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PREDICTING PRESENCE AND ABUNDANCE OF A SMALL MAMMAL SPECIES: THE EFFECT OF SCALE AND RESOLUTION

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Abstract. Management of small mammal communities in forest ecosystems requires a working knowledge of the scales at which species presence and abundance can best be predicted. Habitat-based models were developed to characterize the distribution of a boreal relict, the southern red-backed vole, *Clethrionomys gapperi,* in the southern Appalachian Mountains, USA, at three hierarchical scales of analysis. Vole presence and abundance were most evident at the high-resolution (macrohabitat) scale, followed by the intermediate-resolution scale. The low-resolution model was the least effective for predicting presence or abundance and reflects the need for more resolute landscape classification systems if small mammal populations are to be accounted for in an ecologically relevant manner. Tree and shrub communities indicative of suitable vole habitat included *Fraxinus pennsylvanica* and *Tsuga canadensis* in the canopy and *Carpinus caroliniana* in the understory. Vole abundance increased with incidence of tree species such as *Betula alleghaniensis, Pinus rigida,* and *Prunus serotina* in the canopy, and *Acer spicatum* and woody vines in the understory. Voles were associated with northwest-facing high-elevation sites with abundant rocky substrate, likely a reflection of physiological water and thermal requirements, biogeographic influences, and the importance of substrate complexity for decreasing inter- and intraspecific interactions and avoidance of predators.

Identification of the most effective resolution of landscape characterization improves habitat-based models of *C. gapperi* population dynamics in managed landscapes. Low-resolution habitat classifications may suffice for detecting suitable vole habitats within forest types, but prediction of vole abundance is most accurate at the greatest resolution, i.e., the macrohabitat scale. The utility of forest communities and habitats at various scales to predict vole presence and abundance suggests that *C. gapperi* may be a useful indicator species for identification and assessment of habitat important for rare small mammal species in the southern Appalachians.

Key words: Appalachian Mountains, USA; Clethrionomys gapperi; *habitat selection; indicator species analysis; landscape classification; logistic regression; population ecology.*

INTRODUCTION

Habitat selection affects the distribution of animals across landscapes (Pulliam and Danielson 1991, Dunning et al. 1992). Knowledge of the way in which organisms select habitat is useful for understanding the components that govern ecological systems and for predicting changes in community structure that might follow natural or anthropogenic alterations of ecosystems (Dunning et al. 1995). Because processes that govern habitat selection vary across landscapes and scales of analysis (Thomas and Taylor 1990), ignoring scale risks drawing incorrect conclusions regarding habitat use and importance (Wiens et al. 1987). The measurement of landscape characteristics (Levin 1992) and the perception of density-dependence in a landscape are scale-dependent (Bowers and Matter 1997). Simply, ''reality is size dependent'' (S. Vogel as quoted in LaBarbera 1989), and examining the habitat-specific responses of organisms should utilize a scalar approach to yield the most ecologically relevant conclusions (Morris 1987*a*, Stapp 1997).

Spatially explicit models, which incorporate landscape structure and habitat utilization to predict population responses to landscape change (Dunning et al. 1995, Turner et al. 1995), could benefit from increased predictive ability conferred by using appropriate scales of habitat characterization (Pulliam et al. 1994, Dunning et al. 1995). Understanding how populations are affected by neighboring populations (Pulliam et al. 1994) and how barriers, corridors, and neighboring patches are detected in the landscape depends upon accurate description of landscape boundaries as perceived by study organisms (Dunning et al. 1995). Once the scales of importance have been determined, managers can find a balance between economy of landscape analysis and predictive power with the population of interest.

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Populations of interest are often composed of rare organisms of special management concern (Wiser et al. 1998). The creation of predictive models with more abundant indicator species provides a tool that managers can use to identify areas where rare species are likely to be found. In this case, one study may address several important issues, i.e., examining the scales at which presence and abundance are best predicted for an indicator species allows us to unravel the ecology of the indicator species and provides a means to assess habitat quality for more rare species. Because of moderate dispersal ability (Couch 1998), relative ease of capture, and known association with rare species (Pagels and Tate 1976, Payne et al. 1989, Pagels 1990), the southern red-backed vole, *Clethrionomys gapperi,* provides a model study organism for addressing these issues.

Clethrionomys gapperi is an arvicoline rodent whose distribution ranges from the northern reaches of Canada to the southern portion of the Appalachian Mountains in the eastern United States (Merritt 1981). Once more widespread, post-Pleistocene warming caused *C. gapperi* to withdraw to higher elevation areas in the southern Appalachians (Guilday 1971, Handley 1971). *Clethrionomys* inhabits boreal, mesic forests, as well as recent clearcuts (Steblein 1984, Kirkland 1990). Previous research has noted the characteristics of vole habitat (Fisher 1968, Miller 1970, Merritt 1981, Steblein 1984). However, the response of voles to managed habitats varies (summary in Kirkland 1990), suggesting that habitat selection of *C. gapperi* is not yet completely understood. Morris (1989) and Knight and Morris (1996) have examined vole distribution at multiple scales in Canada, but utilized only a few different habitat types to discern the scales of importance. Our examination extends their work, seeking to identify how *C. gapperi* is distributed within a highly managed landscape composed of many habitat types over a wide expanse.

Our study investigated habitat attributes important for *Clethrionomys* presence and abundance at three scales across a managed landscape with forests of varying species and age composition. Because scale is composed of several characteristics, we examined habitats at varying degrees of resolution, i.e., while the geographic magnitude (extent) remained the same (E. J. Cushing, *personal communication*), information was added regarding the habitats at each subsequent level of analysis, resulting in a gradient from coarse- to fine-grained descriptions of habitat. The habitat analysis was performed in a hierarchical manner (Johnson 1980, Kolasa 1990, Kotliar and Wiens 1990): (1) low-resolution analysis treated the landscape as being composed of seven habitat types; (2) intermediate-resolution analysis treated the landscape as being composed of 15 habitat types; and (3) high-resolution (macrohabitat scale, sensu Morris 1987*a*) analysis treated landscape as being composed of 349 sampling sites. We suspected that presence and abundance of voles might be most evident at different scales of analysis. As such, we examined presence and abundance separately to determine whether red-backed voles perceive these components of habitat differently. If hierarchical selection was applicable, we expected presence to be most evident at lower resolution, while vole abundance should respond to local habitat factors most evident at higher resolution, i.e., the macrohabitat scale.

Red-backed voles are habitat associates of rare small mammals in the region including *Sorex palustris* (Pagels and Tate 1976), *Microtus chrotorrhinus* (Pagels 1990), and *Glaucomys sabrinus* (Payne et al. 1989), and other investigators have suggested that *C. gapperi* might serve as a useful indicator species (Nordyke and Buskirk 1988). As such, models useful for identifying habitat with abundant *C. gapperi* may be useful for the management of rare mammal as well as amphibian species (Pagels et al. 1994, Mitchell et al. 1997). To maximize utility, models were generated using information readily taken from forest inventory data or easily measured by field technicians, such as tree and shrub species, substrate characteristics, and field capacity. Promising management protocols based upon integration of field data, satellite imagery, and GIS technology are still limited in their ability to discern fine-scale differences in habitat. Hence, our large-scale models represent those that could be detected with such technology (He et al. 1998). Through these models, we hoped to determine the utility of large-scale management techniques as they pertain to examining small mammal populations and provide suggestions for their improvement.

The null hypothesis states that *C. gapperi* select habitats equally at all scales, and an examination of habitats at all resolutions will be equally effective in predicting *C. gapperi* presence and abundance. Our objectives were to determine: (1) the scale at which the pattern of red-backed vole distribution was most evident; (2) the ecological factors responsible for red-backed vole distribution patterns; and (3) if both were evident at the same scale of analysis.

MATERIALS AND METHODS

Study area

The survey area consisted of a 160-km^2 portion of the George Washington and Jefferson National Forests in the southern Appalachian Mountains between 38°28′–38°02′ N and 79°40′–79°50′ W. The sampling area was located on, or adjacent to, a portion of the Allegheny Mountain that extends from Hightown to Mountain Grove, Virginia. Sampling sites (hereafter referred to as sites) within the area were chosen randomly within 25 age/habitat classes as defined using United States Forest Service Continuous Inventory of Stand Condition (CISC) data. The number of sites placed in a given habitat type was proportional to the area of that habitat type in the study region, i.e., most habitats were assessed according to their relative availability (Thomas and Taylor 1990). We manually increased the number of rare habitat types sampled to maintain a minimum number of replicates for subsequent analysis; 349 sites were established. Boundaries of all sites were at least 250 m apart and at least 20 m from the edge of the given habitat type. Site location was determined with a Trimble GPS Pathfinder Pro XL and coordinates were corrected using base station data from the Harrisonburg, Virginia office of the U.S. Forest Service.

Survey and collection methodology

Each site was a circular area, 22 m in diameter, with trap stations established within the site at each cardinal direction near the site perimeter. At each station, two $8 \times 9 \times 23$ cm Sherman live traps (H. B. Sherman Traps, Tallahassee, Florida, USA) were placed at likely capture spots within a 2-m radius extending from the site perimeter towards the center. A single $21 \times 21 \times 62$ cm Tomahawk live trap (Tomahawk Live Trap Company, Tomahawk, Wisconsin, USA) was placed within each site. Sherman live traps were baited with whole oats covered with either peanut butter or peanut oil. Tomahawk traps were baited with sunflower seeds. Synthetic bedding material was placed in all traps, and traps were covered with a roofing shingle or leaf litter to provide shelter. A pitfall array was installed within each sample site consisting of a center pitfall surrounded by three other pitfalls spaced 1 m from the center (Type 1B of Handley and Kalko 1993). Each 0.5-L pitfall was connected to the center pitfall by a drift fence made of a 0.3 m high aluminum screening. Pitfalls were filled with ~5 cm of water during trapping and were closed after use.

A 7-d trap session was conducted at each site; a typical session included 30 sites of various habitat types. Pitfall traps were open for seven consecutive days; live traps were pre-baited for two days and then opened for five consecutive days. All traps were checked daily for captures and live traps rebaited as necessary. Specimens were marked with a No.1 monel eartag (National Band and Tag Company, Lexington, Kentucky, USA), and species, sex, age, and mass recorded before release. Dead specimens were injected with 10% formalin solution and deposited in the Virginia Commonwealth University Mammal Collection.

Climatological data were obtained from the weather station at the Bath County Hydroelectric Pump/Storage Facility located near the center of the study area. Trapping sessions were partitioned into seasons by examining plots of data for mean monthly minimum, maximum, and daily temperatures in 1996 and 1997. Sites trapped between 12 May and 10 June were designated spring, those trapped between 26 June and 14 August were designated summer, and autumn sites were trapped between 31 August and 12 September. Sites were partitioned into spring (113 sites), summer (158 sites) and autumn (78 sites). Daily temperatures in the spring (14.6° ± 0.3°C, mean ± 1 SE), summer (21.4° ± 0.6°C), and autumn (19.6°± 0.2°C) were significantly different (paired t tests, $P < 0.01$).

Site analysis

Slope was determined using a Suunto PM-51360 clinometer, and aspect was determined with a compass by estimating the direction water would flow from the center of a site. All woody plants >1 m in height within the site were counted and identified to species. The diameter at breast height (dbh; breast height ~1 m) was recorded for all trees, defined as woody plants with a dbh >0.04 m and height >1 m. Canopy openness, ground cover, and substrate composition were determined using the line-transect method of Canfield (1941). Two transects were established that divided the study area into four equal quarters, bisecting in the center. Along each transect, 40 observations were made using an ocular tube. We tallied observations in the following categories: herbaceous material, leaf litter, bare soil, rock, woody debris, moss, lichen, and whether the canopy was open or closed. One sample point along a transect could yield several tallies, e.g., if a moss-covered rock was shaded by herbaceous vegetation. Tallies of rock were sized according to the following scheme: size 1 <0.2 m, size 2 = 0.2–0.4 m, size 3 = 0.41–0.8 m, and size 4 > 0.8 m. We considered woody debris to be any portion of a woody stem or trunk regardless of the size; the diameter of large woody debris (diameter estimated to be >0.1 m) along the transect was estimated and recorded. In addition to transect data, we counted all downed logs with a diameter >10 cm within each site (Table 1).

Soil was sampled by taking random core samples to a depth of 0.1 m using a 2 cm diameter galvanized pipe section driven into the soil; rocky conditions necessitated use of a pick mattock at some sites. We collected one sample of the top mineral soil horizon from each quadrant of the site, excluding the top layer of organic material and humus. All soil samples were stored on ice and subsequently frozen until laboratory analysis. Prior to analysis, soil samples (excluding the humus layer) were pooled for each site. Moisture holding capacity (field capacity) was determined as in Salter and Williams (1967).

Data treatment

Aspect data were transformed as outlined in Beers et al. (1966) to derive a linear score from the original circular aspect data. In this manner, a score between 0 (southeast aspect) and 2 (northwest aspect) represented aspect at each site. Proportional basal area and proportional abundance of each tree species were summed to generate the importance values for tree species at each site. Importance values were standardized, and the resulting proportions were arcsine square-root trans-

TABLE 1. Variables used to quantify habitat characteristics at study sites in the southern Appalachian Mountains, USA, and the respective abbreviations used in the text.

Scale of analysis	Variable name	Description
Low resolution	n/a	Design variable representing one of seven habitat types
Intermediate resolution	n/a	Design variable representing one of 15 habitat types
High resolution		
Topographic position	ASPECT	Aspect transformed to a value between 0 and 2
	ELEV	Elevation as determined by GPS data
	SLOPE	Inclination of site taken along aspect
Woody components	n/a	Importance value of a tree species
	CANPY	Degree of canopy closure
	SHBTOT	Count of woody shrubs dbh <4 cm and height <1 m
	TOTDBH	Sum of basal area of trees within site
	TRE410	Count of trees with dbh 4–10 cm
	TRE1125	Count of trees with dbh 11–25 cm
	TRE2660	Count of trees with dbh 26–60 cm
	TRE61	Count of trees with dbh >60 cm
	VINES	Sum of importance values for woody vines
Substrate	FC	Field capacity (moisture-holding ability of soil at a site)
	HERB	Percentage of incidence of herbaceous vegetation
	HMHAB	Shannon index measure of substrate diversity
	LEAF	Percentage of incidence of leaf
	LICHEN	Percentage of incidence of lichen
	LOGS	Count of all downed logs diameter >10 cm
	MOSS	Percentage of incidence of moss
	ROCK1	Percentage of incidence of rock <20 cm wide
	ROCK2	Percentage of incidence of rock 20–40 cm wide
	ROCK3	Percentage of incidence of rock 41–80 cm wide
	ROCK4	Percentage of incidence of rock >80 cm wide
	SOIL	Percentage of incidence of bare soil
	WDYDEB	Percentage of incidence of woody debris
	WOODSUM	Sum of estimated diameter of woody debris >10 cm

Notes: Variables were transformed as described in *Materials and methods: Data treatment.*

formed to more approximate normality (Zar 1996). Additional macrohabitat variables representing density of shrubs and trees of various size classes (Table 1) were also examined for relationships with vole presence or abundance. Macrohabitat variables representing substrate components (Table 1) were also standardized and arcsine square-root transformed. Prior to use in regression analysis, all variables were examined for linear responses with the dependent variable. If a nonlinear relationship was detected, variables were transformed or additional variables were added to represent squared or cubed components of the polynomial (Hosmer and Lemeshow 1989, Jongman et al. 1995). Outliers, heteroscedasticity, independence, and normality were assessed using methods outlined in Fox (1991).

Description of scales

Cluster analysis using relative Euclidean distance (Jongman et al. 1995) and the flexible beta linkage method, with $\beta = -0.25$ (Lance and Williams 1967) was used to create low- and intermediate-resolution habitat types based upon tree importance values at each site. The number of final groups was determined by examining group placement in ordination space with detrended correspondence analysis (DCA, McCune and Mefford 1995) and was statistically evaluated using Indicator Species Analysis (Dufrêne and Legendre 1997).

Low-resolution habitat types consisted of seven habitat types; intermediate-resolution habitat types consisted of 15 habitat types (Table 2; Fig. 1). Because the analysis was hierarchical, three of the habitats at the low-resolution scale were split, while the remaining four groups were more homogeneous and remained intact in the intermediate-resolution classification (Table 2). Habitat types loosely follow Eyre (1980), which should be consulted for further description of canopy and understory species associated with each habitat type. These groups were categorized by dominant tree species in each stand type and coded as design variables (Hosmer and Lemeshow 1989) for entry into regression analyses. With the exception of the mixed mesophytic group, these groups will be referred to within the text by the common name of the dominant tree species within the group.

Macrohabitat (high-resolution) models were generated using importance values and variables relating biotic and abiotic structure (Table 1). Variables were entered without the use of data reduction via factoring as found in other studies (Morris 1984, 1987*a*, Adler and Wilson 1987, Knight and Morris 1996). Although factoring techniques combine collinear variables and attempt to discern underlying environmental gradients, all factoring methods have inherent shortcomings (Jongman et al. 1995, McCune and Mefford 1995). Because no final model suffered from excessive mul-

TABLE 2. Classification of habitats based upon flexible beta clustering of tree importance values using relative Euclidean distance.

Low resolution			Intermediate resolution		
Habitat type (code)	No. sites	Dominant tree species	Habitat type (code)	No. sites	Dominant tree species
Mixed mesophytic (MM)	59	*Betula alleghaniensis* *Fraxinus americana* *Fagus grandifolia*	Yellow birch (YB)	7	*Betula alleghaniensis* *Acer spicatum*
			Black cherry (BC)	7	*Prunus serotina* *Carya* spp.
			Green ash (GA)	12	*Fraxinus americana* *Quercus rubra*
			American basswood (AB)	9	*Tilia americana* *Fraxinus pennsylvanica*
			Black birch (BB)	11	*Betula lenta* *Acer pensylvanicum*
			American beech (BE)	13	*Fagus grandifolia* *Tilia americana*
Sugar maple (SM)	55	*Acer saccharum* *Magnolia acuminata* *Tilia americana*	Sugar maple (SM)	55	*Acer saccharum* *Magnolia acuminata* *Tilia americana*
Eastern hemlock (EH)	24	*Tsuga canadensis* *Betula* spp.	Eastern hemlock (EH)	24	*Tsuga canadensis* *Betula* spp.
Northern red oak (NRO)	70	*Quercus rubra* *Acer rubrum*	Northern red oak (NRO)	28	*Quercus rubra* *Acer saccharum* *Ostrya virginiana*
			Red maple (RM)	42	*Acer rubrum* *Quercus rubra*
Chestnut oak (CO)	64	*Quercus prinus* *Kalmia latifolia* *Acer rubrum*	Chestnut oak (CO)	64	*Quercus prinus* *Kalmia latifolia* *Acer rubrum*
White oak (WO)	33	*Quercus alba* *Pinus rigida* *Pinus strobus*	White oak (WO)	33	*Quercus alba* *Pinus rigida* *Pinus strobus*
Table mountain pine (TMP)	44	*Pinus pungens* *Pinus virginiana*	Table mountain pine (TMP)	5	*Pinus pungens* *Pinus virginiana* *Quercus prinus*
			Hickory (Hic)	21	*Carya* spp. *Quercus prinus* *Cornus floridana*
			White pine (WP)	18	*Pinus strobus* *Pinus virginiana* *Quercus prinus*

Notes: Habitats are arranged from the most mesic to the most xeric as determined by mean field capacity of sites grouped at low resolution. Intermediate-resolution groups were created by separating the low-resolution groups.

ticollinearity based upon collinearity statistics described in Myers (1990), use of individual variables was justified and should provide the most informative, ecologically interpretable models.

Statistical analyses

The distribution of voles among habitats and habitat factors indicative of vole presence or absence were determined using stepwise multiple logistic regression (Hosmer and Lemeshow 1989). Design variables were entered into the stepwise procedure except a reference group that represented the lowest suitability vole habitat (Hosmer and Lemeshow 1989). Variables (Table 1) were chosen for retention in the models using subjective interpretation of preliminary models in conjunction with the backwards selection method and the log-ratio selection criterion (Hosmer and Lemeshow 1989). The goodness-of-fit of each model was assessed using the Hosmer-Lemeshow test (Hosmer and Lemeshow 1989).

Factors indicative of vole abundance were identified using multiple linear regression, using only sites where voles were captured. Vole abundance was determined using the minimum-number-alive method (Krebs 1966); juveniles were excluded from analyses. Design variables were treated as described for multiple logistic regression. Final high-resolution models were generated using backwards stepwise multiple linear regression with conventional and relaxed selection criteria (Myers 1990). The relationship between R^2 and adjusted R^2 values was used to gauge the goodness-of-fit of multiple linear regression models, and prediction sums of squares (PRESS) statistics were utilized to select models with the greatest amount of predictive ability. Generally, the smaller the absolute value of the PRESS statistics, the more accurate the model (Myers 1990).

Preliminary statistical analyses, including *t* tests and regression analyses were executed using the SPSS advanced statistics software package (Norusis 1993) and the NCSS statistics package (Hintze 1998). Indicator species analysis (Dufrêne and Legendre 1997), cluster analysis, and DCA were performed using PC-ORD for WINDOWS software (McCune and Mefford 1995). Results were deemed statistically significant if $P \leq 0.05$.

RESULTS

Trapping

A total of 6893 captures of small mammals was recorded during 25 550 trap-nights of effort between 12 May and 5 September 1996 and between 17 May and 5 September 1997. Twenty species were captured at least once; nine species composed 99% of the initial captures. There were 372 initial captures of *Clethrionomys gapperi* at 127 of the sample sites.

Number of voles per site was greatest in the summer (3.3 ± 0.4, mean ± 1 SE), followed by autumn (2.8 ± 0.9) and spring (2.5 ± 0.5). While the variation in vole abundance was not significant (ANOVA, $P = 0.39$), this should be interpreted cautiously because different habitats were sampled during these seasons.

Vole presence

Voles were distributed nonrandomly among habitats ($P < 0.001$). Vole presence or absence was predicted with 69.2% accuracy at low resolution, 67.5% accuracy at intermediate resolution, and 80.1% accuracy at high resolution (Table 3). All models significantly ($P < 0.001$) affected the determination of *Clethrionomys* presence within a site, and fit the data well as measured by the Hosmer-Lemeshow (1989) test of goodness of fit (Table 3).

At low resolution, *Clethrionomys* was most likely to be absent in white oak or table mountain pine stands. At intermediate resolution, *Clethrionomys* was most likely to be present in sugar maple (*Acer saccharum*), mixed mesophytic, eastern hemlock (*Tsuga canadensis*), American beech (*Fagus grandifolia),* and white ash (*Fraxinus americana*) stands. *Clethrionomys* was most likely to be absent from white oak (*Quercus alba*) stands at intermediate resolution.

Macrohabitats characterized by green ash (*Fraxinus pennsylvanica*), black cherry (*Prunus serotina*), and eastern hemlock (*Tsuga canadensis*) in the canopy and American hornbeam (*Carpinus caroliniana*) in the understory were most likely to contain *C. gapperi.* The probability of vole presence was least at very low or very high values of TRE61 (Table 3). Voles were also more likely to be present in habitats as ASPECT approached northwest, ELEV and FC increased, and ROCK2, ROCK4, and WDYDEB increased. Conversely, red-backed voles were least likely to be found in habitats characterized by high WOODSUM, ROCK1, and TRE1125 and coverage of *Vaccinium* spp. shrubs (Table 3).

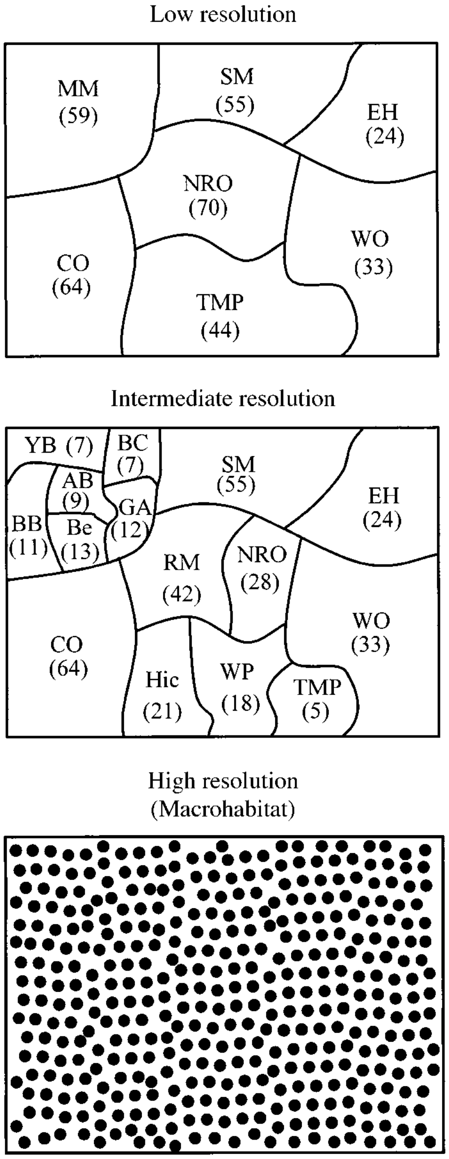

FIG. 1. Levels of resolution used in the analysis. Each square represents the 160-km^2 study area. The number of sites in each habitat type is indicated in parentheses. At low resolution, sites were classified into one of seven habitat types. At intermediate resolution, the seven low-resolution habitat types were further dissected, resulting in 15 habitat types. Note that some habitat types remained undivided, i.e., some habitat types were relatively homogenous. Habitat types are abbreviated using the initial letters of the common names as (see codes in Table 2). At high resolution, all sites ($N = 349$) were considered individually. Note that this figure is greatly simplified for clarity. In reality, habitat types were not one continuous patch as suggested by the low- and intermediate-resolution depictions. Rather, there were many replicates of each habitat type within the study landscape.

Vole abundance

The high-resolution multiple linear regression model accounted for the most variance in red-backed vole abundance at sample sites ($R^2 = 0.67$, $P < 0.001$; Table

TABLE 3. Summary of models predicting the presence and abundance of *Clethrionomys gapperi* in the southern Appalachians, USA, at several spatial scales using logistic regression.

Scale of prediction	Significant variables	Relationship	Model statistics χ^2	P	Percentage correct	Goodness of fit
Low resolution	Mixed mesophytic	Linear (+)	50.3	<0.001	69.2	0.99
	Sugar maple	Linear (+)				
	Eastern hemlock	Linear (+)				
	Northern red oak	Linear (+)				
	Chestnut oak	Linear (+)				
Intermediate resolution	Yellow birch	Linear (+)	19.2	<0.001	67.5	0.99
	American beech	Linear (+)				
	Sugar maple	Linear (+)				
	Eastern hemlock	Linear (+)				
	White oak	Linear (−)				
Macrohabitat	American hornbeam	Linear (+)	129.4	<0.001	80.1	0.97
	Green ash	Linear (+)				
	Eastern hemlock	Linear (+)				
	Blueberry (shrub)	Linear (−)				
	TRE1125	Linear (−)				
	TRE61	Unimodal				
	ASPECT	Linear (+)				
	ELEV	Linear (+)				
	FC	Linear (+)				
	ROCK1	Linear (−)				
	ROCK2	Linear (+)				
	ROCK4	Linear (+)				
	WDYDEB	Linear (+)				
	WOODSUM	Linear (−)				

Notes: Variables were treated and selected as described in *Materials and Methods*. The number of sites used in the analysis was 349.

4). The intermediate-resolution model explained 23% of the variance in vole abundance ($R^2 = 0.23$, $P < 0.001$), followed by the low-resolution model ($R^2 = 0.09$, $P = 0.001$).

At low resolution, vole abundance increased as habitats resembled the mixed mesophytic stand type to a greater degree. Vole abundance increased as habitats more closely resembled the yellow birch, white ash, and American basswood stand types at intermediate resolution (Table 4). *Clethrionomys* abundance increased in macrohabitat comprised of *Betula alleghaniensis, Pinus rigida,* and *Prunus serotina* (Table 4). Vole abundance also increased as *Acer spicatum,* mountain laurel (*Kalmia latifolia*), and vines (*Lonicera* spp. and *Vitis* spp.) increased in the understory. *Clethrionomys* abundance increased with ELEV and ROCK3. Vole abundance decreased as TRE1125 increased.

TABLE 4. Summary of models predicting the presence and abundance of *Clethrionomys gapperi* in the southern Appalachians, USA, at various resolutions using multiple linear regression.

Scale of prediction	Significant variables	Relationship	Model statistics F	P	R^2	Adjusted R^2	PRESS
Low resolution	Mixed mesophytic	Linear (+)	11	0.001	0.09	0.08	184.3
Intermediate resolution	Yellow birch	Linear (+)	11.5	<0.001	0.23	0.21	171.1
	Green ash	Linear (+)					
	American basswood	Linear (+)					
Macrohabitat	Striped maple (shrub)	Linear (+)	24.1	<0.001	0.67	0.64	132.7
	Yellow birch	Linear (+)					
	Mountain laurel	Linear (+)					
	Pitch pine	Linear (+)					
	Black cherry	Linear (+)					
	TRE1125	Linear (−)					
	VINES	Linear (+)					
	ELEV	Linear (+)					
	ROCK3	Linear (+)					

Notes: Variables were treated and selected as described in *Materials and Methods*. The number of sites used in the analysis was 127.

DISCUSSION

Predicting vole presence and abundance

Distribution and abundance of red-backed voles were best predicted using the macrohabitat-scale models. *Clethrionomys* utilized and selected from a relatively discrete portion of the complex landscape, evidenced by decreased accuracy as landscape groups became less resolute (Tables 3 and 4). At the low and intermediate resolutions, habitats viewed as homogenous are composed of an array of habitat patches too heterogeneous at high resolution to accurately predict vole presence or abundance (Fig. 1). This is not surprising considering the large geographic area of the study landscape and the degree of variability introduced by substrate gradients, elevation gradients, and hydrologic interactions.

Large-scale habitat classifications based upon satellite imagery and GIS technology may be useful for predicting habitats suitable for red-backed voles. While large-scale classifications are not useful for predicting *C. gapperi* abundance, such classifications may identify suitable habitats that would be good candidates for macrohabitat-scale investigation. Additionally, macrohabitat data useful for predicting vole abundance can be gathered with a minimal investment of field time, as plant communities and site attributes are relatively easy to quantify. In this manner, managers can assess habitats in a hierarchical manner and can identify areas of concern in a relatively efficient manner. Use of low-resolution classifications may be effective for predicting suitable and quality habitats for generalist small mammal species, such as *Peromyscus* species (Adler and Wilson 1987), which operate at a coarser grain than do specialists (Kolasa 1990). Species of special concern in the region, such as the rock vole (Pagels 1990), water shrew (Pagels and Tate 1976), and northern flying squirrel (Payne et al. 1989), are often associated with habitats where voles are abundant and that are likely to elude low-resolution models. In this regard, the accuracy with which suitable vole habitat can be located supports the utility of *C. gapperi* as a potential indicator species (Nordyke and Buskirk 1988) for locating habitat suitable for these rare species. As technology allows the creation of more resolute classification schemes, managers and modelers alike may be able to better understand how species view and interact with the landscape.

Patterns of vole distribution

Vole presence and abundance were characterized by abiotic and biotic indicators of water availability and high levels of moisture at all scales examined. The physiological basis for selection of moist habitats lies in the dilute urine produced by *C. gapperi* that increases water requirements to between twice (Getz 1968) and nearly ten times (Odum 1944) that of other small mammals such as white-footed mice (*Peromyscus leucopus*) and deer mice (*P. maniculatus*). Downed woody debris provides sheltered runway areas (Miller and Getz 1973, Tallmon and Mills 1994) and provides moist microsites and substrates, favoring growth of hypogeal fungi often consumed by *Clethrionomys gapperi* (Maser et al. 1978, Clarkson and Mills 1994, Waters et al. 1997). The finding that suitability is positively associated with downed woody debris, but negatively associated with the quantity of large (>10 cm) downed woody debris, may reflect the more heterogeneous substrate provided by an abundance of small twigs and branches. Rocky areas provide much-needed components of vertical and horizontal cover that allow *C. gapperi* to avoid capture by predators (Wywialowski 1987) (in light of their poor climbing ability [Getz and Ginsberg 1968] and relatively slow ground speed [Layne and Benson 1954]), and may offer preferred nesting areas (Wywialowski 1987, Stewart 1991). Rocky, talus slopes maintain a thermally stable environment (Hack and Goodlett 1960), moist substrates are more thermally stable (Hack and Goodlett 1960), and suitable vole habitat is characterized by increased cover and an aspect that minimizes solar irradiance.

Requirements for suitable vole habitat provide a characterization of the niche utilized by *C. gapperi* and are similar to the findings of Steblein (1984). Suitable macrohabitats are mesic habitats at moderate elevation with complex substrates. Once these conditions are met, vole abundance increases as elevation increases and evergreen shrub cover (mountain laurel) increases. It is likely that evergreen shrub cover may consistently reduce predation pressure on voles, which are active all year (Merritt 1981). Additionally, the presence of an evergreen shrub layer may also contribute to a sheltered, thermally stable microclimate during temperate seasons. The increase in vole abundance with elevation reflects the ecological conditions under which *C. gapperi* evolved (Guilday 1971).

Implications for habitat selection

Couch (1998) found that voles are not dispersal limited in the southern Appalachians, suggesting that macrohabitat selection is the primary factor constraining vole distribution in the study area, i.e., voles discriminate among habitat patches at this scale (Morris 1987*a*). The efficacy of the high-resolution models suggests that the functional grain (degree of patchiness) at which voles perceive habitat (Kotliar and Wiens 1990) is at the macrohabitat scale. Because habitats were not assessed at a more resolute scale, it is unknown whether voles select habitat at a more resolute grain, although results of this study and those by Morris (1996) and Knight and Morris (1996) suggest not. While the degree to which vole movement is altered by landscape characteristics (Buechner 1989, Dunning et al. 1992, Anderson and Danielson 1997) is unknown, the association of voles with specific macrohabitat features suggests that voles have access to all habitats within the study area, perhaps with the exception of low-elevation habitats. The increasing ability to predict suitable vole habitat with increasing resolution suggests that voles moving across the landscape of the southern Appalachians utilize hierarchical habitat selection (Kotliar and Wiens 1990), although this hypothesis was not specifically tested.

Vole habitat in the study region was composed of relatively distinct ecological conditions at the macrohabitat scale, and vole abundance was related with habitat variables at that scale. When interpreting a landscape, managers must consider changes in patches at high resolution to predict population-level impacts of management on *C. gapperi.* Alteration of macrohabitat is likely to alter population structure, even if dispersal allows colonization of disturbed habitats. Smaller patches of suitable macrohabitat would support smaller populations of *C. gapperi*, with implications that follow from island biogeography theory (MacArthur and Wilson 1967), such as increased probability of local extinction, loss of heterozygosity (Loxterman et al. 1998), and decreased resistance to environmental change (Via and Lande 1985). Landscape effects would include decreased fitness due to increased costs of foraging both in time and increased predation risk (Morris 1987*b*). While the degree to which metapopulation dynamics apply to *C. gapperi* is unknown, macrohabitat size and availability certainly should be considered in this context as well (Hanski and Gilpin 1997). Our research indicates that macrohabitat integrity is essential for vole abundance among a wide variety of habitat types, although abundance also responds to intermediate-resolution variation to a lesser degree. Because habitats with abundant *C. gapperi* often contain a diverse assemblage of small mammals (Pagels et al. 1994), alteration of such habitats may also have serious effects on rare macrohabitat specialists, especially isolated populations (Pagels 1990) and vertebrates of limited dispersal ability (Mitchell et al. 1997).

It is likely that voles exploit different portions of the macrohabitat, if only because resource requirements, predation risk, and social status vary with sex and age (Nordahl and Korpimäki 1998). It is also possible that the scales of habitat use and selection vary among individuals of different sex and age, i.e., perception of opportunities and subsequent selection may be a function of each vole's position in the social hierarchy (Mihok 1979, Bondrup-Nielsen 1987). While our work has identified factors associated with vole presence and abundance, a profitable next step would be to follow cohorts of voles within various habitats in manipulated landscapes to clarify the roles of demographic status, age, habitat quality, and landscape structure in affecting habitat selection by the individual.

Clethrionomys gapperi exhibits macrohabitat selection across a wide geographic range (this study, Knight and Morris 1996, Morris 1996) within a variety of forest types and treatments, providing a framework for understanding how vole populations should be investigated (Morris 1987*a*, Wiens et al. 1987, Dunning et al. 1992). Vole presence and abundance were best predicted at the macrohabitat scale, although presence was also predictable at larger scales of analysis. *Clethrionomys* was associated with specific tree and shrub communities indicative of mesic soil conditions with high field capacity and complex, heterogeneous substrates of rocky talus, woody debris, and cover. Voles were abundant in habitats containing the most complex substrates and poorly drained soils, with an aspect that minimized solar load and reduced thermally induced water stress. Although they may satisfactorily identify areas where voles are present, satellite-imaging systems currently lack the resolution to characterize habitats at a scale fine enough to predict vole abundance within habitats. Therefore, such systems are also limited in their ability to identify areas of habitat in which rare small mammal specialists in the region are often found. The incorporation of macrohabitat-scale forest community patterns with satellite imagery to create spatially explicit models is a promising avenue for bridging the gap between the large-grained scale at which management best operates and the scale at which small mammal distributions are regulated.

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