

Special Section: The Value and Utility of Presence–Absence Data to Wildlife Monitoring and Research

MODELING PATCH OCCUPANCY BY FOREST RODENTS: INCORPORATING DETECTABILITY AND SPATIAL AUTOCORRELATION WITH HIERARCHICALLY STRUCTURED DATA

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Abstract: Widespread conversion of deciduous forests to agriculture in the midwestern United States has resulted in landscapes whose remaining native habitats are highly fragmented, with well-documented consequences for wildlife community structure. We analyzed trap data for 5 forest rodent species from 525 sites in 35 study landscapes throughout the upper Wabash River basin, which is dominated by agricultural use and drains >20% of Indiana. We used a recently developed likelihood approach and multi-model inference to obtain unbiased estimates of occurrence probabilities for a species when detection rates are <1, and we used hierarchical generalized linear modeling to evaluate random effects associated with nested data structure. Inclusion of a spatial autocovariate term had important effects on model selection results for 4 of 5 species and improved fit of models. Eastern chipmunks (*Tamias striatus*), although previously described as sensitive to fragmentation, were nearly ubiquitous in our study region and had greater occupancy rates in smaller woodlots. Fox squirrels (*Sciurus niger*) are well adapted to patchy landscapes, and their occupancy rates actually increased with patch isolation. Gray squirrels (*S. carolinensis*) are adversely affected by forest fragmentation; we observed a threshold decline in occupancy rates beyond ~15 km from the Wabash River, which harbors the only source of contiguous habitat within the entire river basin. Red squirrels (*Tamiasciurus hudsonicus*) exhibited greater abundance in sites without gray squirrels. Moreover, their occupancy rates were positively related to habitat and landscapes considered suboptimal (e.g., lower basal area of hard-mast bearing trees, more isolated patches); this was further evidence for negative effects of gray squirrels on red squirrel populations. White-footed mice (*Peromyscus leucopus*) were nearly ubiquitous; although occurrence rates in less forested landscapes increased with distance from edge and greater volume of woody debris.

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Habitat loss and fragmentation are serious and ongoing threats to native biodiversity, particularly in landscapes intensively used by humans for food production. The problem is exemplified in the midwestern United States by the vast conversion from deciduous forest and tallgrass prairie to agriculture. Across the states of Illinois, Indiana, Iowa, Minnesota, Missouri, Ohio, and Wisconsin, approximately 60% of forest and >99% of prairie habitat have been lost since pre-European settlement levels (Smith et al. 1994, Robertson et al. 1997). Loss of native vegetation has resulted in local extinctions of mammalian fauna. Illinois lost 25% of its mammalian species (Mankin and Warner 1997, Hoffmeister 1989), and Indiana lost nearly 20% (Mumford and Whitaker 1982). Of the 55 remaining native mammal species in Indiana (S. Knapp et al. 2003), 2 are federally endangered

(Indiana bat [*Myotis sodalis*], gray bat [*M. grisescens*]), an additional 8 are state endangered, and another 13 are state species of special concern (<http://www.in.gov/dnr/fishwild/endangered/mammal.htm>).

Having lost those species most sensitive to habitat reduction and human disturbance, extant Midwestern mammal communities now comprise many species that are tolerant of or even benefit from human alteration of landscapes (Swihart et al. 2003). However, mammalian population responses could lag behind the actual moment of landscape change, depending on species-specific variation in sensitivity to fragmentation and rate of population dynamics (Tilman et al. 1994). Thus, a species negatively affected by habitat fragmentation might continue to exist in a highly fragmented landscape, but be on a slow path to local extinction (ter Braak et al. 1998). Similarly, species might exhibit threshold responses to fragmentation so that a disturbed landscape still

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capable of supporting a species might become completely unsuitable following slight additional disturbance (Fahrig 2001). These factors necessitate research to evaluate possible future consequences of prior land-use change for extant species, and to measure the relative sensitivity of species to various degrees of habitat fragmentation.

Logistic regression is a common approach for assessing the relationship between environmental characteristics and species presence-absence data collected from a number of sites. However, ordinary logistic regression can be problematic in this context for several reasons. First, non-detection of a species at a site does not mean the species is absent unless detection probability = 1 (MacKenzie et al. 2002, Tyre et al. 2003). Non-detection error leads to biased parameter estimates in logistic regression (Gu and Swihart 2004) or metapopulation incidence function models (Moilanen 2002), and if associated with site-specific covariates, the consequences of nondetection error are more severe (Gu and Swihart 2004). MacKenzie et al. (2002) developed a likelihood-based approach for simultaneously obtaining unbiased estimates of site-occupancy rates (ψ) and detectability (p) when $p < 1$. An overview of this approach and review of its recent applications and extensions is provided by MacKenzie (2005).

A second limitation of ordinary logistic regression for modeling spatial patterns of species presence-absence is that these are often positively autocorrelated; i.e., locations closer together in space are likely to exhibit more similar attributes than are far-apart locations. This phenomenon results in violation of independence assumptions of most classical statistical models, with consequences that include artificially narrow confidence intervals for parameter estimates and erroneous conclusions about the importance of predictor variables (Legendre 1993). Augustin et al. (1996) introduced an approach to explicitly model spatial autocorrelation in a logistic regression framework, but in spite of its greater statistical validity compared to ordinary logistic regression, relatively few wildlife studies have modeled spatial autocorrelation of binary response data (but see Osborne et al. 2001, Klute et al. 2002, R. Knapp et al. 2003).

A similar non-independence problem arises when data are hierarchically structured. For example, if n sample sites are nested within a smaller number of landscapes, then performing a site-level analysis where attributes of each landscape are repeatedly assigned to all constituent

sites often will violate independence assumptions and bias standard error estimates. Hierarchical generalized linear models (HGLMs) are more appropriate for this data structure because they partition information into level-1 (site) and level-2 (landscape) components, each with appropriate degrees of freedom, and they estimate a unique random effect for each level-2 unit that appropriately adjusts standard errors of other parameter estimates (Sullivan et al. 1999, Raudenbush and Bryk 2002). The HGLM is an intuitive extension of the generalized linear model, and parameters may be estimated using maximum likelihood methods available in user-friendly software (e.g., HLM for Windows, SAS Proc Glimmix); however, with the exception of recent studies using more sophisticated hierarchical Bayesian techniques (e.g., Hooten et al. 2003, Thogmartin et al. 2004), we are unaware of HGLM applications in the wildlife literature.

Our goal was to evaluate multi-scale effects of habitat fragmentation on forest rodent community structure, while accounting for imperfect detection, spatial autocorrelation, and the hierarchical structure of multiscale data. We used the occupancy estimation module based on the model of MacKenzie et al. (2002) as implemented in program MARK (White and Burnham 1999) to evaluate the importance of local, patch, and landscape-level predictors of forest-site occupancy by 5 granivorous rodent species (eastern chipmunk, fox squirrel, eastern gray squirrel, red squirrel, and white-footed mouse) in an agriculturally dominated region of north-central Indiana. Previous research at local scales (e.g., within a single major watershed, <40 sites) elucidated variable effects of fragmentation on these species (Rosenblatt et al. 1999, Nupp and Swihart 2000, Goheen et al. 2003a), but these have not been evaluated at larger scales (e.g., landscape or watershed) or in conjunction with habitat effects, so our understanding of such processes even at local scales is incomplete. The larger scope of our study enabled us formally and more adequately to evaluate hypotheses concerning multi-scale processes. By explicitly modeling detectability and spatial autocorrelation, our occupancy models should yield less biased conclusions than previous models, and should aid in designing more effective field studies of these species in the future. Because sites were nested within landscapes, we also used HGLM to evaluate whether there remained any unique landscape effects not described by predictor variables that could lead

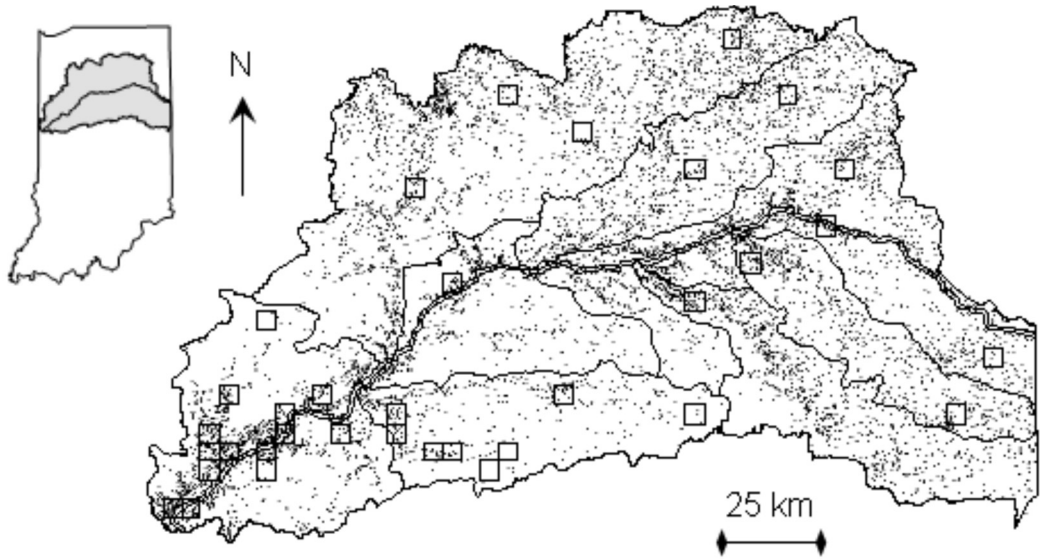


Fig. 1. Map of upper Wabash River basin, Indiana, USA. Enlargement shows distribution of forest cover, Wabash River (double line), boundaries of the basin's 8 major watersheds, and locations of 35 23-km² study landscapes studied 2001–2003.

to artificially small standard errors for parameters estimated in nonhierarchical MARK models.

STUDY AREA

The upper Wabash River basin in north-central Indiana (Fig. 1) contains the longest free-flowing stretch of navigable water in the United States east of the Mississippi River and drains an area >20,000 km², representing >20% of the state (Swihart and Slade 2004). The basin underwent extreme transformation following colonization by Europeans; at the time of our study, approximately 96% of the land area was privately owned, and 88% of the area was in agricultural use, primarily for corn and soybean production. Only about 8% of the basin was forested, compared to 19% statewide. Pre-settlement forest cover statewide was 87% (Smith et al. 1994). The remaining native forests (predominantly oak–hickory–maple [*Quercus-Carya-Acer*]) in the basin were highly fragmented. Relatively large contiguous forest tracts in the basin were confined to major drainages where floodplains or locally steep topography made land unsuitable for agriculture (Fig. 1).

METHODS

Field Sampling

Selection of Sample Sites.—Forest cover was patchily distributed throughout the upper Wabash River basin and varied from 0.25% to

56% (mean = 9%, median = 7%) across ~800 23-km² (4.8 × 4.8-km) grid cells that we overlaid on a map of the region. To capture the range of landscape variation when selecting our study areas, we characterized each grid cell according to several Geographic Information System (GIS) layers, including a classified land use layer for the percentages of forest, farmland, water, urban, and grassland cover. Because we designed our sampling to meet the goals of 2 complementary projects in the region (Swihart and Slade 2004), nearly two-thirds of the selected cells were located in the 2 southwest-most watersheds (Fig. 1); however, the selection algorithms for both projects were based on assigning cells into multiple strata based on GIS classification and selecting cells to span the range of landscape variation. We ultimately selected for biological sampling 35 cells (hereafter, landscapes), representing all 8 major watersheds in the basin (Fig. 1). Across these 35 landscapes, 75% of forest patches were <5 ha, 50% were <2 ha, and only 1% of patches were >100 ha.

Within each study landscape, we stratified forest cover into 1 of 3 categories based on natural cut-points in the distribution of forest-patch size: small (<5 ha), medium (5–50 ha), and large (>50 ha). We randomly allocated up to 45 total points per landscape across the 3 strata in proportion to the log of their respective areas, with the constraint that points were separated by ≥200 m. The

number and location of points actually sampled depended on total forest area, accuracy of image classification, and cooperation of private landowners. We sampled for small mammals at ≥ 32 forest sites per landscape. Two landscapes had only 4 sample points because of low percentage forest cover; all others had ≥ 9 sample points (median = 14). Seventy percent of sampled patches contained only 1 sample site, and 96% of sampled patches contained ≤ 3 sites.

Mammal Sampling.—We trapped small mammals in forest patches in 5, 18, and 12 separate study landscapes from late May to early August 2001, 2002, 2003, respectively. Four to 8 field crews conducted trapping each year so that multiple landscapes received trapping effort simultaneously, and effort for a given landscape was spread across the entire summer. At each sample point, we placed a grid of Fitch live traps (2001), Sherman live traps (2003), or a mixture of the 2 (2002), with trap spacing of 15 m. In 2001, grid dimensions were 3×3 or, less commonly, 7×7 . In 2002 and 2003, grids were 5×5 when forest-patch size permitted and 4×4 or 3×3 otherwise. We placed Tomahawk squirrel traps with every other Sherman or Fitch trap (30-m spacing) so that 7×7 Sherman/Fitch grids contained 4×4 Tomahawk grids; 5×5 Sherman/Fitch grids contained 3×3 Tomahawk grids; and 4×4 and 3×3 Sherman/Fitch grids contained 2×2 Tomahawk grids. We baited Sherman and Fitch traps with black-oil sunflower seed, and squirrel Tomahawk traps with black walnuts. A trap session consisted of a 3-day pre-bait period during which traps were locked open, and then a 5-day trap-check period, during which we checked traps twice daily (i.e., 4 afternoon and 4 morning checks). We only trapped each site for a single session during the course of the study.

For each trap check, we recorded the number of empty traps that had been disturbed (tipped, missing, or sprung but empty) and whether or not rain had fallen since the previous trap check. For occupancy analysis, we built encounter histories for each site, recording a 1 for each trapping day when the focal species was detected, or a 0 for each day when it was not detected. We only included trapping days 2-5 in encounter histories for white-footed mice, since we rarely caught this nocturnal species during the first trap-day, which began with an afternoon check.

Explanatory Variables.—For each 23-km² landscape and a surrounding 1.6-km buffer, we digitized major land-cover types (forest, grassland/

pasture, water, urban, agriculture) and secondary land-cover types (roads, streams, corridor elements) as vector data from U.S. Geological Survey digital orthophotos (DOQs) of 1-m resolution. The important role of buffers was to ensure that patches near the edge of each study cell were properly evaluated for estimates of patch size and isolation metrics. We defined treed habitat <30-m wide as corridor rather than forest. The implication was that larger forest patches connected by narrow wooded habitat were defined as separate patches rather than a single patch for calculating patch and landscape metrics. We recognize that corridors may support residents of some species (e.g., eastern chipmunks, Bennett et al. 1994; white-footed mice, Merriam and Lanoue 1990) and that the cutoff width defining corridor will vary with species. However, narrow landscape elements, even if suitable as residential habitat for a species, are still distinct from larger wooded patches because of structural differences in vegetation and dominating influence of edge. Thus, our construct should provide a more biologically meaningful interpretation of the landscape for most taxa than assuming all connected wooded area represents contiguous homogeneous habitat.

After converting vector data to 3-m raster data, we used Fragstats 3.3 (McGarigal and Marks 1995) to calculate patch and landscape metrics. We chose a 3-m grid resolution because it was the largest pixel size that preserved narrow landscape features (roads, streams, forest-corridors) separating otherwise connected habitat patches. For each patch, we calculated AREA (ha), SHAPE (perimeter of patch relative to maximally compact patch), ENN (distance to nearest patch), and PROX (sum of area in forest patches <400-m away, weighted by distance⁻²). For each landscape, we calculated the total area forested (including the buffer area), mean AREA, mean SHAPE, mean ENN, mean PROX, SHEI (Shannon's evenness index, which varies from 0 for landscapes dominated by a single cover type to 1 for a landscape in which area of each cover type is equal), and distance to the Wabash River. Eighty-six percent of forest patches >100 ha in size were within 15 km of this major drainage, so we considered this a possible source area for dispersal-limited rodents.

We used field sampling techniques to measure all site-level variables except distance to nearest habitat edge (EDGD), which we measured in the GIS. We conducted a rapid-assessment survey of vegetation at the center of each sample site to

coarsely characterize vegetation structure and relative biomass of nut-bearing trees (e.g., *Quercus*, *Carya*, *Juglans* species). We indexed basal area (m²/ha) of nut-trees (MAST) from a single variable-radius plot using a 10 basal-area-factor (BAF) prism (Husch et al. 1982). We indexed downed woody debris (DWD) by measuring the length and diameter of all log sections >5 cm in diameter within a 10-m radius, estimating volume for each section, and summing the volumes. We indexed understory density with 2 measures. For the variable STEMS, we counted all woody stems <5 cm in diameter at breast height within a 5-m radius. To estimate the variable DENS, we raised a vertical board 3 m tall by 0.3 m wide at each of 4 subsample points (5 m in each cardinal direction from plot center). We divided the board into 4 sections of unequal length and drew a checkerboard pattern on each section (5 squares wide by 3–10 squares tall). An observer hunched over at the plot center to count the number of checkerboard-squares at least half obstructed visually by vegetation (Noon 1980). We did this for each section of the board, and we averaged measures across sections and the 4 sub-sample points.

Analysis of Detection-Nondetection Data

Initial Model Construction.—We began by building models of detectability (*p*) and occupancy rate (ψ) sensu MacKenzie et al. (2002) without inclusion of a spatial autocovariate term. We considered models with combinations of the following effects on *p*: (1) trap occasion, estimated as a linear trend (OCC) for white-footed mice (only captured during the 4 morning trap occasions) and as a quadratic function (OCC + OCC²) for other species because days 1 and 5 of trapping were only half-days; (2) trapping year (YR); (3) number of days of rain recorded at a site (RAIN);

(4) an index of trap effort at each site (EFF), equaling the number of traps multiplied by the number of trap occasions, minus the number of traps disturbed; (5) an integer variable (SEAS) indicating timing of trapping (1 = first 2 weeks of field season ... 5 = last 2 weeks). Previous trapping experience in the region suggested that trap success for most species was greatest during the middle of each trapping season, so we modeled the effect of season as a quadratic function (SEAS + SEAS²). We modeled this effect as a linear trend (SEAS) for white-footed mice, however, because they became increasingly detectable over the course of summer as densities increased (Nupp 1997). Candidate predictor variables for ψ included site- and patch-level variables that we described in the previous section, and principal components that we derived from landscape-level variables (see below, Table 1). We also tested 2 competition-effect variables for red squirrels (number of gray squirrels captured [GNUM] and detection or nondetection of gray squirrels [GPRES]) based on previous evidence of competition between these species (Nupp and Swihart 2001). Prior studies of coexistence between gray squirrels and fox squirrels suggest that these species are not competitors in the Midwest (Brown and Batzli 1984, Nupp and Swihart 2001), so we did not test for this interaction.

For each species, we took several steps to develop a finite set of possible models for subsequent evaluation in program MARK. For tree squirrels we eliminated DWD and EDGD from consideration because we did not expect these variables to affect site-occupancy rates. All 7 landscape-level variables were correlated with at least 1 other landscape variable (0.57 < *r* < 0.93), so we used principal components analysis with varimax rotation to reduce these to 5 orthogonal principal compo-

Table 1. Principal components following varimax rotation of landscape-level variables for 35 23-km² landscapes in the Upper Wabash River Basin, Indiana, USA, 2001–2003.

Principal component	Eig ^a	% var ^b	Factor loading for each landscape variable ^c							Interpretation: PC value increases for landscapes...
			SHEI	Total forest area (ha)	Mean AREA	Mean SHAPE	Mean ENN	Mean PROX	Dist (km) to river	
pcFOR	2.44	34.9	0.20	0.74	0.87	0.45	-0.21	0.90	-0.29	...with more forest
pcNODIV	1.25	17.9	-0.94	-0.43	-0.20	-0.09	0.34	-0.09	0.10	...with lower cover-type diversity
pcNEARW	1.09	15.6	0.09	0.21	0.21	0.21	-0.26	0.24	-0.91	...closer to Wabash River
pcENN	1.07	15.3	-0.25	-0.39	-0.11	-0.20	0.86	-0.14	0.23	...with longer inter-patch distances
pcSSHP	1.00	14.3	-0.07	-0.15	-0.33	-0.84	0.19	-0.27	0.18	...with simpler patch shapes

^a First 5 eigenvalues of the correlation matrix of landscape variables.
^b Percentage of variation in landscape variables contained in each principal component.
^c Correlations between the principal component and each landscape variable.

nents that captured 98% of the variation in these predictor variables and were easily interpretable based on factor loadings (Table 1). For each species we reduced further the candidate set of variables by running ordinary logistic regression analysis in SAS using PROC LOGISTIC with Selection = SCORE to identify the top 15 variable combinations based on likelihood scores adjusted for the number of parameters. We considered all variables included in at least 1 of the 15 best logistic regression models for model selection in occupancy models in MARK. Any variable included in all 15 top logistic models was forced into subsequent MARK occupancy models after verifying its importance via large (>4) ΔAIC_c (Akaike's Information Criterion [1973]) scores of models without this variable. For each species, this left us with 2–5 variables that were of potential but uncertain importance and that formed a reasonably small set (4–32) of models for testing in MARK.

We acknowledged model selection uncertainty by performing multi-model inference (MMI) based on AIC with a bias-correction term for small sample size (AIC_c ; Hurvich and Tsai 1989) and AIC_c weights (w_i ; Burnham and Anderson 2002). We only included models with $\Delta AIC_c < 4$ in the final confidence set (Burnham and Anderson 2002), which we used for MMI. We rescaled weights (w_i) to models in the confidence set and performed model averaging to estimate parameters:

$$\tilde{\beta}_j = \sum_{i=1}^R w_i I_j(g_i) \hat{\beta}_{j,i},$$

where

$$w_i = \frac{\exp(-\frac{1}{2} \Delta_i)}{\sum_{r=1}^R \exp(-\frac{1}{2} \Delta_r)}$$

and

$$I_j(g_i) = \begin{cases} 1 & \text{If predictor } x_j \text{ is in model } g_i, \\ 0 & \text{otherwise} \end{cases}$$

This estimator shrinks estimates toward 0 for parameters not included in all models in the confidence set, thereby reducing estimation bias associated with model selection uncertainty and spurious effects and serving to stabilize inference (Burnham and Anderson 2002). We calculated model-averaged standard errors as:

$$\widehat{se}(\tilde{\beta}_j) = \sum_{i=1}^R w_i \sqrt{\widehat{\text{var}}(\hat{\beta}_{j,i} | g_i) + (\hat{\beta}_{j,i} - \tilde{\beta}_j)^2}$$

We evaluated the relative importance of variables by summing AIC_c weights for all models in the confidence set where variable j occurred (i.e., w_{+j} ; Burnham and Anderson 2002). We standardized continuous predictor variables for analysis in MARK, so $\tilde{\beta}_j$ could be interpreted as the amount of change in the log-odds (logit) of p or ψ following a 1-standard deviation change in the variable from its mean.

We evaluated model goodness-of-fit for each species by comparing the observed deviance from our most general model to the mean deviance from 100 parametric bootstrap simulations of data generated from parameter estimates in the general model (Cooch and White 2004); i.e.,

$$\hat{c} = \frac{\text{Deviance}_{\text{Observed}}}{\text{Deviance}_{\text{Expected}}}$$

This approach is not available in MARK for models with individual covariates, so we bootstrapped using our most parameterized model that was biologically meaningful but did not include individual covariates: $\{p(\text{trap occasion})\psi(\cdot)\}$. This reduced model represents a special case of more general models, so model fit will only be greater for a more general model (G. White, Colorado State University, personal communication). For all species, we found $0.9 < \hat{c} < 1.1$ ($0.4 < P < 0.6$), indicating adequate fit of our models to the data.

Modeling Spatial Autocorrelation.—To assess the degree of spatial autocorrelation in response variables not accounted for by predictor variables, we calculated Moran's I (R version 2.0.1) for residuals from occupancy models across a set of distance categories (Cliff and Ord 1981). We based residuals on model-averaged estimates and calculated them as the observed values at site i (detection = 1, nondetection = 0) minus the predicted probabilities of detecting the species at least once:

$$\hat{D}_i = \psi_i p_i^*$$

where

$$p_i^* = 1 - \prod_{k=1}^K (1 - p_{ik}),$$

and K = number of trap occasions. Distance categories were 0–400 m, 400–800 m, ..., 4,400–4,800 m. We chose 400-m categories because this was twice the minimum separation distance between sample sites, and 4,800 m was the width of each study landscape. For species with positively corre-

lated residuals, we calculated an autocovariate (ACOV) term:

$$autocov_i = \frac{\sum_{j=1}^{J_i} w_{ij} y_j}{\sum_{j=1}^{J_i} w_{ij}},$$

where $y_j = 1$ for all occupied sites in a set J_i defined as neighbors of site i , and $w_{ij} = 1/h_{ij}$, where h_{ij} was the distance between site i and j . This autocovariate was based on methods introduced by Augustin et al. (1996), but we modified it for our models following Klute et al. (2002) so that it is calculated only from data at sampled sites rather than from estimated presences-absences (via Gibbs sampling) in a complete lattice of surrounding grid cells (Augustin et al. 1996). We examined correlograms of Moran's I values to assess the maximum distance where residuals were autocorrelated and used this distance to define the neighborhood of sites J_i .

There are caveats concerning use of this autocovariate in species occupancy models; both are related to measurement error. First, Augustin et al. (1996) noted that the autocovariate cannot be properly estimated for each i unless presence-absence data exist for every neighboring site j . Augustin et al. (1996) used Gibbs sampling to circumvent this problem, but the Gibbs sampler requires predictor variable data for all sites in the neighborhood (e.g., obtained from remote sensing). When a census is not possible, we recommend increasing the number of neighbor sites sampled to improve accuracy of the autocovariate estimate. Second, since estimation of the autocovariate depends on observed detections/nondetections at a set of neighbor sites, its accuracy, like that of ψ , depends on detectability (p), which we were not modeling in its calculation. However, we suggest this may not be very problematic if detectability over the course of the trapping session (p_i^*) was either close to 1, or similar across sites so that the number of detections and true presences in J_i correlated strongly and consistently across sites i . For reasons above, the autocovariate we calculated may be better viewed as an index. Significant improvement in fit of our models when we included the autocovariate (see Results) suggest that this term was worthwhile to incorporate, in spite of these concerns.

Hierarchical Generalized Linear Modeling.—We modeled occupancy at the site-level in MARK, assigning the same landscape-variable values to all sites within the same landscape. This may vio-

late assumptions of independence and could lead to erroneous conclusions concerning the importance of our predictor variables, particularly at the landscape level. Therefore, we used program HLM for Windows 6.0 to evaluate HGLMs that included variables in our lowest-AIC_c MARK occupancy models (except OCC or OCC², which are specific to trap occasion) before and after inclusion of the autocovariate term. Let the log-odds (logit) of observing a species at site i in landscape z be:

$$\eta_{iz} = \ln\left(\frac{D_{iz}}{1 - D_{iz}}\right),$$

where D_{iz} is a composite variable analogous to D_i above (since ψ_{iz} and p_{iz}^* are not estimated separately here). The level-1 model including multiple site- and patch-level predictors is:

$$\eta_{iz} = \beta_{0z} + \beta_1(x_1)_{iz} + \dots + \beta_m(x_m)_{iz} + r_{iz},$$

where r_{iz} is an error term representing a unique effect for site i in landscape z . Assuming the level-1 intercept (but not slope coefficients) varies across landscapes, the level-2 model is:

$$\beta_{0z} = \gamma_{00} + \gamma_{01}W_{1z} + \dots + \gamma_{0s}W_{sz} + u_{0z},$$

$$u_{0z} \sim \text{Normal}(0, \tau_{00}),$$

where γ_{00} is the average logit across landscapes, γ_{0s} is the level-2 slope coefficient for landscape-level variable W_s , and u_{0z} is the unique random effect of landscape z on the mean logit. For details on HGLM, see Raudenbush and Bryk (2002). Here, we simply highlight the importance of the level-2 variance component τ_{00} , which may be tested via a χ^2 statistic to determine whether it is significantly different from 0 after accounting for covariate effects in the model. If $\tau_{00} \neq 0$, then we assume each landscape is imparting a unique but undescribed effect on the response variable, so site-level data are not independent, and standard errors of parameter estimates are adjusted accordingly. If $\tau_{00} = 0$, we may assume that any variation in landscape mean-logits is fully described by predictor variables, so site-level data may be considered independent and landscape variables may be treated as fixed effects.

Model Validation

We evaluated accuracy of our occupancy models, both without and with inclusion of the spatial autocovariate, using receiver operator characteristic (ROC) curves. The ROC plots describe the

Table 2. Model selection results for MARK models of forest rodent occupancy in the Upper Wabash River Basin, Indiana, USA (2001–2003) that do not include a spatial autocovariate, and estimates of γ_{00} and τ_{00} for the HGLM containing variables in low-est-AIC_c MARK model. γ_{00} is the log-odds of observing the species during the first 2 weeks of trapping in 2003 when continuous covariates equal their standardized mean (0) and when random effect (u_{02}) = 0. Residual between-landscape variance in the logit, after controlling for covariates, is τ_{00} . χ^2 tests $H_0: \tau_{00} = 0$.

Model, by species	MARK				GLM				
	ΔAIC_c	w_i	# Par	Deviance	γ_{00}	τ_{00}	χ^2	df	P
Eastern chipmunk									
$p^a \psi$ (YR + STEM – MAST – AREA – pcNEARW)	0.0	0.53	15	2,678.0	1.15	0.58	84	33	<0.001
$p^a \psi$ (YR + STEM – AREA – pcNEARW)	0.6	0.39	14	2,680.7					
$p^a \psi$ (YR + STEM – MAST – pcNEARW)	3.7	0.08	14	2,683.8					
Fox squirrel									
$p^b \psi$ (YR – DENS + ENN)	0.0	0.78	11	1,917.3	-0.84	0.09	42	34	0.17
$p^b \psi$ (YR + ENN)	2.5	0.22	10	1,921.8					
Gray squirrel									
$p^c \psi$ (YR – ENN + pcNEARW + pcFOR + pcSSHP)	0.0	0.87	11	705.9	-2.18	0.79	53	31	0.008
$p^c \psi$ (YR – ENN + pcNEARW + pcFOR)	3.8	0.13	10	711.7					
Red squirrel									
$p^a \psi$ (YR + DENS – STEM – pcNEARW + pcSSHP – pcFOR)	0.0	0.75	16	1,614.5	-1.48	0.76	93	31	<0.001
$p^a \psi$ (YR + DENS – STEM – pcNEARW + pcSSHP)	2.2	0.25	15	1,618.8					
White-footed mouse									
$p^d \psi$ (YR + EDGD + DWD – SHAPE + pcFOR + pcSSHP)	0.0	0.30	15	2,369.6	1.30	<0.001	21	32	>0.50
$p^d \psi$ (YR + EDGD + DWD + pcFOR + pcSSHP)	0.4	0.25	14	2,372.1					
$p^d \psi$ (YR + EDGD + DWD – SHAPE + pcFOR)	1.1	0.17	14	2,372.8					
$p^d \psi$ (YR + EDGD + DWD + pcFOR)	2.3	0.09	13	2,376.1					
$p^d \psi$ (YR + EDGD + DWD + pcSSHP)	2.9	0.07	13	2,376.7					
$p^d \psi$ (YR + EDGD – SHAPE + pcFOR + pcSSHP)	3.1	0.06	14	2,374.8					
$p^d \psi$ (YR + EDGD + pcFOR + pcSSHP)	3.4	0.05	13	2,377.2					

^a $p(YR + OCC - OCC^2 + SEAS - SEAS^2 + EFF)$
^b $p(YR + OCC - OCC^2 + EFF)$
^c $p(OCC - OCC^2 - RAIN)$
^d $p(YR - OCC + SEAS - RAIN + EFF)$

false-positive classification rate (1 – specificity) and true-positive classification rate (sensitivity = 1 – false-negative rate) for predicted values (in our case, \hat{D}_i) across a full range of success-threshold values between 0 and 1 (Fielding and Bell 1997). Area under the ROC curve (AUC) varies from 0.5 for a model that performs no better than a null model to 1.0 for a perfect fit to the data. The AUC may be directly interpreted as the probability that $\psi_i p_i^*$ was greater for a randomly selected site where the species was detected than for a randomly selected site where the species was not detected.

RESULTS

Of 525 forest sites sampled from 2001 to 2003, we detected eastern chipmunks at 392 sites (74%), fox squirrels at 222 sites (42%), eastern gray squirrels at 70 sites (13%), red squirrels at 171 sites (33%), white-footed mice at 408 sites (78%), and southern flying squirrels (*Glaucomys volans*) at only 3 sites (0.6%). Because of low sample size, we did not develop models for flying

squirrels, but we noted all detections were <6km from the Wabash River. Initial modeling in MARK suggested important landscape-level effects on occupancy rates (ψ_i) for all species except fox squirrels (Table 2). However, HGLMs revealed significant data-dependence between sites nested within the same landscape for eastern chipmunks, gray squirrels, and red squirrels. Residual between-landscape variance (τ_{00} ; Table 2) was significantly >0 for these species, indicating a unique and undescribed random effect for each landscape on occupancy rates of constituent sites. Further evidence for a landscape effect is provided by Moran’s *I* correlograms (Fig. 2, panels A, C, D) that showed that residuals for MARK analyses were positively correlated over the approximate width of a study landscape (4–5 km). Residuals from the fox squirrel model also were correlated (Fig. 2, panel B) but only over relatively short distances (<1 km), suggesting spatial dependence at a more local scale. Residuals from the model for white-footed mice were not spatially correlated.

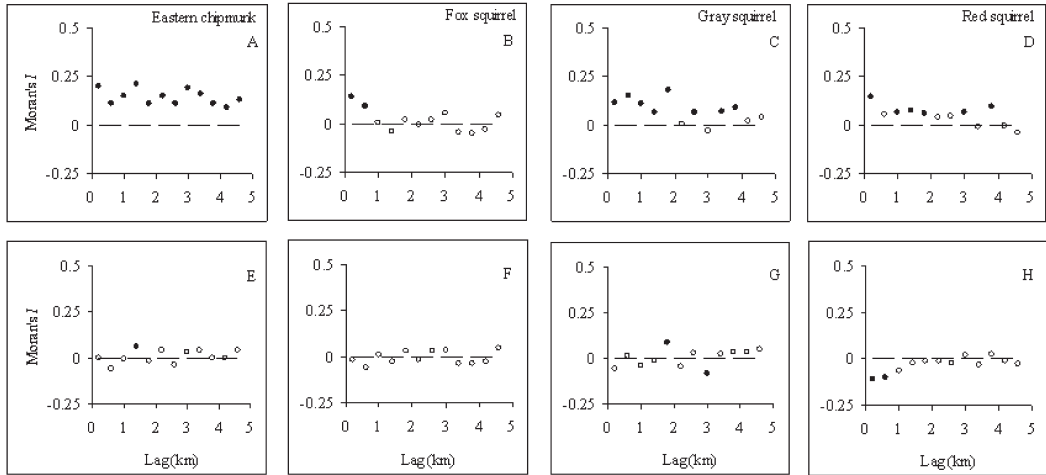


Fig. 2. Moran's *I* correlograms of residuals from MARK models of forest rodent occupancy in the Upper Wabash River Basin, Indiana, USA, 2001–2003, before (A–D) and after (E–G) inclusion of spatial autocovariate term. Filled circles indicate Moran's *I* values statistically different from 0 ($P < 0.10$).

The spatial autocovariate effectively controlled for intra-landscape data dependence. Following inclusion of this term, residuals from MARK analy-

sis were no longer autocorrelated (Fig. 2, panels E–H), and τ_{00} for HGLMs were no longer different from 0 (Table 3), providing justification for the

Table 3. Model selection results for MARK models of forest rodent occupancy in the Upper Wabash River Basin, Indiana, USA (2001–2003) that include a spatial autocovariate, and estimates of γ_{00} and τ_{00} for the HGLM containing variables in lowest-AIC_c MARK model. γ_{00} is the log-odds of observing the species during the first 2 weeks of trapping in 2003 when continuous covariates equal their standardized mean (0) and when random effect (u_{0z}) = 0. Residual between-landscape variance in the logit, after controlling for covariates, is τ_{00} . χ^2 tests $H_0: \tau_{00} = 0$.

Model, by species	MARK				GLM				
	ΔAIC_c	w_i	# Par	Deviance	γ_{00}	τ_{00}	χ^2	df	<i>P</i>
Eastern chipmunk									
$p^a \psi$ (YR + ACOV + STEM – AREA – pcNEARW)	0.0	0.37	13	2,535.4	1.17	0.0001	29	33	>0.5
$p^a \psi$ (YR + ACOV + STEM – AREA)	0.7	0.25	12	2,538.3					
$p^a \psi$ (YR + ACOV + DENS – AREA)	1.1	0.21	12	2,538.7					
$p^a \psi$ (YR + ACOV – AREA)	1.6	0.17	11	2,541.2					
Fox squirrel									
$p^b \psi$ (ACOV – DENS + ENN)	0.0	0.47	10	1,872.9	-0.79	0.0002	29	34	>0.5
$p^b \psi$ (ACOV + ENN)	0.1	0.44	9	1,875.1					
$p^b \psi$ (ACOV)	3.4	0.08	8	1,880.5					
Gray squirrel									
$p^c \psi$ (YR + ACOV + MAST + AREA – ENN + pcNEARW)	0.0	0.26	12	665.6	-2.57	0.0002	25	33	>0.5
$p^c \psi$ (YR + ACOV + AREA – ENN + pcNEARW)	0.04	0.25	11	667.8					
$p^c \psi$ (YR + ACOV + MAST + AREA + pcNEARW)	1.2	0.14	11	668.9					
$p^c \psi$ (YR + ACOV + MAST – ENN + pcNEARW)	1.3	0.14	11	669.0					
$p^c \psi$ (YR + ACOV + AREA + pcNEARW)	1.5	0.12	10	671.3					
$p^c \psi$ (YR + ACOV – ENN + pcNEARW)	2.1	0.09	10	671.9					
Red squirrel									
$p^a \psi$ (ACOV – MAST – PROX)	0.0	0.45	12	1,555.4	-1.09	0.0004	21	34	>0.5
$p^a \psi$ (ACOV – MAST)	0.2	0.41	11	1,557.7					
$p^a \psi$ (ACOV + DENS – PROX)	3.75	0.07	12	1,559.1					
$p^a \psi$ (ACOV – PROX)	3.84	0.07	11	1,561.3					

^a p (YR + OCC – OCC² + SEAS – SEAS² + EFF).
^b p (YR + OCC – OCC² + EFF).
^c p (OCC – OCC² – RAIN).

Table 4. Model-averaged slope estimates from final MARK occupancy models of forest rodent occupancy in the Upper Wabash River Basin, Indiana, USA (2001–2003). p -intercept is the log-odds of detection (given occurrence) on first day of a trap session during first 2 weeks in 2003, holding other covariates for p at standardized mean 0. Coefficients predict logit-change with 1-SD change in a continuous variable. Interpretation of ψ -intercept is similar. $w_+(j)$ is the sum of weights (w_j) for models containing coefficient j (shown for continuous predictors of ψ).

Covariate	Eastern chipmunk			Fox squirrel			Gray squirrel			Red squirrel			White-footed mouse		
	$\tilde{\beta}_j$	SE	$w_+(j)$	$\tilde{\beta}_j$	SE	$w_+(j)$	$\tilde{\beta}_j$	SE	$w_+(j)$	$\tilde{\beta}_j$	SE	$w_+(j)$	$\tilde{\beta}_j$	SE	$w_+(j)$
p															
INTERCEPT	0.74	0.19		-1.49	0.21		-0.90	0.26		-1.74	0.32		0.12	0.17	
YR															
2001				-1.17	0.30					0.17	0.32		-0.35	0.19	
2002				0.50	0.18					0.83	0.23		0.33	0.14	
OCC	2.11	0.20		0.87	0.23		1.29	0.41		1.13	0.26		-0.31	0.05	
OCC ²	-0.39	0.03		0.87	0.23		-0.21	0.07		-0.17	0.04				
SEAS	1.03	0.21								0.97	0.31		0.12	0.04	
SEAS ²	-0.18	0.14								-0.15	0.05				
EFF	0.17	0.06		0.55	0.08					0.14	0.08		0.79	0.07	
RAIN															
ψ															
INTERCEPT	1.20	0.12		0.55	0.18		-2.38	0.38		-0.80	0.12		4.25	1.23	
YR															
2001							-2.37	1.08					-2.46	0.87	
2002							-0.32	0.38					-0.23	0.80	
ACOV	0.78	0.12	1.00	0.77	0.17	1.00	1.04	0.18	1.00	1.18	0.13	1.00			
STEM	0.15	0.17	0.62												
DENS	0.04	0.07	0.21	-0.09	0.12	0.47				0.01	0.03	0.07			
EDGD													1.05	0.50	1.00
MAST							0.13	0.17	0.54	-0.27	0.15	0.86			
DWD													2.85	2.07	0.88
AREA	-0.27	0.10	1.00				0.22	0.18	0.77						
ENN				0.36	0.22	0.92	-0.59	0.58	0.73						
SHAPE													-0.24	0.27	0.59
PROX										-0.14	0.17	0.59			
pcNEARW	-0.08	0.12	0.37				0.72	0.29	1.00						
pcFOR													0.82	0.48	0.93
pcSSHHP													0.35	0.33	0.68

MARK analyses that treated landscape predictors as fixed site-level effects. The autocovariate improved fit of models as well; deviances of MARK models with the autocovariate were ~40–140 units lower than in models without the autocovariate (compare Tables 2, 3), and AUC for ROC plots increased 3–11% for models with the autocovariate: from 0.70 to 0.74 for eastern chipmunks, 0.78 to 0.81 for fox squirrels, 0.89 to 0.92 for gray squirrels, and 0.73 to 0.81 for red squirrels. The AUC for the white-footed mouse model was 0.85. Model selection results differed substantially for 3 of 4 species after inclusion of the autocovariate (compare Tables 2, 3). All species except white-footed mice were much more likely to occur at a site if surrounding sites in the landscape were also occupied, as indicated by the relatively large coefficient estimates for ACOV (Table 4, Fig. 3). The following results are based on final model selection in MARK.

For eastern chipmunks, there was strong support for an inverse relationship between ψ_i and

patch AREA, which occurred in all 4 candidate models (Tables 3, 4). There was moderate support ($w_+[j] = 0.62$) for a positive effect of STEM density on ψ_i , and weak support for a positive effect of vegetation density (DENS; $w_+[j] = 0.21$), which only occurred in the third-lowest AIC model. Collectively, these models suggested that chipmunks were more likely to occur in smaller patches with denser understory (Fig. 3). The landscape-level predictor pcNEARW varied negatively with ψ_i in the lowest-AIC model, suggesting higher occupancy rates in landscapes further from the Wabash River; however, this predictor occurred in no other models, so overall support for this effect was relatively weak ($w_+[j] = 0.37$).

Fox squirrel occurrence did not vary with landscape-level predictors. Within a landscape, this species was more likely to occur in more isolated patches, as evidenced by strong model support ($w_+[j] = 0.92$) for a positive relationship between ψ_i and nearest patch-neighbor distance (ENN; Tables

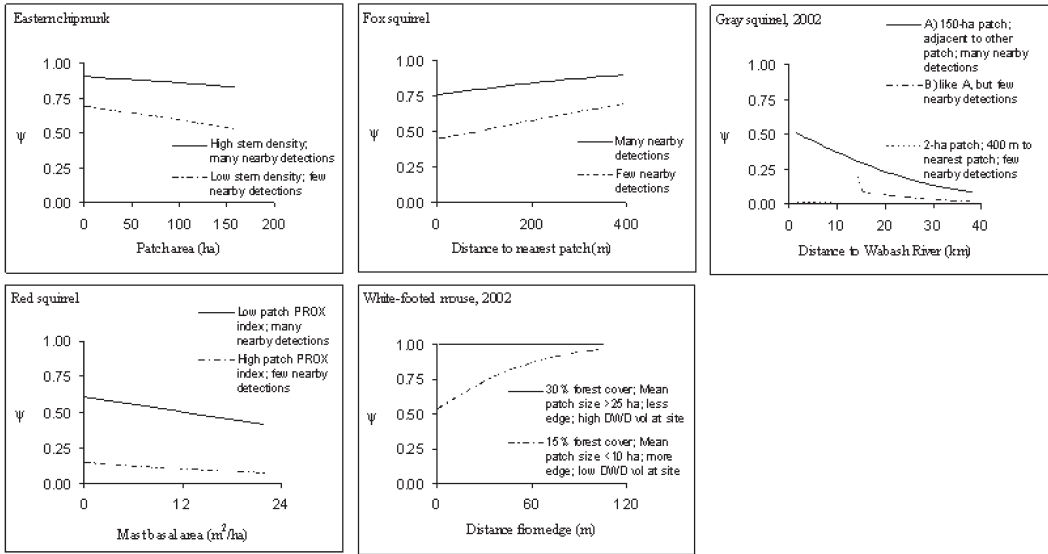


Fig. 3. Predicted occupancy rates of forest rodents in the Upper Wabash River Basin, Indiana, USA, 2001–2003, as a function of predictor variables. Estimates are shown across a range of observed variation (5th to 95th percentiles) in environmental predictors and for 2 values of the spatial autocovariate (25th and 75th percentiles, denoted few or many nearby detections, respectively). Strongest environmental predictor (based on $w_+[j]$) is on x-axis. Other variables with $w_+(j) > 0.5$ are represented together in prediction curves. Estimates for gray squirrels and white-footed mice varied annually, so only those for 2002 are shown. The 2 dotted lines for gray squirrels contrast ψ_i for large and small autocovariates beyond 15 km from the Wabash River. The lower of these (B) depicts pattern of occupancy we observed.

3, 4; Fig. 3). Fox squirrels also showed strong evidence of fine-scale spatial dependence; ψ_i increased as the number of detections (weighted by inverse distance) at sample sites within 800 m of i (ACOV) increased. There was also weak-to-moderate support ($w_+[j] = 0.47$) for a negative effect of STEM density on ψ_i , suggesting higher occupancy rates at sites with more open understory.

Gray squirrel occupancy rates were strongly affected by the landscape-level predictor pcNEARW, which occurred in all 6 candidate models, indicating the importance of proximity to the Wabash River corridor for occurrence of this species (Tables 3, 4). There was also fairly strong support for a positive effect of patch AREA ($w_+[j] = 0.77$) and a negative effect of inter-patch distance (ENN; $w_+[j] = 0.73$) on ψ_i . Of 70 sites where we detected gray squirrels, only 7 (10%) were in patches smaller than 5 ha, and only 3 (4.3%) were in patches separated by >60 m from the nearest-neighbor patch. We also found moderate support ($w_+[j] = 0.54$) for a positive relationship between basal area of MAST trees and ψ_i . Taken together, important patch and landscape variables resulted in a strong regional threshold effect (Fig. 3); we detected gray squirrels at only 3 of 179 sites >15 km from the Wabash

River and at none of 157 sites >21 km from the river. This result was closely concordant with the spatial distribution of large forest patches; 86% of the river basin's forest area occurring in patches >100 ha was within 15 km of the river. More striking, of the 17 landscapes where we detected gray squirrels, 13 were in the southwest-most watershed (Middle Wabash–Little Vermillion; MWLV). This watershed only comprised 14% of the entire basin's land area but 40% of its larger forest-patch area. Of the 21 study landscapes located <15 km of the river, all 13 in the MWLV had gray squirrel detections whereas 5 of 8 landscapes outside the MWLV did not. Only 29% of our sample sites were in this watershed, but 91% of our gray squirrel detections occurred there.

For red squirrels, there was strong support ($w_+[j] = 0.86$) for an inverse relationship between basal area of hard-mast trees (MAST) and ψ_i . Red squirrels also were more likely to occur in more isolated patches, as indexed by PROX ($w_+[j] = 0.59$; Tables 3, 4). A positive effect of vegetation density occurred only in the third of 4 candidate models, so support for this relationship was weak. Red squirrel occupancy was not predicted by any landscape-level variables, nor did we find direct evidence that gray squirrel occupancy or abun-

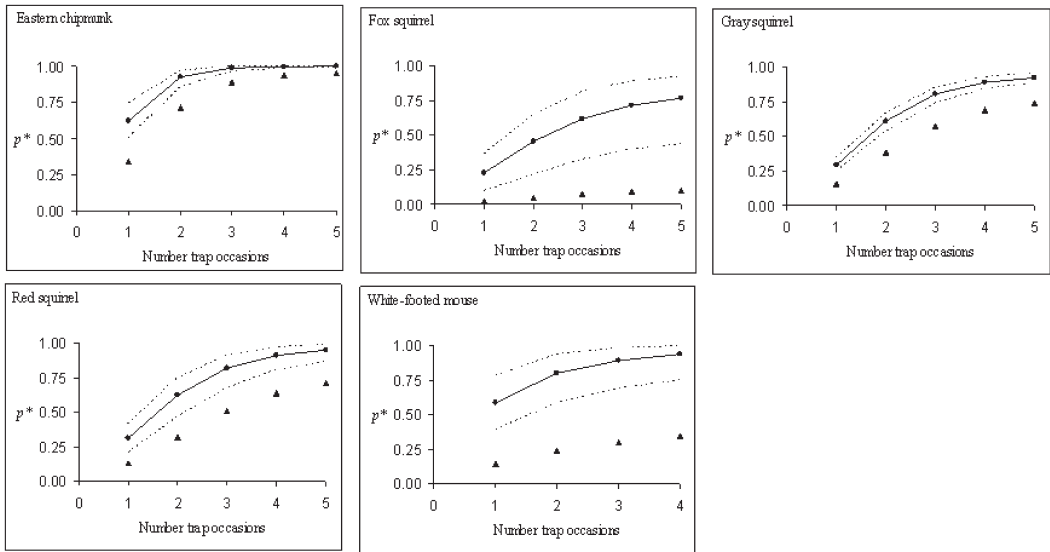


Fig. 4. Variation in species detection probabilities (given occurrence) as a function of number days trapped. Graph depicts average (solid line), ± 1 SD (dotted lines), and minimum (\blacktriangle) of predicted values across 525 study sites in upper Wabash River basin, Indiana, USA, summer 2001–2003.

dance affected red squirrel occupancy rates. However, naïve estimates of red squirrel densities (number of individuals captured) were 3 times higher at sites without gray squirrels ($\bar{X}_{resq} = 1.53 \pm 0.15$ [SE], max = 18, $n = 455$) than with gray squirrels ($\bar{X}_{resq} = 0.46 \pm 0.11$, max = 4, $n = 70$; Mann-Whitey Z-score = 1.95, $P = 0.025$). Further, ψ_i for these 2 species varied oppositely with MAST-tree basal area and patch isolation indices.

Several variables garnered modest to strong support as predictors of white-footed mouse occurrence (Tables 2, 4). At the site level, we observed strong positive relationships with volume of DWD ($w_+[j] = 0.88$) and EDGD ($w_+[j] = 1.00$). There was moderate support ($w_+[j] = 0.59$) for a negative effect of increasing SHAPE on site occurrence, which was consistent with a negative edge effect. At the landscape level, there was strong and moderate support for a positive effect of pcFOR ($w_+[j] = 0.93$) and pcSSH ($w_+[j] = 0.68$), respectively, on ψ_i . These predictors suggest higher occupancy rates in landscapes with more total forest cover, larger average patch areas, and simpler patch shapes. In fact, white-footed mice were essentially ubiquitous across sites in highly forested landscapes, with variation across other environmental variables occurring only in less forested landscapes (Fig. 3) and in 2001 when average ψ_i ranged from only 0.58–0.81 across all study landscapes (vs. 0.81–0.999 for all other landscapes; see Table 4 for slope coefficients for YR).

Adjusting for detection probabilities, we estimated the total percentages of sites occupied ($100 * \sum \psi_i / 525$) to be 74% for eastern chipmunks, 61% for fox squirrels, 14% for gray squirrels, 34% for red squirrels, and 89% for white-footed mice. Only for fox squirrels and white-footed mice were these substantial increases (45% and 14%, respectively) over the percentage of sites where the species were detected. These species showed high variation in detection rates by the end of a 5-day trap session (Fig. 4). Eastern chipmunks, by contrast, were very detectable, with estimates of $p_i^* > 0.99$ for nearly all sites. Consequently, the estimated mean log-odds and relevant slope parameters for chipmunk occurrence were nearly identical for the MARK model and HGLM (compare intercepts in Tables 3, 4). MARK models and HGLMs were similarly concordant for mean log-odds of gray squirrel and red squirrel occupancy (more so for gray squirrels), as these species also displayed consistently high detection rates ($p_i^* \geq 0.90$ for 75% of sites). Difference in mean-logits and slope parameters from MARK and HGLMs were substantial for white-footed mice and fox squirrels.

DISCUSSION

Patterns of species occurrence within a landscape are affected by the distribution of suitable habitats, by the spatial context in which habitat patches occur, and by spatially structured popula-

tion processes (e.g., dispersal limitation, disease outbreaks; Legendre 1993). Previous studies of the species we considered have documented the important effects of attributes of habitat (Cummins and Vessey 1994, Derge and Yahner 2000) or patches (Rosenblatt et al. 1999, Nupp and Swihart 2000) on patterns of occurrence or density, but few have simultaneously addressed site-, patch-, and landscape-level predictors over a larger region within a multi-scale analysis framework. Thus, our study builds on previous work by expanding the scale of investigation and by explicitly modeling nondetection error and spatial autocorrelation effects. Spatial autocorrelation of initial-model residuals revealed landscape-level structuring of occupancy rates for eastern chipmunks, gray squirrels, red squirrels, and fox squirrels beyond that which could be described by environmental predictor variables. Although controlling for such spatial dependence (via autocovariate analyses or HGLMs) was important for improving model fit, model selection inference, and statistical validity, spatial autocorrelation was interesting in its own right because it revealed the presence of spatially heterogeneous demography in these species.

Eastern chipmunks have been described as fragmentation-sensitive (Henein et al. 1998; Nupp and Swihart 1998, 2000) because of lower apparent survival rates observed in smaller woodlots (Nupp and Swihart 1998) and a reported intolerance of nonwooded habitat (Bennett et al. 1994). These factors suggest frequent local extinctions in forest patches that cannot be recolonized unless they are connected to another source patch via vegetated corridor. However, Nupp and Swihart (1998, 2000) reported higher chipmunk densities in smaller habitat patches, and Henderson et al. (1985) described rapid recolonization of woodlots following local extinction, even for woodlots that required crossing 20–60 m of pasture to get to. Further, Bowman and Fahrig (2002) found that the probability of translocated eastern chipmunks returning to home ranges did not vary across gap distances of 0 (continuous forest) to 240 m, and they concluded that isolated woodlots without vegetated corridors were functionally connected in their landscape. Perhaps lower apparent survival rates in smaller patches (Nupp and Swihart 1998) are the result of higher dispersal rather than mortality rates. We found no negative effect of fragmentation on chipmunk occupancy rates; in fact, occupancy rates were inversely related to patch area. Model

results do not necessarily imply a preference by chipmunks for smaller patches, just as higher densities in smaller woodlots (Nupp and Swihart 1998, 2000) do not necessarily indicate such preference (Van Horne 1983). However, rapid colonization of unoccupied patches, higher densities and occupancy rates of smaller woodlots, and the high overall occupancy rates (74%) across all study sites suggest that the upper Wabash River basin, which we characterized as an extreme case of forest fragmentation, was suitable for persistence of eastern chipmunks. Our finding that occupancy rate increased with stem density was consistent with Nupp's (1997) finding that the probability of occupancy and population density increased in patches with dense understory.

Consistent with earlier studies, we found no negative effect of landscape fragmentation on fox squirrel occurrence patterns. As was observed by Nupp and Swihart (2000), fox squirrels in our study were actually more likely to occur in more isolated woodlots. The ability and willingness of fox squirrels to move through open landscapes and utilize agricultural fields is well documented (e.g., Shepard and Swihart 1995, Goheen et al. 2003a) and consistent with their evolution in open savannah-like conditions (Koprowski 1994). Lack of model support for an effect of basal area of mast-producing trees may be an artifact of the time at which we sampled. Nupp (1997) found that fox squirrel densities and occurrence rates in spring were positively related to mast-tree variables; however, this result may have reflected a tie to overwinter resources, namely cache locations of nuts. We would expect the same during masting in autumn but not during our summer sampling if fox squirrels are then using other resources throughout the landscape.

Human alteration of the midwestern landscape has negatively affected eastern gray squirrel populations (Rosenblatt et al. 1999, Nupp and Swihart 2000). Across the upper Wabash River basin, gray squirrels were rare. We estimated them to occur at only 14% of sampled sites, and they were essentially absent in study landscapes >15 km from the Wabash River. Most occurrences were in a single, relatively heavily forested watershed (MWLV). Dependence of gray squirrels on proximity to the Wabash River corridor probably reflects multiple factors at work. Consistent with previous studies (Nupp and Swihart 2000, Goheen et al. 2003a), we found that gray squirrel occurrence rates were higher in larger patches, which occurred mostly near the Wabash River, especially

in the MWLV watershed. Nonetheless, patches up to 90 ha occurred throughout the basin but were unoccupied away from the river. Absence from these sites likely resulted from gray squirrels' unwillingness or inability to disperse through non-forest habitat (Goheen et al. 2003a). This should make gray squirrels sensitive to isolation, as vacant patches following local extinctions cannot be readily colonized. Consistent with this prediction, we found lower occupancy rates of sites in patches with greater nearest-neighbor distances. Collectively, our results point to the importance of a concentrated habitat network for the persistence of gray squirrel populations. Thus, riparian forest of the Wabash River, especially within the MWLV, may support a source population of gray squirrels, with sink populations existing only near this connected network of larger habitat patches. It is surprising then that other landscape principal components were not supported in our models after controlling for a distance-from-Wabash effect. However, this may be explained by the fact that a landscape's distance from the Wabash River was also negatively correlated ($R^2 \sim 0.3$) with all other measures of landscape forestation and connectivity.

We also found support for a positive effect of mast-tree basal area on gray squirrel occupancy rates, even though sampling occurred in summer when nuts were not available. Unlike fox squirrels, gray squirrels do not make use of habitats between patches; rather, they restrict use and movements to within a forest patch because of dispersal limitation. Thus, dependence of gray squirrel occurrence on habitats with high mast abundance may be reflected in their distributions all year.

The red squirrel is a relatively recent colonist of deciduous forest habitats of the midwestern United States and has expanded its range throughout northern Indiana concurrent with reduction in gray squirrel distribution (Mumford and Whitaker 1982, Goheen and Swihart 2003). Red squirrels and gray squirrels that co-occur in Indiana exhibit considerable overlap in diet breadth (Ivan and Swihart 2000). However, gray squirrels are more efficient at using nuts (Goheen et al. 2003b), and Nupp and Swihart (2001) found some evidence of negative competitive effects of gray squirrels on red squirrel densities. We did not find direct evidence of competition in our occupancy models. However, a variety of mechanisms may explain coexistence of competitors where there are species-related tradeoffs in resource-use efficiency and movement ability (Tilman 1994, Tilman et

al. 1997) especially in the presence of spatially or temporally structured resources (e.g., Brown 1989). All of these attributes characterize the red squirrel-gray squirrel system in northern Indiana. So, rather than full exclusion of a species by a superior competitor, we might simply observe inferior competitors existing at lower densities (Tilman 1994). Indeed, we found significantly greater red squirrel densities at sites without gray squirrels. Further, our models suggest that probability of red squirrel occurrence is greater at presumably suboptimal sites (i.e., those with lower basal area of mast-bearing trees) and in more isolated patches. We suspect that our model has not described site characteristics preferred by red squirrels but rather characteristics of sites that are less favorable to gray squirrels.

White-footed mice are habitat generalists and have been considered possible benefactors of forest fragmentation (Nupp and Swihart 1998, Henein et al. 1998), and high overall occurrence rates of white-footed mice across forest sites in our study clearly indicate a tolerance for the current agricultural landscape. Some previous studies have reported mouse densities to be greater in forest-edge habitat than forest-interior habitat (Cummings and Vessey 1994) and to vary inversely with woodlot size (Nupp and Swihart 1996, 1998). However, Wolf and Batzli (2002) found greater densities in forest interior than in edge habitat, and greater parasitism and predation rates in edge habitat than in forest interior (Wolf and Batzli 2001, 2004). In the latter study, food abundance was not greater in forest edge, nor was the reproductive effort of white-footed mice. Wolf and Batzli (2004) thus concluded that habitat quality of forest-edge was inferior to forest-interior for this species. Our data also suggested a negative response to edge by white-footed mice; several edge-related variables were supported in our occupancy models, including distance from edge, patch-shape complexity, and average patch-shape complexity in the landscape. We also found fairly strong evidence that occupancy rates were lower and more variable in landscapes that were less forested overall. This is not surprising; Middleton and Merriam (1981) suggested that post-winter patch extinctions may be relatively common in a landscape in Ottawa, Canada, and substantially lower occupancy rates in the first year of our study revealed the susceptibility of this species to temporal fluctuations in the environment. Although white-footed mice are known to use most habitats in agricultural landscapes to

some degree, the rate of colonizing unoccupied patches through agriculture fields should be limited before growth of crops each year (Cummings and Vessey 1994). Most of our sampling occurred before crops reached substantial height or cover.

MANAGEMENT IMPLICATIONS

The Wabash River corridor and Middle Wabash–Little Vermillion watershed in particular are only areas in the upper Wabash River basin with relatively contiguous forest habitat. The remaining agricultural landscape of northern Indiana seems unsuitable for persistence of dispersal-limited forest species such as gray squirrels and southern flying squirrels. Gray squirrels are valued for esthetics and as a game species. As prime dispersers of mast-producing trees, they serve an important role in forest regeneration (Steele and Smallwood 2002). For a region that has lost nearly 20% of its native mammal diversity over the past 2 centuries, we urge managers and land-use planners to recognize the importance of maintaining and restoring ecological integrity of this river corridor.

Methodologically, we showed the importance of modeling detection probabilities for species with low or variable detection rates (e.g., fox squirrels, white-footed mice) and of modeling spatial autocorrelation or mixed effects (random and fixed) for hierarchically structured data. All of these approaches were important for reducing bias in parameter estimates and model selection, and should be used in other studies. Detectability estimates, which reveal the amount of sampling effort required to achieve high detection rates, can assist in designing subsequent studies and should be used to correct simple presence-absence indices that do not otherwise account for heterogeneous nondetection error.

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LITERATURE CITED

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