Am. Midl. Nat. 151:388–398

Small Mammal Communities of High Elevation Central Appalachian Wetlands

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ABSTRACT.—We surveyed small mammal assemblages at 20 high-elevation wetlands in West Virginia and Maryland and examined relationships among mammal capture rates, richness and evenness and landscape features at multiple spatial scales. In 24,693 trap nights we captured 1451 individuals of 12 species. Small mammal species richness increased with wetland size and was negatively correlated with trail density. Generalists, such as meadow voles (*Microtus pennsylvanicus*) and shrews (*Sorex cinereus*, *Blarina brevicauda*), dominated larger, more open wetlands, whereas southern red-backed voles (*Clethrionomys gapperi*) were more prevalent at smaller sites surrounded by mixed coniferous-deciduous forest stands. Furthermore, meadow voles were captured more often at sites with higher road density and lower trail density. Southern bog lemmings (*Synaptomys cooperi*) were captured at less than half the sites, all of which were surrounded by a high proportion of deciduous forest. Although significant relationships were found, landscape features explained <20% of total variation at any spatial scale. Other factors, such as land use history or competition, likely have exerted a greater influence in small mammal abundance and distribution at these sites.

INTRODUCTION

In recent years, the field of landscape ecology has grown, emphasizing relationships between animal species within a given habitat (*i.e.,* wetlands) and surrounding land use patterns. Issues of dispersal corridors, fragmentation and isolation of suitable habitat have been widely researched for mammals (Bennett, 1990; Andren, 1994; Beier and Noss, 1998; Barrett and Peles, 1999). Small mammals have been used as model organisms in landscape ecology studies for many reasons, including well-known biology and natural history, and the relative ease of mark/recapture and telemetry studies. Additionally, mammal movement often is spatially restricted and their short life span allows for multi-generational studies of dispersal, colonization and extinction rates in relatively short time periods (Barrett and Peles, 1999).

The impact of anthropogenic landscape alteration has been investigated thoroughly for many biological groups, including plants, birds, herpetofauna and small mammals (*e.g.,* Getz *et al.*, 1978; Kozel and Fleherty, 1979; Findlay and Houlahan, 1997; deMaynadier and Hunter, 2000). Roads have facilitated the introduction and spread of exotic species and have caused fragmentation of suitable landscape, habitat loss, wildlife disturbance due to vehicular traffic and wildlife mortality due to vehicle collisions (Canaan Valley National Wildlife Refuge, 2002). Additionally, deMaynadier and Hunter (2000) found that logging roads served as partial barriers to movement of several amphibian species.

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Findlay and Houlahan (1997) found that road density and timber harvesting up to 2 km from study wetlands in Ontario significantly decreased herpetofaunal, avian and plant species richness. Studies by Mitchell *et al.* (1997) and Russell *et al.* (2002) support these findings, concluding that species diversity is linked intrinsically to surrounding land use (*e.g.,* timber harvesting) and landscape structure (*e.g.,* distance to other wetland habitats). In some cases, a disturbance such as timber removal around aquatic breeding sites may lead to amphibian population declines (Mitchell *et al.*, 1997).

The relationship between mammals and surrounding land use, however, is less clear than for herpetofauna and varies greatly among habitat types. In wetlands, Findlay and Houlahan (1997) found that road density did not significantly affect mammal richness or diversity, but mammal species richness significantly increased with greater forest cover. This richness-forest cover relationship, however, typically does not hold true for mammals outside of wetlands. In Kirkland's (1990) review of small mammal responses to clearcutting in North American temperate forests, species abundance and diversity increased immediately following harvest, but overall species richness was not significantly affected. In bottomland hardwoods, Menzel *et al.* (*in press*) found increases in small mammal species richness, diversity and overall abundance following a group selection timber harvest. Small mammal richness increased in new forest gaps that were larger and closer to early successional or oldfield habitats, due to gap invasion by oldfield specialists (Menzel *et al.*, *in press*). These studies demonstrate that generalizations cannot be made about mammalian response to disturbance without considering the surrounding habitat types, the available small mammal species pool and the habitat tolerance of species in the pool of potential colonizers.

High elevation wetlands in West Virginia and Maryland are similar to boreal bogs and fens of the northern United States and Canada in terms of climate, vegetation and chemical characteristics (Francl *et al.*, *in press*). However, little is known regarding the faunal communities of these unique habitat types (*e.g.,* Boynton, 1994; Murdock, 1994; Rossell and Rossell, 1999). Previous surveys have documented the presence of uncommon small mammal species, such as the southern bog lemming and water shrew (*Sorex palustris*), in wetlands of the region (E. Michael, West Virginia University, pers. comm.; D. Feller, Maryland Department of Natural Resources, pers. comm.), but little is known about small mammal communities as a whole.

The goal of our research was to survey small mammals at central Appalachian wetlands to determine if the associated small mammal communities are unique and/or wetland-dependent. We also examined landscape features surrounding the wetlands at several spatial scales to determine the influence of local and regional land use on community structure. Given existing data on mammal communities in central and southern Appalachian wetlands, plus previous trapping effort, we hypothesized that non-wetland species (*i.e.,* generalists or oldfield obligates) would dominate the majority of wetland sites, with wetland obligate species constituting a small but persistent portion of the community. We additionally predicted that, similar to Findlay and Houlahan (1997), species richness would not be related to road density and that meadow vole captures would be higher at sites with higher road densities.

METHODS

Site selection.—Twenty high-elevation wetlands, 17 in Randolph and Tucker counties, West Virginia and 3 partially (portion of one site in Preston County, West Virginia) or entirely in Garrett County, Maryland, were selected for this study (Table 1). Wetlands were located on the Monongahela National Forest, Canaan Valley National Wildlife Refuge, Canaan Valley Resort State Park and properties owned by The Nature Conservancy and were identified

TABLE 1.—Locality information for 20 wetland sites in West Virginia and Maryland surveyed 2001–2002

Code	Site name	County	Elevation (m)	Area (ha)
ABER	Canaan Valley State Park, Abe Run Trail	Tucker, WV	960	3.0
ALDR	Alder Run	Tucker, WV	1164	5.0
BEAL	Canaan Valley NWR, Beall Tract	Tucker, WV	954	1.2
BIGR	Big Run Bog	Tucker, WV	982	15.0
COND	Condon Run	Randolph, WV	918	3.0
CRSW	Cranesville Swamp	Preston, WV/Garrett, MD	794	225.0
FISH	Fisher Springs Run	Tucker, WV	1158	25.0
GLAD	The Glades	Garrett, MD	775	240.0
HAMM	Hammel Glade	Garrett, MD	737	20.0
HERZ	Canaan Valley NWR, Herz Tract	Tucker, WV	983	10.0
HIGH	High Ridge	Tucker/Randolph, WV	1216	28.0
MAIN	Canaan Loop, Main Rd.	Tucker, WV	1111	30.0
MOOR	Moore Run	Randolph, WV	991	2.0
NORT	Canaan Loop, North Rd.	Tucker, WV	1076	15.0
POWR	Canaan Loop, Powerline	Tucker, WV	1099	0.08
REDR	Canaan Loop, Red Run	Tucker, WV	1085	0.4
TRL1	Canaan Loop, Trail 101	Tucker, WV	1038	0.4
TRL2	Canaan Loop, Trail 109/108	Tucker, WV	1067	0.2
TRL3	Canaan Loop, Trail 109/701	Tucker, WV	1085	1.3
YELL	Yellow Creek	Randolph, WV	952	2.5

from communication with natural resource personnel and from appropriate GIS coverages. Sites were categorized as wetlands based on the frequency and duration of inundation and the presence of wetland vegetation. Several of the larger sites have been studied in terms of vegetation, soils or biochemistry (Robinette, 1964; Walbridge 1944). Elevations ranged from 737–794 m at the Maryland sites and 918–1216 m in West Virginia (Table 1).

Small mammal sampling.—We sampled small mammals in 28 × 28 m grids, with trapping stations set approximately 7 m apart (25 stations per grid). To reduce trap bias (Rana, 1982; Mengak and Guynn, 1987), we used a combination of 7.6 × 8.9 × 22.9-cm Sherman live traps, Museum Special snap-traps and 32-oz. pitfalls (964 cm^3) placed in visible mammal runways, along logs or at the bases of hummocks or shrubs within 1 m of the trapping station marker. Trapping permits prohibited lethal traps (Museum Specials) in Maryland, so each trapping station at The Glades and Hammel Glade (Garrett County, Maryland) contained only a Sherman and a pitfall. Traps were baited with rolled oats and peanut butter (snap traps) or only rolled oats (Museum Specials). At each site, traps were set for 5 consecutive nights between May–July 2001 and checked every morning.

We installed 1–12 trapping grids at each site depending on wetland size, visible habitat diversity and amount of trappable area. We first established grids within every vegetative community type present and then laid out additional grids proportionately according to the dominance hierarchy of the habitat types (Sutherland, 1996; Silva *et al.*, 2000). Small wetland sites were sampled at approximately 1 grid/ha. Because larger sites could not be sampled with this same intensity, at least one grid representing each physiognomic type present (*i.e.,* shrub-scrub, open mossy, open grassy and forested patches) was surveyed. To account for variability in trapping effort across sites, results were analyzed using captures per trap night.

All live mammals captured were sexed, aged (juvenile vs. adult), weighed and released. Deceased mammals were prepared as voucher specimens and deposited in the University of Georgia's School of Forest Resources teaching collection or the Georgia Museum of Natural

History. For each site we calculated mean capture per trap night for each small mammal species as a relative index of species abundance. Additionally, we calculated species richness and species evenness (Silva *et al.*, 2000) for each site. Because of unequal trapping effort among sites, we expected that greater sampling effort would yield higher species richness values. Therefore, we employed a rarefaction estimator (Krebs, 1999) to recalculate species richness and evenness. If we found n species at a smaller, less sampled wetland, rarefaction took hypothetical subsamples of n organisms from a larger, more intensively sampled wetland and calculated the average species richness in these subsamples.

GIS analysis.—We mapped the boundaries of mammal trapping grids using a Trimble GeoExplorer 3 (Trimble Navigation Limited, Sunnyvale, CA), differentially corrected the polygons and input our grids as a data layer in ArcView 3.2 (Environmental Systems Research Institute, 1999). We obtained GIS data layers of landscape features surrounding wetlands, including roads, trails and land cover (West Virginia GIS Technical Center, http://www.wvgis.wvu.edu/). Land cover categories were determined from landuse/landcover (LULC) data layers (WebGIS, http://www.WebGIS.com) and Digital Orthophoto Quarter Quadrangle (DOQQ) maps (Maryland Department of Natural Resources, http://www.MSGIC.state.md.us; West Virginia Department of Environmental Protection, http://www.dep.state.wv.us). All layers were either downloaded as or converted to the UTM, NAD83 coordinate system, except for the Maryland DOQQ maps (MD State Plane, NAD83) for analysis. To optimize recognition of wetland land cover classes, we overlaid the smaller scale National Wetlands Inventory (NWI) layer onto the LULC layer, so that NWI designations took precedence over broader LULC wetland categories. If specific NWI wetland types (*i.e.,* emergent or shrub-scrub wetlands) were not designated as LULC categories, we created them in the land cover table.

We constructed buffers of 250 m, 500 m and 1000 m radius around the trapping grids in ArcView. In wetlands where there was a single grid, the buffers were centered on the grid. In wetlands where there were multiple grids, the grids were grouped and buffers were centered on the collection of grids. We overlaid separate layers containing roads, trails and land cover and calculated proportion of each land cover category, road density (m/km^2) and trail density (m/km^2) at each buffer scale.

Statistical analysis.—Pearson product-moment correlations ($\alpha = 0.05$), performed in SYSTAT 9.0 (SPSS, Inc. 1998), were used to examine relationships among small mammal captures and rarified species richness and evenness, and land cover category proportions, road and trail density, wetland size and elevation at each scale. We used canonical correlation analysis and canonical redundancy analysis to examine multivariate relationships between mammal and landscape variables across sites at each scale. Canonical correlation analysis (CCA) combines multiple regression and correlation analyses on a multivariate scale and examines the linear relationship between two sets of variables, creating canonical variables (linear combinations from each set with the strongest between-set correlation). Canonical redundancy analysis (CRA) examines how well the original variables could be predicted from the canonical variables. Separate CCAs and CRAs were performed in SAS 8.02 (SAS Institute, Inc., 2001) correlating a matrix containing small mammal captures per trap night, rarified richness and rarified evenness versus matrices containing land cover proportions, road and trail density, elevation and wetland size for the 250 m, 500 m and 1000 m buffers.

RESULTS

In 24,693 trap nights, we trapped 1451 individuals of 12 small mammal species (Table 2). Overall mammal trap success was 6.7%. Meadow voles (MIPE) and masked shrews (SOCI)

Table 2.—Mean small mammal captures per trap night by species, rarified richness and rarified evenness at 20 wetland sites in West Virginia and Maryland, 2001 and 2002. Site codes are given in Table 1 and species codes are given in the text

Site	BLBR	CLGA	COCR	MIPE	PELE	PEMA	SOCI	SOFU	SYCO	TAHU	TAST	ZAHU	Rarified richness	Rarified evenness
ABER	0.023	0.001	—	0.039	0.004	0.039	0.033	—	—	0.003	—	0.001	9.5	0.71
ALDR	0.015	0.001	—	0.054	0.002	0.002	0.009	—	0.001	—	—	—	9.0	0.50
BEAL	0.018	<0.000	—	0.014	—	0.038	0.011	—	0.003	—	0.007	—	9.4	0.69
BIGR	0.003	0.001	—	0.019	0.001	0.003	0.006	—	—	0.001	—	0.001	7.9	0.67
COND	—	0.004	—	0.008	0.001	0.007	0.009	0.001	—	—	0.001	0.002	7.4	0.69
CRSW	0.003	0.006	—	0.013	—	0.001	0.017	0.002	0.001	—	—	—	9.0	0.67
FISH	0.008	0.003	—	0.036	0.002	0.008	0.009	<0.000	0.001	0.001	—	—	10.2	0.62
GLAD	0.001	—	0.001	0.039	0.003	0.006	0.021	0.002	—	0.001	0.002	—	10.9	0.57
HAMM	0.029	0.001	0.001	0.052	—	—	0.021	—	—	—	0.001	—	9.0	0.54
HERZ	0.011	—	—	0.007	—	0.001	0.011	0.001	—	—	0.001	0.001	8.3	0.64
HIGH	0.022	0.001	—	0.011	0.001	0.014	0.006	—	0.001	0.001	—	0.003	9.1	0.74
MAIN	0.015	0.001	—	0.014	0.001	0.002	0.010	—	—	0.001	0.001	0.001	9.0	0.52
MOOR	0.003	—	—	0.031	0.003	0.003	0.008	—	0.003	—	—	—	7.4	0.61
NORT	0.012	0.002	—	0.006	0.001	0.006	0.015	—	0.001	—	0.003	—	9.1	0.76
POWR	0.011	0.016	—	—	—	0.029	0.019	0.003	—	—	—	—	6.7	0.75
REDR	0.005	0.024	—	—	—	0.027	0.008	—	—	—	—	—	6.5	0.64
TRL1	0.019	0.005	—	—	0.024	0.021	0.016	—	—	—	0.003	—	7.0	0.83
TRL2	0.005	0.019	—	—	0.008	0.019	0.011	—	—	—	—	—	6.3	0.82
TRL3	0.003	0.016	—	—	0.008	0.008	0.029	—	—	0.003	—	—	6.5	0.79
YELL	0.003	0.001	—	0.001	—	0.004	0.002	0.008	0.003	—	—	—	6.3	0.86
Mean	0.011	0.006	0.001	0.023	0.004	0.012	0.014	0.002	0.002	0.001	0.002	0.001	8.23	0.68

dominated the majority of the sites. Other commonly captured species included deer mice (*Peromyscus maniculatus*; PEMA), white-footed mice (*P. leucopus*; PELE), northern short-tailed shrews (BLBR) and southern red-backed voles (CLGA). Star-nosed moles (*Condylura cristata*; COCR), smoky shrews (*Sorex fumeus*; SOFU), southern bog lemmings (SYCO), red squirrels (*Tamiasciurus hudsonicus*; TAHU), chipmunks (*Tamias striatus*; TAST) and meadow jumping mice (*Zapus hudsonius*; ZAHU) were captured at fewer than 10 sites. Rarified richness varied from 6.3–10.9 per site with a mean of 8.2 over all sites, and rarified evenness ranged from 0.50–0.86 with a mean of 0.68 (Table 2).

Correlation analyses indicated that rarified species richness increased with wetland size, decreased with trail density at all scales and decreased with proportion of mixed (coniferous and deciduous) forest cover at the 500 and 1000 m scales (Table 3). Rarified evenness increased with trail density at the 250 and 1000 m scales. Captures of meadow voles, the most common species captured, increased with higher road density (500 m, 1000 m), lower trail density (250 m, 1000 m) and greater proportion of agricultural land (250 m). Two common shrews, the northern short-tailed shrew and the masked shrew, were captured more frequently at sites with higher road density (500 m, 1000 m for *Blarina*, 1000 m for *Sorex*). Southern red-backed vole capture was greater in areas with a higher proportion of mixed forest at all scales, but was lower at sites with more deciduous forest at the 1000 m scale. Capture of southern bog lemmings was greater at sites surrounded by a higher trail density (500 m) and deciduous forest (all scales). Eastern chipmunks also were associated with deciduous forest at all scales. Star-nosed moles, captured at only two sites, were positively correlated to agricultural land. Only the smoky shrew showed a preference for any wetland type (forested wetland at 500 and 1000 m), and capture was positively correlated to wetland size.

Canonical correlation analyses demonstrated strong relationships (squared canonical correlations ranged 0.979–0.999) between first canonical components of the mammal and landscape matrices. This correlation was significant ($P < 0.01$) for the first canonical component for each landscape matrix, except for the 500 m buffer ($P = 0.22$). However, despite the strong correlations, canonical redundancy measures were extremely low, explaining no more than 17% of total variance for any pair combination. Thus, landscape variables explained a relatively small amount of the variation in mammal species captures per trap night, rarified richness and rarified evenness at any scale.

DISCUSSION

As hypothesized, we found that upland mammals, such as meadow voles, masked shrews and deer mice, comprised a disproportionately large percentage of individuals at our sites. Southern bog lemmings, a species commonly associated with wetlands in the region, were present at less than half of the sites and water shrews, a wetland obligate, were not captured. We expect that both species are present in greater numbers than results indicate. For example, extensive tunneling and active bog lemming latrine sites were observed at some sites, indicating the presence of multiple individuals. Additionally, data from the West Virginia Natural Heritage Program indicate that northern water shrews have been captured at Cranesville Swamp several times in the past 70 y, as recently as 1986 (Jennifer Wykle, West Virginia Department of Natural Resources, pers. comm.).

Similar to Findlay and Houlahan (1997), we found a positive relationship between wetland area and rarified mammal species richness. Large open wetlands appeared to function as early successional oldfield habitats, dominated by meadow voles and masked shrews. Judging by species composition, smaller sites were more influenced by surrounding land cover types. Woodland species, such as southern red-backed voles, were most common

TABLE 3.—Pearson's correlations (r, with P-values in parentheses) among small mammal captures/trap night, rarified richness, rarified evenness and landscape features for 20 sites in West Virginia and Maryland, surveyed 2001–2002. Significant correlations($P \leq 0.05$) indicated in bold

	Rarified richness	Rarified evenness	BLBR	CLGA	COCR	MIPE	PELE	PEMA	SOCI	SOFU	SYCO	TAHU	TAST	ZAHU
Roads														
250	0.009	−0.128	0.275	0.064	0.057	−0.054	−0.391	0.340	0.094	0.005	−0.351	0.121	−0.053	0.488
	(0.968)	(0.590)	(0.241)	(0.790)	(0.811)	(0.821)	(0.089)	(0.142)	(0.695)	(0.982)	(0.129)	(0.611)	(0.825)	(0.029)
500	0.382	−0.365	**0.625**	−0.168	**0.499**	**0.510**	−0.352	0.197	0.382	−0.172	−0.295	0.255	−0.099	0.293
	(0.096)	(0.113)	**(0.003)**	(0.479)	**(0.025)**	**(0.022)**	(0.128)	(0.405)	(0.097)	(0.467)	(0.206)	(0.278)	(0.679)	(0.210)
1000	0.389	−0.299	**0.457**	−0.250	0.439	**0.481**	−0.327	0.088	**0.526**	0.011	−0.212	0.367	−0.122	0.269
	(0.090)	(0.200)	**(0.043)**	(0.288)	(0.053)	**(0.032)**	(0.159)	(0.712)	**(0.017)**	(0.963)	(0.369)	(0.112)	(0.608)	(0.252)
Trails														
250	**−0.624**	**0.557**	−0.198	0.362	−0.296	**−0.467**	0.409	0.402	−0.105	0.105	0.419	−0.190	0.231	−0.370
	(0.003)	**(0.011)**	(0.402)	(0.116)	(0.205)	**(0.038)**	(0.074)	(0.079)	(0.659)	(0.660)	(0.066)	(0.422)	(0.327)	(0.108)
500	**−0.492**	0.413	−0.134	0.224	−0.292	−0.365	0.381	0.392	−0.170	0.038	**0.524**	−0.282	0.367	−0.404
	(0.028)	(0.070)	(0.574)	(0.343)	(0.211)	(0.114)	(0.098)	(0.088)	(0.475)	(0.875)	**(0.018)**	(0.229)	(0.112)	(0.078)
1000	**−0.610**	**0.530**	−0.178	0.410	−0.323	**−0.522**	0.372	**0.446**	−0.090	−0.006	0.405	−0.230	0.405	−0.421
	(0.004)	**(0.016)**	(0.453)	(0.073)	(0.165)	**(0.018)**	(0.107)	**(0.049)**	(0.707)	(0.979)	(0.077)	(0.330)	(0.077)	(0.065)
Agriculture														
250	0.272	−0.399	0.415	−0.240	**0.876**	**0.444**	−0.158	−0.298	0.258	0.024	−0.256	−0.102	0.077	−0.101
	(0.247)	(0.081)	(0.069)	(0.309)	**(0.001)**	**(0.050)**	(0.507)	(0.202)	(0.272)	(0.921)	(0.277)	(0.669)	(0.748)	(0.671)
500	0.347	−0.095	0.411	−0.296	**0.718**	0.415	−0.180	−0.181	0.329	0.058	−0.243	−0.009	0.129	−0.050
	(0.133)	(0.691)	(0.072)	(0.206)	**(0.001)**	(0.069)	(0.448)	(0.444)	(0.157)	(0.859)	(0.302)	(0.970)	(0.588)	(0.833)
1000	**0.521**	−0.272	0.198	−0.313	0.315	0.328	−0.186	0.039	0.434	0.304	−0.142	0.134	0.255	−0.031
	(0.019)	(0.246)	(0.404)	(0.179)	(0.176)	(0.159)	(0.432)	(0.870)	(0.056)	(0.192)	(0.551)	(0.572)	(0.278)	(0.897)
Forest: deciduous														
250	0.253	0.072	0.265	−0.207	−0.039	−0.066	−0.202	0.388	−0.131	−0.039	**0.551**	−0.144	**0.719**	0.086
	(0.282)	(0.764)	(0.259)	(0.382)	(0.870)	(0.784)	(0.392)	(0.091)	(0.582)	(0.870)	**(0.012)**	(0.546)	**(0.001)**	(0.718)
500	0.200	0.050	0.271	−0.266	0.042	−0.052	−0.246	0.319	−0.175	−0.033	**0.648**	−0.172	**0.670**	0.074
	(0.399)	(0.834)	(0.248)	(0.258)	(0.861)	(0.828)	(0.296)	(0.170)	(0.460)	(0.889)	**(0.002)**	(0.469)	**(0.001)**	(0.756)
1000	0.282	−0.026	**0.468**	**−0.449**	0.281	0.187	−0.325	0.300	−0.057	−0.102	**0.602**	−0.029	**0.526**	0.322
	(0.228)	(0.915)	**(0.037)**	**(0.047)**	(0.231)	(0.429)	(0.163)	(0.198)	(0.810)	(0.670)	**(0.005)**	(0.905)	**(0.017)**	(0.167)

TABLE 3.—Continued

	Rarified richness	Rarified evenness	BLBR	CLGA	COCR	MIPE	PELE	PEMA	SOCI	SOFU	SYCO	TAHU	TAST	ZAHU
Forest: mixed														
250	−0.418	0.182	−0.351	**0.474**	−0.376	−0.245	0.394	0.080	0.001	−0.125	−0.221	0.108	−0.282	−0.265
	(0.067)	(0.444)	(0.130)	**(0.035)**	(0.102)	(0.299)	(0.085)	(0.737)	(0.996)	(0.599)	(0.349)	(0.651)	(0.229)	(0.258)
500	**−0.470**	0.157	−0.296	**0.444**	−0.292	−0.197	0.360	0.019	−0.072	−0.197	−0.223	0.081	−0.356	−0.144
	(0.037)	(0.507)	(0.206)	**(0.050)**	(0.212)	(0.404)	(0.119)	(0.935)	(0.763)	(0.405)	(0.344)	(0.735)	(0.123)	(0.545)
1000	**−0.516**	0.190	−0.258	**0.443**	−0.231	−0.253	0.318	−0.095	−0.214	−0.233	−0.179	−0.062	−0.358	−0.176
	(0.020)	(0.423)	(0.271)	**(0.050)**	(0.328)	(0.281)	(0.172)	(0.691)	(0.366)	(0.322)	(0.450)	(0.795)	(0.121)	(0.458)
Wetland: emergent														
250	0.094	0.143	−0.313	−0.174	−0.148	0.003	−0.204	−0.266	−0.365	0.136	0.314	−0.128	−0.251	0.000
	(0.693)	(0.548)	(0.179)	(0.463)	(0.533)	(0.989)	(0.389)	(0.258)	(0.114)	(0.568)	(0.177)	(0.591)	(0.286)	(0.998)
500	0.290	−0.097	−0.257	−0.107	−0.142	0.159	−0.178	−0.263	−0.139	0.227	0.080	−0.118	−0.239	−0.086
	(0.215)	(0.686)	(0.275)	(0.653)	(0.551)	(0.502)	(0.452)	(0.262)	(0.599)	(0.335)	(0.737)	(0.650)	(0.309)	(0.717)
1000	0.273	−0.107	−0.182	−0.128	−0.162	0.155	−0.182	−0.148	0.040	0.264	0.068	0.043	−0.276	−0.032
	(0.245)	(0.654)	(0.442)	(0.591)	(0.496)	(0.514)	(0.444)	(0.533)	(0.867)	(0.261)	(0.775)	(0.858)	(0.239)	(0.895)
Wetland: forested														
250	−0.067	0.401	−0.125	−0.110	−0.120	−0.064	−0.071	0.149	0.005	0.231	0.168	0.245	−0.220	0.402
	(0.778)	(0.080)	(0.599)	(0.645)	(0.613)	(0.788)	(0.765)	(0.531)	(0.834)	(0.327)	(0.478)	(0.299)	(0.351)	(0.079)
500	0.340	0.080	−0.194	−0.212	−0.002	0.196	−0.060	0.052	0.303	**0.496**	−0.038	0.302	−0.075	0.252
	(0.140)	(0.737)	(0.413)	(0.369)	(0.993)	(0.408)	(0.801)	(0.827)	(0.195)	**(0.026)**	(0.874)	(0.196)	(0.752)	(0.340)
1000	0.350	−0.103	−0.238	−0.220	0.065	0.204	−0.029	0.025	0.277	**0.504**	0.038	0.252	0.058	0.022
	(0.130)	(0.667)	(0.311)	(0.352)	(0.785)	(0.388)	(0.904)	(0.917)	(0.237)	**(0.023)**	(0.873)	(0.283)	(0.808)	(0.928)
Wetland: shrub-scrub														
250	0.258	−0.270	−0.027	−0.341	−0.238	0.036	−0.318	−0.394	−0.183	0.110	−0.094	−0.081	−0.262	0.326
	(0.273)	(0.250)	(0.911)	(0.141)	(0.313)	(0.880)	(0.172)	(0.086)	(0.441)	(0.643)	(0.694)	(0.734)	(0.266)	(0.161)
500	0.207	−0.206	0.018	−0.244	−0.197	−0.102	−0.284	−0.340	−0.115	0.157	−0.155	−0.091	−0.221	0.260
	(0.380)	(0.383)	(0.941)	(0.300)	(0.406)	(0.669)	(0.225)	(0.142)	(0.630)	(0.507)	(0.614)	(0.702)	(0.350)	(0.269)
1000	0.112	−0.134	−0.015	−0.181	−0.183	−0.185	−0.233	−0.227	−0.115	0.079	−0.059	−0.127	−0.027	0.078
	(0.639)	(0.574)	(0.949)	(0.446)	(0.597)	(0.436)	(0.322)	(0.293)	(0.630)	(0.741)	(0.805)	(0.595)	(0.911)	(0.742)
Wetland	**0.509**	−0.265	−0.291	−0.154	0.123	0.222	−0.116	−0.288	0.191	**0.614**	−0.153	−0.026	0.041	−0.116
size	**(0.022)**	(0.259)	(0.214)	(0.516)	(0.606)	(0.347)	(0.627)	(0.218)	(0.420)	**(0.004)**	(0.519)	(0.912)	(0.865)	(0.627)
Elevation	−0.215	0.172	0.066	0.253	−0.578	−0.280	0.118	0.186	−0.301	−0.418	0.060	0.079	−0.244	0.228
	(0.363)	(0.468)	(0.782)	(0.282)	(0.008)	(0.231)	(0.620)	(0.433)	(0.197)	(0.067)	(0.803)	(0.742)	(0.299)	(0.936)

at small forest gap wetlands bordered entirely by mixed forest. These trends concur with previous research, demonstrating that early successional habitats, whether created naturally or anthropogenically, exhibit higher species diversity values than late successional habitats (*e.g.,* Golley *et al.*, 1965; Kirkland, 1990).

This dominance-habitat size trend by early successional species is not uncommon among small mammals. For example, hispid cotton rat (*Sigmodon hispidus*) densities tend to increase with larger oldfield patch sizes (Foster and Gaines, 1991; Yates *et al.*, 1997), whereas western harvest mice (*Reithrodontomys megalotis*), prairie voles (*Microtus ochrogaster*) and deer mice exhibit increased densities in smaller patch sizes (Foster and Gaines, 1991). Other species, such as oldfield mice (*Peromyscus polionotus*), white-footed mice (*P. leucopus*) and meadow voles show no clear relationship to patch size (Dooley and Bowers, 1996; Yates *et al.*, 1997). Although number of meadow voles captures was not related to wetland size in our study, meadow voles generally were absent from the smaller wetlands (<1.3 ha).

Rarified species richness was inversely related to trail density at all scales, but rarified evenness was positively related to trail density at the 250 and 1000 m scales. Trail density was highest at sites surrounding the small forest bog complexes. Unlike the large bogs, which effectively functioned as oldfield habitats, small bog complexes generally contained a limited number of species associated with the surrounding forested habitats, such as southern red-backed voles. Thus, lower species richness in areas with high trail densities is more likely related to bog size rather than a direct result of trail density. The positive relationship between trail density and rarified evenness is a result of these few forest-associated species being common and in similar abundances in all of the smaller bogs.

As expected, we found that meadow voles were more common at sites with higher road density at the larger scales. The meadow vole is primarily a grassland species and commonly uses grassy roadsides as dispersal routes (Getz *et al.*, 1978). Meadow voles were less common in areas with higher trail densities at the 250 and 1000 m scales. Many of the wetlands with high trail densities were small forest gap bogs surrounded by mixed forest and connected only by a trail system (trail width 1–2 m). We suggest that either these trails were unsuitable corridors for meadow vole movement (LaPolla and Barrett, 1993; Andreassen *et al.*, 1996), or meadow voles were out competed for food and space by southern red-backed voles, which dominated these smaller wetlands (*e.g.,* Grant, 1969; Morris and Grant, 1972; Crowell and Pimm, 1976; Galindo and Krebs, 1985).

We note that mammal-habitat relationships are not consistent across all scales. We often found correlations with the 500 and 1000 m buffers, but not the 250-m buffer. Rarely were all three buffers correlated with a single variable. The most likely explanation for the lack of consistency across scales is the distributional patterns of the wetlands on the landscape. Most of the wetlands occurred in complexes of multiple wetlands within a relatively small area. Thus, the land cover proportions within the 250-m buffers commonly contained a large proportion of wetland types, whereas the larger buffer categories contain only a small proportion of wetland types surrounded by large tracts of upland areas.

The paucity of consistent relationships between mammal capture rates, richness and evenness, and landscape features, indicates that none of these species are completely dependent on wetlands in this region. The sites we examined were dominated by either generalist mammals not constrained by specific habitat requirements or by specialists of surrounding habitat that are utilizing available food and space in the wetlands. Many of the captured species (*e.g.,* southern red-backed voles, deer mice and northern short-tailed shrews) are commonly associated with northern hardwoods and mixed forests within the central and southern Appalachians (*e.g.,* Webster *et al.*, 1985; Healy and Brooks, 1988; Orrock *et al.*, 2000) and are common in the areas surrounding the wetlands. Boynton (1994)

noted a lack of wetland obligate species in southern Appalachian wetlands, suggesting that the small size and patchy distribution of regional wetlands results in the rarity of such species. As with global plant species distributions (Partel, 2002), local patterns in small mammal richness and diversity may be shaped by regional evolutionary history, rather than by local landscape features.

We acknowledge that when examining multiple factors at multiple scales, single univariate correlations may be inadequate descriptors. In these complex environments many factors likely confound one another. However, multivariate analyses performed poorly in explaining the relationships between the mammal community and landscape features at any scale. Given that no more than 20% of total variance was explained by landscape features in any analysis, other factors such as land use history or regional climatic patterns, may be the dominant influence on the small mammal communities in these wetlands and should be the focus of future studies.

Acknowledgments.—We thank the USDA Forest Service Northeastern Research Station, Georgia Museum of Natural History and the D. B. Warnell School of Forest Resources at the University of Georgia for providing funding and equipment necessary to conduct this research. The Canaan Valley NWR provided housing and field assistance. The Nature Conservancy allowed use of its lands for study and the Maryland branch (in coordination with MD DNR) provided DOQQ and other GIS maps of Garrett County, Maryland. We are grateful to S. Dumpert, R. Kotecki, H. Hadley, K. Warren, R. Smith, N. Castleberry and J. Rodrigue for assistance in the field.

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SUBMITTED 7 FEBRUARY 2003 ACCEPTED 27 OCTOBER 2003