

MESIC DECIDUOUS FOREST AS PATCHES OF SMALL-MAMMAL RICHNESS WITHIN AN APPALACHIAN MOUNTAIN FOREST

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Forests of Southern Appalachia are critical habitats with respect to biodiversity, with a large portion of these forests residing on public multiuse lands. With pressure to extract timber from maturing forests, there is a need to identify the relative importance of forest types within the larger forest matrix. We examined small-mammal populations at 350 sample points across 157 km² of forested habitat in the George Washington and Jefferson National Forests, Virginia, to determine landscape and habitat correlates of species abundance and richness. A total of 3,955 individuals representing 20 species were captured using live trap and pitfall sampling at each point during 1996 and 1997. Nine species were sufficiently common to examine their abundance relative to landscape and habitat features. We found species abundance and richness to be highest in mesic deciduous forest types, with the exception of *Peromyscus leucopus*. Soil moisture capacity and the proportion of mesic habitat within 100 m of the sample point were also important for several species. If mesic deciduous forest can be considered patches within a matrix of xeric forest, then the abundance of 4 species and species richness could be predicted based on the distance of the sample point to the nearest mesic patch and the abundance of 3 species inside mesic patches was related to patch size. At least 73% of mesic patches within this forest were <25 ha and separated from other patches by >100 m. Our results indicate that mesic forest patches contain the bulk of the species richness for small mammals in the Southern Appalachian ecotype. Designing timber harvests that minimize use of mesic deciduous forest type and that does not decrease patch numbers would achieve the largest benefits to small mammals within the region.

Key words: biodiversity, *Clethrionomys*, forest ecology, landscape ecology, metapopulation theory, *Napaeozapus*, *Peromyscus*, *Sorex*

There is demand to identify lands in managed forests that are suitable for timber harvest and lands where timber harvest should be avoided. Part of this decision-making process is mapping species richness across the landscape and identifying habitat types that differ in their capacity to support diverse communities (Carey and Curtis

1996; Seymour and Hunter 1999). Small mammals are a frequent measure of biodiversity because of their relative abundance, ease in identification, and their critical role in many ecosystems (Entwistle and Stephenson 2000; Lomolino and Perrault 2000). Lomolino and Perrault (2000) reported that small-mammal communities reflect past anthropogenic events on managed forestland of the Olympic Peninsula in Washington.

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Most public land in the eastern United States is forested (McWilliams et al. 2002), and several small-mammal species are common across most forest types and ages (DeGraaf et al. 1991; Healy and Brooks 1988; Linzey 1998; Webster et al. 1985).

There is abundant evidence that small mammals respond to forest loss or are sensitive to the configuration of forest patches within a nonforest matrix (Cummings and Vessey 1994; Laurance 1990; Lomolino and Perault 2000; Mills 1995; Nupp and Swihart 1996; Songer et al. 1997). Predicting the response of small mammals to fragmentation may be confounded by scale and dispersal abilities (Bowers and Matter 1997), but concepts of island biogeography (MacArthur and Wilson 1967) and metapopulation theory (Hanski 1999; Hanski and Simberloff 1997; Levins 1969) are useful for explaining patterns of small-mammal richness within fragmented landscapes (Krohne 1997). Krohne (1997) described a spectrum of landscapes where species varied in their dispersal ability and habitats in their heterogeneity. Using Krohne's criteria, most eastern forests appear to qualify as large expanses of deciduous or coniferous forest with no obvious barriers to dispersal.

Metapopulation theory considers animals to exist in subpopulations of favorable patches that are connected through dispersal (Hanski and Simberloff 1997). Ancillary to this theory is the concept of source and sink populations, with high-quality habitats producing surplus animals that fill low-quality habitats during seasonal or multiannual periods (Pulliam 1988; Pulliam and Danielson 1991). Some mammal populations qualify as metapopulations. Black-tailed prairie dogs (*Cynomys ludovicianus*—Roach et al. 2001) and pikas (*Ochotona princeps*—Smith and Gilpin 1997) are both colonial species that exist in subpopulations that periodically go extinct and are recolonized through dispersal.

Small-mammal species within eastern forested landscapes have been described as microhabitat specialists (Dueser and Shu-

gart 1978; Morris 1979; Orrock et al. 2000) or habitat generalists (DeGraaf et al. 1991; Healy and Brooks 1988) for whom events at larger scales may be irrelevant. The finding that small-mammal populations do not respond consistently to forest management, such as timber harvest (R. T. Brooks and W. M. Healy, in litt.; DeGraaf et al. 1991; Ford and Rodrigue 2001; Healy and Brooks 1988; Kirkland 1990; Sekgorane and Dilworth 1995) or fire (Ford et al. 1999; Kirkland et al. 1996), reinforces the idea that if suitable microhabitat persists, so will most small-mammal species. Their high dispersal ability would allow all available patches to be quickly filled. The insensitivity of small mammals to landscape manipulation within large forest blocks argues against metapopulation theory being a useful concept for management of these species.

For the metapopulation paradigm to be useful for small mammals in eastern forests, the distribution of a species would have to be controlled at 2 scales, e.g., broad habitat requirements that restrict animals to forests, but seemingly homogeneous populations within forests would also exhibit clusters with similar demographic and genetic attributes. High-quality forest patches are colonized through dispersal of animals across a low-quality, or inhospitable, forest matrix. Management practices that reduce dispersal across the landscape or that reduce the proportion of productive patches may significantly decrease species richness without significant reductions in the amount of forest available.

The Southern Appalachians are characterized by complex topography and landform that create a diversity of habitats and forest types (Braun 1950; Eyre 1980). Steep slopes associated with 2nd- and 3rd-order streams create rapid changes from mesic to xeric habitat, with accompanying changes in forest composition. The most diverse habitat with respect to woody plants is mesic deciduous forest, and this forest type is only a small portion of the overall landscape (Braun 1950; Eyre 1980). Mesic de-

ciduous forests, rather than xeric forests, do support higher population levels for at least 2 species, *Clethrionomys gapperi* (Orrock et al. 2000) and *Peromyscus maniculatus* (Long 1996). If mesic and xeric forests are endpoints along a continuum in habitat suitability, the complex topography of many Southern Appalachian forests creates a matrix of habitats with abrupt changes along this continuum. Animals must transverse xeric habitats to colonize mesic habitats, setting the stage for possible metapopulation dynamics.

Two management paradigms are possible for large forest blocks; either small-mammal populations are metapopulations that reside within source or high-quality habitats connected by dispersal, or most small mammals are landscape generalists and are ubiquitous within all suitable microhabitats. Management based on the 1st paradigm must identify high-quality habitats and maintain dispersal corridors or pathways between these patches. Under the 2nd paradigm, managers must pay attention to the proportion of habitats available but not necessarily to the characteristics of the landscape.

Adopting the proper management paradigm is important because the Southern Appalachians are considered an important region for conservation of biodiversity (Ricketts et al. 1999); yet, much of the forested land is either public forest designated for multiple use or private forest owned by timber companies (McWilliams et al. 2002). If the region is >90% forested and annual harvests remove <1% of current forest cover, the management paradigm selected would influence the pattern of the annual harvests. If populations are homogenous because of high dispersal abilities, then timber management should emphasize rotation schedules that ensure that all forest-age groups are represented. If small mammals are arrayed in metapopulations centered around patches of favorable habitat such as mature or mesic forest, then timber management must also maintain source habitats

and the potential for dispersal between habitat patches.

We sampled the small-mammal community across a broad expanse of public forest in western Virginia. Our objective was to measure small-mammal abundance and species richness with respect to landscape features. We tested whether common species are found disproportionately in select habitats and whether their abundance was influenced by the configuration of these habitat types across the landscape. Our goal is to provide concrete advice for timber harvest practices that would conserve small-mammal species based on use of the correct management paradigm.

MATERIALS AND METHODS

Study site.—The survey area consisted of a 157-km² 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 Allegheny Mountain that extends from Hightown to Mountain Grove, Virginia (Fig. 1). Sampling points within the area were chosen within 25 age and habitat classes as defined using United States Forest Service Continuous Inventory of Stand Condition data (Table 1). The study area was divided into 0.58-km² blocks, and within each block a single point was placed in the largest habitat polygon. When 2 points were <250 m apart, the point in the more abundant habitat class was eliminated. This stratified sampling resulted in 300 sample points. We manually placed 50 additional points to increase the number of rare habitat types sampled. This selection process resulted in habitats being assessed according to their relative availability (Thomas and Taylor 1990). All points were located and fixed with a GPS (Pathfinder Pro XL, Trimble, Sunnyvale, California), and coordinates were corrected using data from a base station in Harrisonburg, Virginia (<100 km away).

Mammal sampling.—Each sampling unit was a circular area, 22 m in diameter; 4 trap stations were established in each unit at cardinal directions near the site perimeter. At each station, 2 Sherman live traps (8 by 9 by 23 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida) were



FIG. 1.—Study areas in the George Washington and Jefferson National Forests, Virginia. Patches of mesic deciduous habitat (>5 ha) are based on classification of 1997 Landsat Thematic Mapper image. Also shown are location of sampling units and streams found within Forest Service Boundary.

placed at likely capture spots. A single Tomahawk live trap (21 by 21 by 62 cm; Tomahawk Live Trap Company, Tomahawk, Wisconsin) was placed within each unit. 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 consisting of a center pitfall trap surrounded by 3 other pitfalls spaced 1 m from the center was installed in each sampling unit (type 1B—Handley and Kalko 1993). Each 0.5-liter pitfall trap was connected to the center pitfall trap by a drift fence made of a 0.3-m-high aluminum screening. Pitfall traps were filled with approximately 5 cm of water during trapping and were closed after use.

A 7-day trapping session was conducted at each sampling unit; a typical session included 30 units of various habitat types. Pitfall traps were open for 7 consecutive days; live traps

TABLE 1.—Cross-tabulation of forest habitat categories created and used at different stages of this project.

| Original unit selection | Forest within Forest Service boundary (%) | | Classification based on vegetation measurements | | Landsat Thematic Mapper image (subsetting to region) | |
|---|---|-----------------------------|---|-------------------|--|------------------------|
| | Preselected sites (n) | Forest Service boundary (%) | Habitat classes | Sites sampled (n) | Forest habitat classes | Forest composition (%) |
| CISC ^a habitat types (Forest-type codes) | | | | | | |
| Xeric oak and pine (15, 16, 20, 32, 33, 38, 39) | 25 | 07 | Table mountain pine | 44 | Xeric pine | 34 |
| Dry oak and pine (10, 42, 45, 47, 48) | 32 | 09 | White oak | 33 | Xeric pine | 18 |
| Chestnut oak (52, 57, 59, 60) | 77 | 25 | Chestnut oak | 64 | Xeric deciduous | |
| Mesic red oak (53, 54, 55) | 130 | 50 | Northern red oak | 70 | Mesic deciduous | |
| Mixed mesophytic (41, 50, 56) | 48 | 04 | Mixed mesophytic | 59 | Mesic deciduous | |
| Northern hardwood and coniferous (3, 8, 81) | 33 | 03 | Sugar maple | 55 | Mesic deciduous | 36 |
| Montane (6, 7) | 5 | <01 | — | 0 | Mesic pine | 11 |

^a CISC, Continuous inventory of stand condition.

TABLE 2.—Summary of dominant canopy tree species and mean tree community characteristics ($\pm SE$) associated with each of 4 habitat types derived from 350 sampling units in Allegheny Mountain Region of the George Washington and Jefferson National Forests, Virginia. Dominant tree species were those with the greatest mean indicator values in a particular habitat type. When significant differences among community characteristics existed (1-way ANOVA, $P < 0.05$), we used Tukey's HSD procedure to compare means. Means that were significantly different ($P < 0.05$) are indicated by different superscripts.

| Characteristic | Forest type | | | |
|---|--|--|--|--|
| | Mesic deciduous | Mesic coniferous | Xeric deciduous | Xeric coniferous |
| Dominant canopy species | <i>Acer saccharum</i> <i>Fraxinus americana</i> <i>Tilia americana</i> | <i>Betula</i> <i>Liriodendron tulipifera</i> <i>Tsuga canadensis</i> | <i>Acer rubrum</i> <i>Quercus alba</i> <i>Quercus rubrum</i> | <i>Quercus prinus</i> <i>Pinus pungens</i> <i>Pinus virginiana</i> |
| Species richness | 8.97 \pm 0.17 | 9.54 \pm 0.48 | 9.26 \pm 0.24 | 8.93 \pm 0.35 |
| Diversity (H') | 1.82 \pm 0.02 ^{ab} | 1.71 \pm 0.07 ^a | 1.87 \pm 0.05 ^b | 1.90 \pm 0.03 ^{ab} |
| Evenness (Simpson's E) | 0.84 \pm 0.01 ^a | 0.76 \pm 0.02 ^b | 0.86 \pm 0.01 ^a | 0.86 \pm 0.01 ^a |
| Diameter at breast height (\bar{X}) | 15.65 \pm 0.28 ^a | 18.71 \pm 0.78 ^b | 14.08 \pm 0.38 ^c | 14.89 \pm 0.57 ^{ac} |
| Number of trees | 37.33 \pm 1.17 ^a | 43.00 \pm 3.24 ^{ab} | 43.97 \pm 1.61 ^b | 42.16 \pm 2.79 ^{ab} |

were prebaited for 2 days and then opened for 5 consecutive days. All traps were checked daily for captures and rebaited as necessary. Specimens were marked with a No. 1 monel ear tag (National Band and Tag Co., Lexington, Kentucky), and species, sex, age, and weight were recorded before release. Dead specimens were injected with 10% formalin solution and deposited in the Virginia Commonwealth University Mammal Collection, Richmond, Virginia. Species accumulation curves for the 9 species used in further analyses indicate that the trapping session was of sufficient effort to indicate a species' presence.

Trapping was conducted during a 5-month period (May–September) in 1996 and 1997. Small-mammal densities would be expected to increase over the annual sample period; so each month, we sampled the habitats in proportion to their abundance in the study area. There was no significant change in the number of sites sampled each month (analysis of variance [ANOVA], $F = 0.15$, $d.f. = 4, 14$, $P > 0.1$), when habitat was considered a covariate, indicating that we did not bias the monthly sampling with regard to habitat type.

Discrimination between *P. maniculatus* and *P. leucopus* was accomplished in the field using tail length, coloration, and pelage characteristics. Although studies suggest that external characteristics are less reliable than genetic and mor-

phometric techniques (Bruseo et al. 1999; Rich et al. 1996), distinctions among external characteristics of species in our study area were noted readily in the field, with intermediate forms rarely encountered.

Several environmental measures were taken at each sampling unit. Slope was determined using a clinometer (Sunto PM-51360, Vantaa, Finland). Aspect was determined with a compass by estimating the direction water would flow from the center of the unit. 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. We collected 1 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. Before analysis, soil samples (excluding the humus layer) were pooled for each unit. Moisture-holding capacity (field capacity) was determined as in Salter and Williams (1967).

Habitat classification.—Before ground sampling, the number of study units in each of 24 age and habitat classes was proportional to the area covered by the class in the data set. After ground sampling, habitats were classified using measurements of tree communities at each site (Table 1). All tree species were identified at each unit, and importance values were calculated us-

TABLE 3.—Total and average number of captures per trap site for each species in each of the 7 habitat types (Orrock et al. 2000). Number of sites sampled is indicated in parentheses under each habitat type. Habitats are arranged from mesic to xeric based on mean field capacity of the sites. Total and average number of captures and species richness for each habitat type are also given.

| Species | All habitats (350) | | | Mixed mesophytic (59) | | | Sugar maple (55) | | | Eastern hemlock (24) | | |
|-------------------------------|-----------------------|-----------|-----------|--------------------------|-----------|-----------|---------------------|-----------|-----------|-------------------------|-----------|-----------|
| | <i>n</i> | \bar{X} | <i>SE</i> | <i>n</i> | \bar{X} | <i>SE</i> | <i>n</i> | \bar{X} | <i>SE</i> | <i>n</i> | \bar{X} | <i>SE</i> |
| <i>Blarina brevicauda</i> | 339 | 0.97 | 0.08 | 77 | 1.30 | 0.22 | 54 | 0.98 | 0.18 | 32 | 1.33 | 0.34 |
| <i>Sorex cinereus</i> | 153 | 0.44 | 0.05 | 35 | 0.59 | 0.16 | 26 | 0.47 | 0.12 | 8 | 0.33 | 0.13 |
| <i>Sorex fumeus</i> | 160 | 0.46 | 0.07 | 46 | 0.78 | 0.17 | 29 | 0.53 | 0.19 | 35 | 1.46 | 0.71 |
| <i>Sorex hoyi</i> | 23 | 0.07 | 0.01 | 5 | 0.08 | 0.04 | 3 | 0.05 | 0.03 | 2 | 0.08 | 0.06 |
| <i>Clethrionomys gapperi</i> | 385 | 1.10 | 0.13 | 141 | 2.39 | 0.53 | 76 | 1.38 | 0.31 | 24 | 0.83 | 0.27 |
| <i>Napaeozapus insignis</i> | 212 | 0.61 | 0.09 | 63 | 1.07 | 0.26 | 68 | 1.24 | 0.34 | 17 | 0.70 | 0.34 |
| <i>Peromyscus leucopus</i> | 1,008 | 2.88 | 0.13 | 123 | 2.08 | 0.28 | 136 | 2.47 | 0.31 | 59 | 2.46 | 0.53 |
| <i>Peromyscus maniculatus</i> | 685 | 1.96 | 0.12 | 159 | 2.69 | 0.36 | 156 | 2.84 | 0.32 | 56 | 2.33 | 0.75 |
| <i>Tamias striatus</i> | 360 | 1.03 | 0.08 | 88 | 1.50 | 0.27 | 55 | 1.00 | 0.20 | 10 | 0.42 | 0.15 |
| Total abundance | 3,361 | 9.60 | | 748 | 12.68 | | 608 | 11.05 | | 250 | 10.42 | |
| Species richness ^a | 17 | 3.65 | 0.08 | 13 | 4.36 | 0.23 | 12 | 3.95 | 0.20 | 13 | 4.10 | 0.29 |

^a Includes in addition to 9 focal species listed *Cryptotis parva*, *Sorex dispar*, *Mustela frenata*, *Microtus chrotorrhinus*, *Microtus pinetorum*, *Synaptomys cooperi*, *Glaucomys volans*, and *Neotoma floridana*.

ing the proportional basal area and proportional abundance of each tree species at a sampling unit. 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 group sites with similar tree compositions (see Orrock et al. 2000 for details).

Landscape classification.—A Landsat Thematic Mapper image was acquired on 10 June 1997 and subsetted to a 369,000-ha region that included the study area. Aerial photographs and 7.5-min Digital Elevation Models (USGS, Rolla, Missouri) were also obtained for the region. The vegetation data from the 350 sampling units were split into 2 equal groups, with half used for classification and half for accuracy assessment. The aerial photos were used to divide the image into forest and nonforest classes; then, the forest class was subdivided into deciduous or coniferous classes. The ERDAS (1997) Imagine program (ERDAS Inc., Atlanta, Georgia) was used for image classification. Imagine's ISODATA algorithm clustered the data into 50 classes, and we conducted a hybrid-supervised classification using the topographical information and the 175 ground-truthed units to combine classes. To classify mixed coniferous–deciduous stands into either xeric or mesic classes, we placed a 50-m buffer along each stream and classified all mixed habitats within the stream buffer as mesic co-

niferous and all mixed habitats outside the buffer as xeric coniferous.

Over 80% of the subsetted image was 1 of 4 forest types: mesic deciduous, 107,363 ha (36%); xeric deciduous, 53,347 ha (18%); xeric coniferous, 102,087 ha (34%); and mesic coniferous, 33,934 (11%; Table 1). Accuracy assessment was accomplished using vegetation data from the 172 sampling units not used in the initial classification. Overall accuracy was 74%, with the highest accuracy for mesic deciduous (93%) and the lowest accuracy for xeric coniferous (65%). The 4 habitat classes are readily recognizable on the ground based on differences in dominant tree composition and standard diversity measures (Table 2).

The habitat classification was combined with other data sets to create a Geographic Information Systems (GIS) coverage of the study region (Arcview 3.2, ESRI, Sunnyvale, California). For small-mammal associations, we used the proportion of each habitat type within a 100-m radius of the sampling unit. From the GIS layers we were able to determine the distance from the site to the nearest stream and to the nearest functional road (abandoned logging trails were not considered roads). We also calculated the distance from the site to the nearest nonforest coverage type.

To examine the distance from sampling units to patches of mesic deciduous habitat, we cre-

TABLE 3.—Extended.

| Northern red oak (70) | | | White oak (33) | | | Chestnut oak (65) | | | Table mountain pine (44) | | |
|--------------------------|-----------|-----------|-------------------|-----------|-----------|----------------------|-----------|-----------|-----------------------------|-----------|-----------|
| <i>n</i> | \bar{X} | <i>SE</i> | <i>n</i> | \bar{X} | <i>SE</i> | <i>n</i> | \bar{X} | <i>SE</i> | <i>n</i> | \bar{X} | <i>SE</i> |
| 71 | 1.01 | 0.18 | 22 | 0.67 | 0.19 | 54 | 0.83 | 0.17 | 29 | 0.66 | 0.16 |
| 37 | 0.53 | 0.11 | 8 | 0.24 | 0.10 | 14 | 0.21 | 0.07 | 9 | 0.19 | 0.05 |
| 20 | 0.28 | 0.08 | 6 | 0.18 | 0.07 | 13 | 0.20 | 0.06 | 11 | 0.25 | 0.10 |
| 5 | 0.07 | 0.04 | 1 | 0.03 | 0.03 | 3 | 0.05 | 0.02 | 4 | 0.09 | 0.04 |
| 77 | 1.10 | 0.26 | 7 | 0.21 | 0.14 | 55 | 0.85 | 0.23 | 9 | 0.21 | 0.07 |
| 40 | 0.57 | 0.17 | 1 | 0.03 | 0.03 | 10 | 0.15 | 0.05 | 13 | 0.29 | 0.19 |
| 214 | 3.06 | 0.32 | 139 | 4.22 | 0.47 | 209 | 3.21 | 0.27 | 128 | 2.91 | 0.33 |
| 168 | 2.40 | 0.25 | 21 | 0.64 | 0.19 | 89 | 1.37 | 0.21 | 36 | 0.82 | 0.15 |
| 86 | 1.23 | 0.18 | 35 | 1.06 | 0.25 | 41 | 0.63 | 0.12 | 45 | 1.02 | 0.18 |
| 725 | 10.36 | | 241 | 7.30 | | 491 | 7.55 | | 286 | 6.50 | |
| 11 | 3.96 | 0.19 | 10 | 2.67 | 0.20 | 11 | 3.09 | 0.16 | 11 | 3.18 | 0.17 |

ated an image with only mesic deciduous habitat, smoothed the image using a 5-by-5 majority neighborhood function, and then resampled the image to include only patches >5 ha in size (Fig. 1). This map was then processed with the patch-analyst extension in Arcview to determine the number of patches, mean patch size, and distance to nearest patch.

Statistical analysis.—Habitat associations for species were determined with ANOVA using the 7 habitat classes based on ground-collected data (see Orrock et al. 2000 for details). Before analysis, the distribution of each species was examined for normality, and any outlier in a stem-and-leaf plot was deleted. If the ANOVA indicated significant differences among classes, a Bonferroni correction was performed to compare all possible pairs of habitat classes. The importance of landscape and habitat variables in determining the presence of a species was examined with logistic regression analysis, with a stepwise backward elimination of variables based on their probability of contributing to a predictive model; all variables with $P > 0.05$ were eliminated. Proportions of habitat around each sampling unit were subjected to an arcsine transformation before analysis. The relationship between landscape and habitat variables, as well as a comparison of the abundance of mammals at each sampling unit, was examined using Pearson’s correlation analysis. All means are given with *SE* unless indicated otherwise.

To determine if there was spatial autocorre-

lation between species abundance, we used a Mantel test (PC-ORD Version 4, MjM Software, Gleneden Beach, Oregon), with the standardized Mantel statistic (*r*) as the measure of similarity between abundance and distance matrices (McCune and Mefford 1995; Sokal and Rohlf 1995). We examined both raw abundance data and residuals of the stepwise regression analysis described above. Residuals were used to eliminate environmental differences between sampling units. Linear regression was used to examine species abundance and distance to the closest patch. Before linear regression, the number of individuals captured at a sampling unit was examined for normality, and data for several species were square-root transformed. The relationship between abundance and patch size for moist deciduous habitat was examined using ANOVA, with patch sizes divided into 3 classes: <21 ha, 21–235 ha, and >235 ha. For division of the sample into classes we used 1 *SD* above and below the mean patch size.

Estimating patch occupancy.—Patch occupancy was estimated in 2 ways, with the 1st being number of patches in which each species was captured. However, not all species have equal density or capture probability, so we also estimated the probability that a patch was occupied even if individuals from that species were not captured during the 1-week trapping session. Fifteen patches were sampled more than once, and 6 of these patches were sampled at >5 different locations and contained all com-

TABLE 4.—Analysis of habitat associations based on 7 habitat classes and abundances listed in Table 2. For each species, mean abundance in each habitat class was compared using ANOVA, with a Bonferroni correction of differences between pairs of classes. Species richness is also shown. Asterisks indicate level of significance.

| Species | <i>d.f.</i> | <i>F</i> -ratio | Significant differences in abundance between classes |
|-------------------------------|-------------|-----------------|--|
| <i>Peromyscus leucopus</i> | 6, 335 | 4.34** | White oak > mixed mesophytic and eastern hemlock |
| <i>Peromyscus maniculatus</i> | 6, 337 | 8.65*** | Sugar maple > chestnut oak, white oak, and table mountain pine; red oak > white oak and table mountain pine |
| <i>Clethrionomys gapperi</i> | 6, 320 | 3.27** | Sugar maple > white oak, and table mountain pine; mixed mesophytic > table mountain pine |
| <i>Tamias striatus</i> | 6, 337 | 2.21* | None |
| <i>Napaeozapus insignis</i> | 6, 343 | 4.20*** | Sugar maple > chestnut oak and white oak; mixed mesophytic > chestnut oak and white oak |
| <i>Blarina brevicauda</i> | 6, 338 | NS ^a | |
| <i>Sorex cinereus</i> | 6, 336 | NS | |
| <i>Sorex fumeus</i> | 6, 338 | 2.54* | Mixed mesophytic > chestnut oak |
| <i>Sorex hoyi</i> | 6, 343 | NS | |
| Species richness | 6, 343 | 8.42*** | Sugar maple > chestnut oak and white oak; red oak > chestnut oak and white oak; mixed mesophytic > table mountain pine, chestnut oak, and white oak; hemlock > white oak |

^a NS, not significant.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

TABLE 5.—Significant predictors of animal abundance based on a stepwise (backward) logistic regression on the landscape and habitat features listed. Significant variables are indicated with a plus or minus symbol indicating direction of relationship. Only variables that were significant contributors to at least 1 equation are listed; additional variables tested were distance to openings, distance to streams, aspect, and landform (“Materials and Methods”). Asterisks indicate level of significance.

| Species | χ^2 statistic | Environmental variables | | | | | | |
|-------------------------------|--------------------|---------------------------------------|------------------|-----------------|-----------------|-------------------|---------------|-----------|
| | | Amount of habitat type (within 100 m) | | | | Distance to roads | Soil moisture | Elevation |
| | | Mesic coniferous | Xeric coniferous | Mesic deciduous | Xeric deciduous | | | |
| <i>Peromyscus leucopus</i> | 6.32* | | | | + | | | |
| <i>Peromyscus maniculatus</i> | 33.90*** | | – | | – | | + | |
| <i>Blarina brevicauda</i> | 4.68* | + | | | | | + | |
| <i>Tamias striatus</i> | 3.37 | | | | | | | |
| <i>Clethrionomys gapperi</i> | 17.51*** | | | | | + | + | |
| <i>Sorex fumeus</i> | 18.75** | + | – | + | – | | + | |
| <i>Napaeozapus insignis</i> | 8.00** | | | | – | | | |
| <i>Sorex cinereus</i> | 14.09*** | | | | | | + | |
| <i>Sorex hoyi</i> | 6.78** | | | | | | + | |

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

TABLE 6.—Spatial autocorrelation (Mantel test) between species abundance at each sampling unit for 350 sites sampled for small mammals during 1996–1997. Residual values are from regression equation using variables found to be important in Table 5. Asterisks indicate level of significance.

| Species | Raw abundance data | | Residual values | |
|-------------------------------|--------------------|----------|-----------------|----------|
| | <i>R</i> | <i>t</i> | <i>R</i> | <i>t</i> |
| <i>Peromyscus leucopus</i> | +0.0183 | 1.11 | -0.0131 | 0.66 |
| <i>Peromyscus maniculatus</i> | +0.0551 | 6.86*** | -0.0512 | 2.20* |
| <i>Clethrionomys gapperi</i> | +0.0071 | 0.41 | -0.0699 | 2.69** |
| <i>Napaeozapus insignis</i> | -0.0288 | 1.23 | -0.0315 | 1.19 |
| <i>Tamias striatus</i> | +0.0000 | 0.05 | +0.0223 | 0.99 |
| <i>Blarina brevicauda</i> | -0.0086 | 0.79 | -0.0154 | 0.66 |
| <i>Sorex fumeus</i> | -0.0747 | 3.47*** | -0.0646 | 2.35* |
| <i>Sorex cinereus</i> | -0.0426 | 2.11* | -0.0279 | 1.07 |
| <i>Sorex hoyi</i> | -0.0008 | 0.03 | -0.0096 | 0.36 |
| Species richness | | | -0.0033 | 0.18 |

* *P* < 0.05, ** *P* < 0.01, *** *P* < 0.001.

mon species. For the 6 patches, we calculated the proportion of units where a species was captured and assumed that the mean of these proportions (*P_c*) was an indication of how density and capture probability influenced our ability to estimate patch occupancy. We estimated patch occupancy (*O_c*) with this formula:

$$O_c = O_c + [(1 - P_c)E_c],$$

where *O_c* is the number of patches where a species was captured and *E_c* is the number of patches where the species was not captured. In summary, species were captured at a portion of sampling units within larger patches; we are assuming that this proportion is an indication of species' density and capture probability and can be used to estimate how many of the smaller patches are occupied, despite the failure to record a species' capture within the patch.

RESULTS

Small-mammal sampling.—A total of 6,894 captures and recaptures of small mammals were recorded during 25,550 trapnights between 12 May and 5 September 1996 and 17 May and 5 September 1997. Twenty nonvolant species were captured at least once; of these, 9 species comprised 98% of the 3,361 individuals captured (Table 3). These 9 species were used to examine habitat and landscape factors, but the total number of small-mammal (i.e.,

weight <500 g) species captured at a unit was used to estimate species richness. Habitat classes differed in soil field capacity (ANOVA, *F* = 8.20, *d.f.* = 6, 343, *P* < 0.001), with mixed mesophytic forest being the wettest habitat.

Habitat associations.—Each of the 9 abundant species was found in all 7 habitat types, but habitats differed in the mean number of species captured at a sampling unit (ANOVA, *F* = 4.20, *d.f.* = 6, 343, *P* < 0.001; Table 3). Three species (*Blarina brevicauda*, *Sorex cinereus*, and *S. hoyi*) were not associated with specific habitats, 1 species (*Tamias striatus*) was habitat specific but not with respect to moisture, 1 species (*P. leucopus*) was found predominately in xeric habitats, and 4 species (*P. maniculatus*, *C. gapperi*, *Napaeozapus insignis*, and *S. fumeus*) were associated with mesic habitats (Tables 3 and 4). Mixed mesophytic and sugar maple habitat types had significantly more mammals than white oak and chestnut oak habitats (Table 3). Total number of individuals captured also followed this soil moisture gradient, with the greatest number of captures in the mixed mesophytic and fewest captured in table mountain pine habitats (Table 3). Overall, captures in the mixed mesophytic habitat were approximately twice the mean number

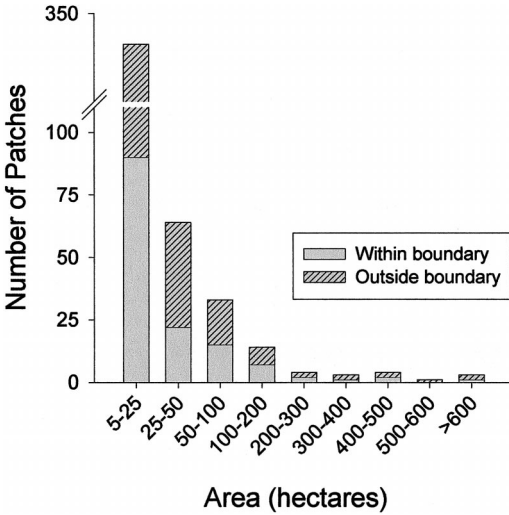


FIG. 2.—Patch size, as shown by the number of mesic deciduous forest patches (>5 ha), found within the study region of each size class. Number of patches that were wholly or partially within the George Washington and Jefferson National Forest boundaries used for this study are indicated in solid gray.

of captures in the table mountain pine habitat. This abundance gradient is obvious despite the large numbers of *P. leucopus* recorded in the 3 more-xeric habitats.

Landscape and habitat features.—We used logistic regression analysis to determine if species' abundance was related to

aspect, elevation, soil moisture, landform index, proportion of each habitat within 100 m of the site, or distance from roads, streams, and forest edges (Table 5). For most species (a notable exception was *P. leucopus*), the proportion of mesic habitats and soil moisture were significant predictors of presence of a species. The 2 xeric habitats, both coniferous and deciduous, were negatively correlated with the presence of 3 species. The landscape variables distance to openings or streams, aspect, and landform were not retained in the final model for any species. One species, *C. gapperi*, was positively associated with roads. *P. leucopus* was positively associated with amount of xeric habitat around the unit.

We examined the correlation between all environmental variables measured using Pearson's *r*. As expected, streams were found near mesic coniferous ($r = 0.28$; $P < 0.01$) and deciduous ($r = 0.17$; $P < 0.05$) habitats, roads were found near forest openings ($r = 0.20$; $P < 0.01$), and xeric deciduous habitat was found near forest openings ($r = 0.28$; $P < 0.01$). The proportions of habitat around a sampling unit were not independent. For example, increased mesic deciduous habitat was negatively correlated with the amount of forest opening ($r = -0.28$; $P < 0.01$) and the amount of xeric deciduous habitat ($r = -0.29$; $P < 0.01$).

TABLE 7.—Number of patches occupied for each species, in the 50 mesic forest patches sampled. Probability of capture (P_c) was the proportion of sites within a patch where the animal was captured based on the 6 patches where we sampled >5 sites.

| Species | Number of patches with capture | Probability of capture within a patch | Estimated number of patches occupied ^a |
|-------------------------------|--------------------------------|---------------------------------------|---|
| <i>Peromyscus leucopus</i> | 47 | 0.74 | 48 |
| <i>Peromyscus maniculatus</i> | 37 | 0.76 | 40 |
| <i>Blarina brevicauda</i> | 30 | 0.52 | 40 |
| <i>Tamias striatus</i> | 29 | 0.45 | 41 |
| <i>Clethrionomys gapperi</i> | 21 | 0.54 | 34 |
| <i>Sorex fumeus</i> | 19 | 0.35 | 39 |
| <i>Napaeozapus insignis</i> | 16 | 0.33 | 39 |
| <i>Sorex cinereus</i> | 23 | 0.31 | 42 |
| <i>Sorex hoyi</i> | 9 | 0.18 | 43 |

^a Estimated patch occupancy = $O_c + ((1 - P_c)E_c)$, where O_c is the number of patches where a species was captured, E_c is the number of patches where the species was not captured, and P_c is the probability of capture in a patch.

TABLE 8.—Comparison of number of individuals captured at each sampling unit and distance from that unit to nearest patch of moist deciduous forest (>5 ha) and mean abundance of each species at sampling units within moist deciduous patches of differing size. Asterisks indicate level of significance.

| Species | Distance to patch | | Patch size | | | d.f. | F-ratio |
|--------------------------------|-------------------|---------|----------------|--------------------|-----------------|--------|---------|
| | d.f. | F-ratio | Small (<21 ha) | Medium (21–235 ha) | Large (>235 ha) | | |
| <i>Peromyscus leucopus</i> | 1, 346 | 4.74* | 3.09 + 0.38 | 2.71 + 0.26 | 2.69 + 0.37 | 2, 131 | 0.41 |
| <i>Peromyscus maniculatus</i> | 1, 346 | 3.68* | 1.58 + 0.28 | 1.86 + 0.23 | 2.70 + 0.32 | 2, 127 | 3.72* |
| <i>Blarina brevicauda</i> | 1, 343 | 0.35 | 0.57 + 0.16 | 0.92 + 0.16 | 0.79 + 0.18 | 2, 133 | 1.26 |
| <i>Tamias striatus</i> | 1, 346 | 0.58 | 0.94 + 0.22 | 0.89 + 0.14 | 1.03 + 0.23 | 2, 129 | 0.13 |
| <i>Clethrionomys gapperi</i> | 1, 327 | 4.79* | 0.47 + 0.16 | 0.55 + 0.11 | 1.00 + 0.17 | 2, 123 | 3.47* |
| <i>Sorex fumeus</i> | 1, 344 | 1.68 | 0.42 + 0.14 | 0.27 + 0.10 | 0.69 + 0.19 | 2, 130 | 4.31* |
| <i>Napaeozapus insignis</i> | 1, 348 | 8.16*** | 0.77 + 0.31 | 0.74 + 0.23 | 0.66 + 0.26 | 2, 133 | 0.04 |
| <i>Sorex cinereus</i> | 1, 345 | 0.78 | 0.29 + 0.10 | 0.36 + 0.90 | 0.32 + 0.09 | 2, 130 | 0.15 |
| <i>Sorex hoyi</i> ^a | 1, 348 | 1.21 | | | | | |
| Species richness | 1, 348 | 9.31** | 3.69 + 0.27 | 3.74 + 0.20 | 4.34 + 1.43 | 2, 133 | 0.13 |

^a Sample size insufficient for analysis of patch size.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

In addition to individual species, we also used linear regression to examine species richness and the same landscape variables (Table 4). Species richness followed the same trends as individual species, with more species found at sites with increased moisture. Xeric forests lacked most species with the exception of *P. leucopus*.

Spatial autocorrelation.—A comparison of the distance matrix for the sampling units and abundance matrix for each species revealed 3 species to be spatially autocorrelated according to a Mantel test (Table 6). For *P. maniculatus*, nearby populations were more similar, but for 2 insectivore species *S. cinerius* and *S. fumeus*, populations farther apart were more similar in abundance. Because several landscape and habitat variables were found to be important in earlier analyses and these factors might obscure spatial patterns, we substituted the abundance matrix for each species with the residuals of the regression formula that best explained each species' abundance. This matrix substitution did not greatly improve our ability to predict abundance based on spatial proximity. Three species were still significant (i.e., *P. maniculatus*, *S. fumeus*, and *C. gapperi*), but the *r*-values for all 3

were negative, meaning farther populations are more similar. In summary, a species' abundance at a unit was not influenced by the species' abundance at nearby units and in some cases may have been significantly dissimilar to the closer survey units.

Mesic deciduous habitat patches.—After resampling the habitat map to include only patches of mesic deciduous forest >5 ha, there were 469 patches within the region, with 141 patches at least partially in the study boundary. The mean patch size for the region was 38.2 ha ±5.6 SD, and the mean distance between patches was 147 m. For patches that were partially or wholly within our study area boundary, the mean size was 54.9 ±15.8 ha, with a mean distance of 118 m between patches. Most mesic patches were relatively small; 73% were <25 ha (Fig. 2). We sampled 50 of the 141 mesic deciduous patches, with 1–32 samples/patch. We did not assume that a species would be captured at every sampling unit within a patch because of species-specific differences in density and ease of capture. For patches sampled at ≥5 locations, we used the proportion of sites occupied as an indication of these 2 factors. When examining all mesic patches, species varied in

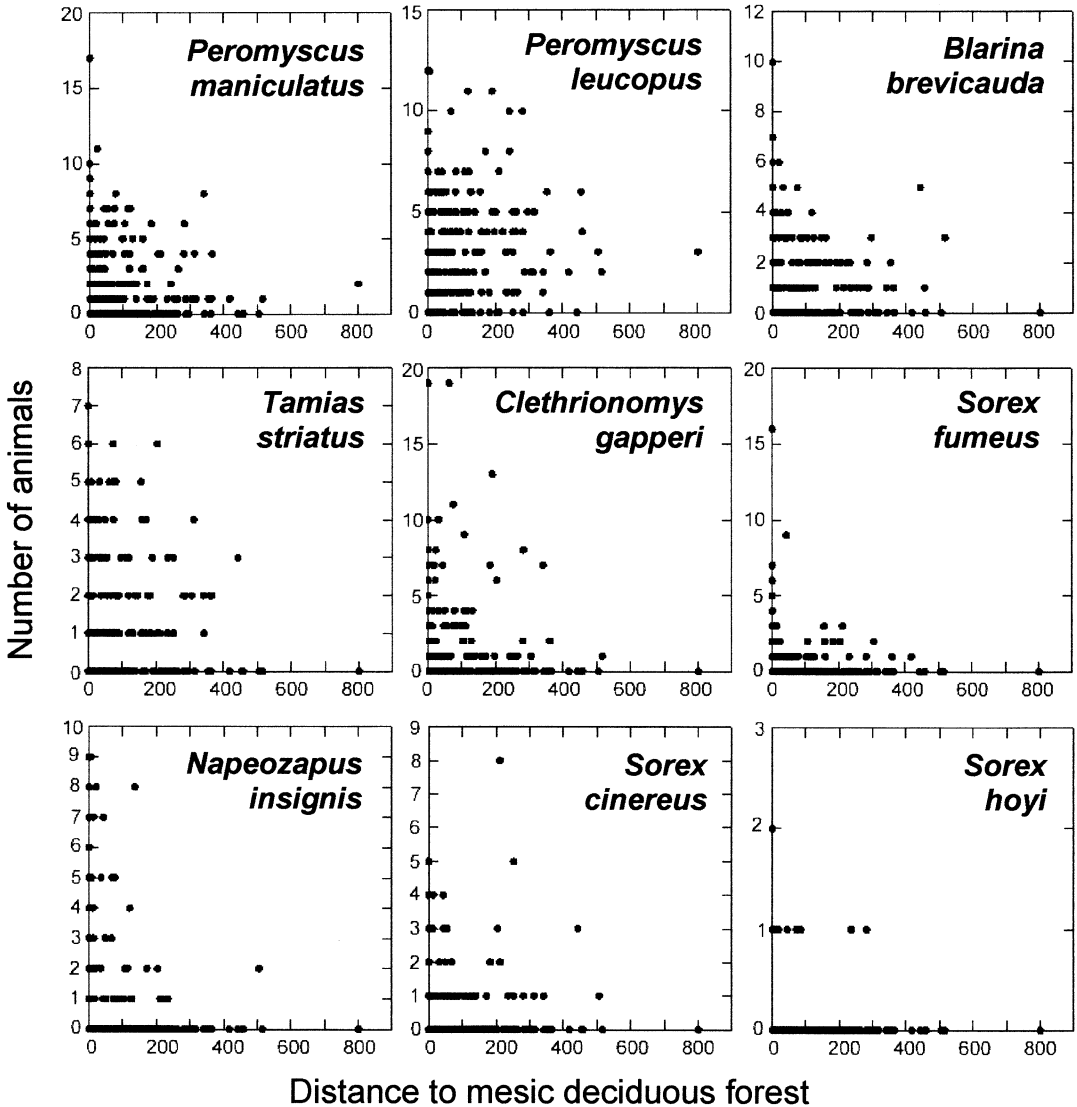


FIG. 3.—Relationship between number of individuals captured at a sampling unit and distance from that unit to a patch of moist deciduous forest, within the George Washington and Jefferson National Forests, Virginia.

the number of patches where they were captured, but most of this variability can be accounted for by the lower capture probability for the rarer species (Table 7).

We examined species abundance at each sampling unit relative to the distance from that unit to the closest patch of moist deciduous habitat (Table 8; Fig. 3). For 4 rodent species, there was a significant relationship between abundance and distance to

moist habitat patches, as identified in the satellite imagery. For 3 of these species, *P. maniculatus*, *C. gapperi*, and *N. insignis*, the relationship was for increased numbers closer to mesic habitat patches; for the 4th species *P. leucopus*, more individuals were captured farther from moist deciduous habitat. For 4 insectivore species and *T. striatus*, there was no significant relationship between captures and distance, although for

insectivores a gradient was evident (Fig. 3). Species richness was also highest at units closest to a moist deciduous patch (Table 8).

For sampling units within moist deciduous patches, we examined relative patch size and each species' abundance. There were significantly more individuals in larger patches for 3 species examined: *P. maniculatus*, *C. gapperi*, and *S. fumeus* (Table 8). Measures for species richness and the remaining species showed no significant trend between patch size and abundance.

DISCUSSION

All common species were found at least once in each habitat type, indicating that these small mammals are habitat generalists at the larger scale. However, for most species, abundance followed a moisture gradient, with mesic habitats containing more individuals and species than do xeric habitats. Habitat association data were reinforced by landscape analysis, with the proportion of mesic or xeric habitat within 100 m of the sampling unit, a common element of the final predictive equation. These findings are in agreement with previous microhabitat studies that found higher abundances in mesic habitats for some of the common species used in this study (DeGraaf et al. 1991; Doyle 1990; Ford et al. 1999; Getz 1994; Orrock et al. 2000).

We used this affinity for mesic sites to identify favorable habitat patches within the landscape. As predicted by a metapopulation model (Hanski 1999), and not by a habitat selection model, not all favorable patches were occupied. Compensating for the species' differences in density and capture probability did not change our findings, but rather most species have an 80% patch occupancy. Outside mesic patches, the closer a sampling unit was to a mesic patch the more likely that the species was present for *P. maniculatus*, *C. gapperi*, and *N. insignis*. Within mesic patches, large patches had more animals per sampling unit than did small patches. All these findings indicate

that for several small-mammal species the most effective management paradigm would be to consider these species as metapopulations.

Hanski (1999) identified 4 criteria for a metapopulation's persistence: breeding populations are discrete, local populations are asynchronous, all populations have a high risk of extinction, and recolonization is possible. There are supporting data that these conditions are met by small-mammal populations within this region, although most studies concern rodent species. Breeding female *Peromyscus* (Wolff 1989) and *Clethrionomys* (Gliwicz and Glowacka 2000) are relatively sedentary. Genetic and demographic differences occur among subpopulations of *P. maniculatus* separated by as little as 350 m (Bowman et al. 2000a). Krohne and Baccus (1985) found genetic and demographic subpopulations in a seemingly continuous population of *P. leucopus*. In our study, the absence of *P. maniculatus*, *C. gapperi*, and *N. insignis* from some favorable patches indicated that these subpopulations were not experiencing equivalent levels of productivity or mortality.

Patch extinction is possible because predators can quickly extirpate local populations (McShea 1990) and are responsible for the majority of rodent mortality in forests (Jedrzejewski and Jedrzejewska 1993) and fields (Dyczkowski and Yalden 1998). A probable predator *Mustela frenata* was captured at 10 sampling units, 7 of which were in mesic deciduous habitat. For predators to limit prey, their scale of movements should match the scale of the prey population, a case often found with mustelids and rodents (Ehrlinge 1983; Ehrlinge et al. 1983). *M. frenata*'s home-range size (18–80 ha—Sheffield 1999) is similar to >70% of the mesic patches in this region.

The recolonization ability of most small mammals, particularly soricids, is unknown. Examination of the density curves (Fig. 3) indicates that most species are not found >350 m from a mesic forest patch. Bowman et al. (2000a, 2001) found a

strong autocorrelation between genetic samples taken at 130 m but not at 500 m for *P. maniculatus*. The same study (Bowman et al. 2000b) reported maximum dispersal distances for *P. maniculatus* (370 m), *N. insignis* (225 m), and *C. gapperi* (224 m) that would indicate that these species are capable of recolonizing vacant patches within our system.

Use of a metapopulation model would have important ramifications for forest managers with respect to how forests are harvested. The most far-reaching implication is that absence of individuals from a patch does not imply that the patch is unfavorable or surplus habitat. Present surveys for threatened or endangered species are usually specific to the land agency involved but originate from mandates within the National Environmental Policy Act (NEPA) of 1969 (42 U.S.C. 4321-4347) or Endangered Species Act (USFWS 1992) to guard against destruction or adverse modification of habitat. In our experience, biologists conducting a NEPA review of a site consider it suitable for harvest or modification if no sign or individual of the rare species is detected. Our data indicate that 20% of all patches are unoccupied at any time, and low-density species were detectable at <30% of the sampling units within occupied patches. Therefore, nondetection of an endangered species within suitable habitat is not a valid criterion for approving harvest or other habitat-modifying activities.

This analysis was conducted on common species primarily to obtain adequate sample size. Most concern in the study area is for the less common boreal forest species such as water shrew (*S. palustris*), Allegheny woodrat (*Neotoma floridana*), northern flying squirrel (*Glaucomys sabrinus*), and rock vole (*Microtus chrotorrhinus*). Given that the habitat and geographic affinities of these species (Pagels 1987; Pagels et al. 1998; Payne et al. 1989) more closely mimic species such as *C. gapperi* (Orrock et al. 2000; Reese et al. 2001) and not *P. leuco-*

pus, we assume that these species also exist within metapopulations.

Our description of eastern deciduous forests does not match a strict definition of metapopulations, where habitable patches are embedded in a nonhabitable matrix (Hanski 1999; Levins 1969). Our xeric forest matrix supported individuals, which may or may not have been breeding, based on our observation that some individuals from all species were captured in each habitat type. Our conception of this forest metapopulation is akin to the current understanding of breeding migratory birds, where many forest habitats are suitable for birds to attempt breeding, but only some forests contain sustainable populations (i.e., source-sink habitats—Pulliam 1988; Pulliam and Danielson 1991). Landscape and regional examinations of bird populations do not focus on whether a species occupies a specific stand but rather on large-scale trends in abundance and productivity (Buford and Capen 1999; Mitchell et al. 2001; Peterjohn and Sauer 1994). Only subsequent research would determine whether some small-mammal populations truly mimic bird populations with respect to population dynamics.

In conclusion, we believe the evidence presented in this article indicates that mesic deciduous patches should be harvested with caution regardless of species occupancy during a specific survey. We encourage research on the productivity, dispersal, and predation pressures of small-mammal subpopulations within large forest tracts to clarify the landscape patterns we observed. If metapopulation theory is the paradigm for managing small-mammal species richness in eastern forests, then the integrity of this patch matrix is more important than the occurrence of a species in a specific patch. Managers of National Forests have the ability to work at the landscape scale: all large mesic patches in this study region were on public lands, and most forestry practices are now planned at the landscape level with biodiversity (Carey and Curtis 1996) or

ecological sustainability (Seymour and Hunter 1999) as a goal. The problem is that most sampling for small mammals, unlike migratory birds, is still being conducted at the stand level, a scale inappropriate for the management issues involved.

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