Biogeography Symposium (R.P. Eckerlin, ed.). Virginia Museum of Natural History, 7:1-258.

LAERM, J., W.M. FORD, M.A. MENZEL, and T.S. MCCAY. 2000b. Analysis of distribution and habitat associations of *Sorex hoyi winnemana* in the southern Appalachians. Pp. 17-26, *in* Fourth Colloquium on Conservation of Mammals in the Southeastern United States (B.R. Chapman and J. Laerm, eds.). Occasional Papers of the North Carolina Museum of Natural Science and the North Carolina Biological Survey, 12:4-16.

LAERM, J., W.M. FORD, D.C. WEINAND, and M.A. MENZEL. 1994. First records of the pygmy shrew, *Sorex hoyi* (Insectivora: Soricidae) in western Maryland and Pennsylvania. Maryland Naturalist, 38:23-27.

LAERM, J., L.T. LEPARDO, T. GAUDIN, N. MONTEITH and A. SZYMCZAK. 1996. First records of the pygmy shrew, *Sorex hoyi winnemana* Preble (Insectivora: Soricidae), in Alabama. Journal of the Alabama Academy of Science, 64:43-48.

LAERM, J., C.H. WHARTON, and W.M. FORD. 1995c. First record of the water shrew, *Sorex palustris* (Insectivora: Soricidae), in Georgia with comments on its distribution and status in the southern Appalachians. Brimleyana, 22:47-52.

LAERM, J., C.H. WHARTON, and W.M. FORD. 1997. First record of *Sorex dispar* in Georgia with comments on its conservation status in the southern Appalachians. Brimleyana, 24:1-5.

LOMOLINO, M.V. 2001. Elevation gradients of species-density: historical and prospective views. Global Ecology and Biogeography, 10:3-13.

MCCAY, T.S., J. LAERM, M.A. MENZEL, and W.M. FORD. 1998. Methods used to survey shrews (Insectivora: Soricidae) and the importance of forest-floor structure. Brimleyana, 25:110-119.

MCCOY, E.D. 1990. The distribution of insects along elevation gradients. Oikos, 58:313-322.

MENZEL, M.A., W.M. FORD, J. LAERM, and D. KRISHON. 1999. Forest to wildlife opening: habitat gradient analysis among small mammals in the southern Appalachians. Forest Ecology and Management, 114:227-232.

MERRITT, J.F., M. LIMA, and F. BOZINOVIC. 2001. Seasonal regulation in fluctuating small mammal populations: feedback structure and climate. Oikos 94:505-514.

MITCHELL, J.C., S.C. RINEHART, J F. PAGELS, K.A. BUHLMAN, and C.A. PAGUE. 1997. Factors influencing amphibian and small mammal assemblages in central Appalachians forests. Forest Ecology and Management, 96:65-76.

NOR, S.M. 2001. Elevations diversity patterns of small mammals on Mount Kinabalu, Sabah, Malaysia. Global Ecology and Biogeography, 10:41-62.

ODOM, R.H., W.M. FORD, J.W. EDWARDS, C.W. STIHLER and J.M. MENZEL. Developing a habitat model for the endangered Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) in the Allegheny Mountains of West Virginia. Biological Conservation, 99:245-252.

PAGELS, J.F. 1987. The pygmy shrew, rock shrew and water shrew: Virginia's rarest shrews (Mammalia: Soricidae). The Virginia Journal of Science, 38:364-368.

PAGELS, J.F. 1991. A high elevation record for the least shrew, *Cryptotis parva* (Say). The Virginia Journal of Science, 42:361-362.

PAGELS, J.F. and C.O. HANDLEY. 1989. Distribution of the southeastern shrew, *Sorex longirostris* Bachman, in western Virginia. Brimleyana, 15:123-131.

PAGELS, J.F., L.A. SMOCK, and S.H. SKLAREW. 1998. The water shrew, *Sorex palustris* Richardson (Insectivora:Soricidae), and its habitat in Virginia. Brimleyana, 25:120-134.

PAGELS, J.F. and C.M. TATE. 1976. Shrews (Insectivora: Soricidae) of the Paddy Knob-Little Back Creek area of western Virginia. Virginia Journal of Science, 27:202-203

PAGELS, J.F., K.L. UTHUS and H.E. DUVAL. 1994. The masked shrew, *Sorex cinereus*, in a relictual habitat of the southern Appalachian Mountains. Pp. 103-110 *in* Advances in the biology of shrews (J.F. Merritt, G.L. Kirkland, Jr., and R. K. Rose, eds.)., Carnegie Museum of Natural History, Special Publication 18: 1-458.

RICKART, E.A. 2001. Elevational diversity gradients, biogeography and the structure of montane mammal communities in the intermountain region of North America. Global Ecology and Biogeography, 10:77-100.

SANCHEZ-CORDERO, V. 2001. Elevation gradients of diversity for rodents and bats in Oaxaca, Mexico. Global Ecology and Biogeography, 10:63-76.

SAS INSTITUTE, INC. 1995. Logistic regression examples using the SAS System. SAS Institute, Inc., Cary, North Carolina. 163 pp.

SHVARTS, E.A. and D.V. DEMIN. 1994. Community organization of shrews in temperate zone forests of northwestern Russia. Pp. 57-66 *in* Advances in the biology of shrews (J.F. Merritt, G.L. Kirkland, Jr., and R. K. Rose, eds.), Carnegie Museum of Natural History, Special Publication 18: 1-458.

STEEL, R. G. D. and J. H. TORRIE. 1980. Principles and procedures of statistics: a biometrical approach. McGraw-Hill, New York. 633 pp.

STOKES, M.E., C.S. DAVIS, and G.G. KOCH. 1995. Categorical data analysis using the SAS System. SAS Institute, Inc., Cary, North Carolina. 499 pp.

TEIXEIRA, J., N. FERRAND and J.W. ARNTZEN. 2001. Biogeography of the golden-striped salamander *Chioglossa lusitanica*: a field survey and spatial modeling approach. Ecography, 24:618-624.