Landscape Ecology 15: 621–631, 2000.
© 2000 *Kluwer Academic Publishers. Printed in the Netherlands.*

Using landscape metrics to model source habitat for Neotropical migrants in the midwestern U.S.

Peter T. Fauth[1]*, Eric J. Gustafson[2] & Kerry N. Rabenold[1]
[1]*Department of Biological Sciences, Lilly Hall, Purdue University, West Lafayette, IN 47907-1392, USA*
[2]*USDA-Forest Service, North Central Research Station, Forestry Sciences Laboratory, 5985 Highway K, Rhinelander, WI 54501, USA*
(author for correspondence and present address: Biology Department, Drew University, Madison, NJ 07940, USA; e-mail: PFauth@drew.edu)

Received 1 November 1998; Revised 15 June 1999; Accepted 29 September 1999

Key words: agricultural landscapes, bird abundance, GIS, landscape structure, midwestern U.S., multivariate models, Neotropical migrants, reproductive success, source-sink dynamics, wood thrushes

Abstract

Size of a forest patch is a useful predictor of density and reproductive success of Neotropical migratory birds in much of eastern North America. Within these forested landscapes, large forest tracts appear to be sources – fragments in which surpluses of offspring are produced and can potentially colonize new fragments including woodlot sinks where reproduction fails to balance adult mortality. Within agricultural landscapes of the midwestern U.S., where forests are severely fragmented, high levels of brood parasitism by brown-headed cowbirds (*Molothrus ater*) and intense predation on nests generally result in low reproductive success for Neotropical migrants regardless of forest size. In some midwestern U.S. landscapes, however, the variation in reproductive success among forest fragments suggests that 'source' habitat could still exist for Neotropical migrants. We used vegetation, fragment and landscape metrics to develop multivariate models that attempt to explain the variation in abundance and reproductive success of Neotropical migrants nesting in an agricultural landscape in northern Indiana, USA. We produced models that reasonably described the pattern of species richness of Neotropical migrants and the abundance of wood thrushes (*Hylocichla mustelina*) and several other Neotropical migrant species within 14 forest fragments. In contrast, we were unable to produce useful models of the reproductive success of wood thrushes breeding in the same forest fragments. Our results suggest that (1) abundance patterns of Neotropical migrants are probably influenced by both landscape- and fragment-scale factors; (2) multivariate analyses of Neotropical migrant abundance are not useful in modeling the corresponding patterns of reproductive success; and (3) the location of any remaining 'source' habitat for Neotropical migrants breeding within agricultural landscapes in North America will be difficult to predict with indirect measures such as vegetation composition or landscape context. As a result, the potential for developing conservation strategies for Neotropical migrants will be limited without labor-intensive, direct measurements of demographic parameters.

Introduction

Growing evidence implicates habitat fragmentation as a major factor contributing to population declines of several Neotropical migratory birds breeding in North American forests (reviewed in Askins et al. 1990; Faaborg et al. 1995). For example, lower reproductive success has been observed in fragmented compared to continuous forests within the same geographical region (e.g., the midwestern U.S.; Donovan et al. 1995) or landscape (e.g., a county; Porneluzi et al. 1993; Hoover et al. 1995). Lower reproductive success in forest fragments (often 0–0.6 fledglings per nesting attempt vs. 1–2 fledglings in continuous forests) occurs primarily because of high levels of brood parasitism by brown-headed cowbirds (*Molothrus ater*) and fre-

quent nest losses due to predators such as blue jays (*Cyanocitta cristata*), raccoons (*Procyon lotor*), and opossums (*Didelphis marsupialis*; e.g., Brittingham and Temple 1983). High densities of cowbirds and predators occur in forest fragments because of their low ratios of forest-interior to forest-edge habitat favored by these species (e.g., Brittingham and Temple 1983; Paton 1994).

Reproductive success of many Neotropical migrants in landscapes with fragmented forests is consistent with source-sink dynamics: some forest patches support stable populations (sources), whereas other patches (sinks) contain populations that are not self-maintaining in the absence of immigration from other forested tracts (Pulliam 1988). In eastern North America, large forest patches appear to be source habitat, whereas small woodlots are typically categorized as sinks for Neotropical migrants (e.g., Porneluzi et al. 1993; Hoover et al. 1995, but see Roth and Johnson 1993; Gale et al. 1997). As a result, forest size is generally a good predictor of the reproductive success of Neotropical migrants in eastern North America (e.g., Hoover et al. 1995). In contrast, forest size does not predict reproductive success in the midwestern U.S. (e.g., Fauth 2000).

Robinson et al. (1995) found that reproductive success of Neotropical migrants in the midwestern U.S. can be predicted by at least one landscape-scale variable: percent forest cover within a 10 km radius of study sites was negatively related to cowbird parasitism and predation rates for several forest-breeding Neotropical migrants. Although conservation strategies for Neotropical migrants in the midwestern U.S. may be most effective at broad scales (i.e. regions within states), the restoration of large blocks of forested land in agricultural landscapes is often impractical. Moreover, in some midwestern U.S. landscapes, reproductive success of Neotropical migrants varies among individual forest patches (Trine 1998; Fauth 2000). In northern Indiana, for example, some forest fragments appear to support populations of Neotropical migrants that produce enough offspring to act as potential sources, although the landscape as a whole appears to be part of a regional, midwestern U.S. sink (Fauth 2000). The ability to identify remaining 'sources' in midwestern U.S. is the first step in conserving Neotropical migrants and reducing the impact of these agricultural landscapes as sinks draining individuals from the regional population (Robinson et al. 1995; Brawn and Robinson 1996).

Recent quantification of the spatial patterns of habitats using Geographic Information Systems (e.g., O'Neill et al. 1988; Turner et al. 1991; Gustafson 1998) has made it easier to investigate the effects of landscape context on distributions, breeding density, and reproductive success of bird populations. For example, Gustafson et al. (1994) found that proximity index, a measure of habitat patch clustering, was effective in classifying the suitability of habitat for wild turkey (*Meleagris gallopavo*) in the midwestern U.S. Flather and Sauer (1996) found that Neotropical migrants were sensitive to regional habitat structure, and stressed the importance of landscape attributes in designing conservation strategies for this group of birds.

In this paper we attempt to model source habitat for wood thrushes (*Hylocichla mustelina*), a common, but declining Neotropical migrant in the midwestern U.S. (Sauer et al. 1997), using landscape and vegetation metrics derived from GIS and traditional sampling methods. Our goal was to explore possible associations of bird abundances and reproductive success with attributes of the study sites including their spatial position in the landscape. In particular, we attempted to identify useful predictors of reproductive success that would allow wildlife managers to readily screen agricultural landscapes for potential source habitat and implement appropriate conservation efforts for wood thrushes and possibly other Neotropical migrants.

Methods

Study sites

We established 15 study sites in 14 different forest fragments ranging from 7 ha to nearly 500 ha in the Indian-Pine Watershed, Tippecanoe and Warren Counties, Indiana, U.S.A. (Fig. 1). Within the 58,000-ha watershed, forests of various sizes remain along drainages embedded in predominately agricultural matrices. Overall, less than 9% of the watershed is forested and 60% is planted in agricultural crops (primarily soybean and corn; Fig. 1).

Dependent variables

We modeled species richness of Neotropical migrants, the abundance of female brown-headed cowbirds, the abundance of all potential hosts to cowbirds, the abundance of individual Neotropical migrant species, and the reproductive success of wood thrushes (Table 1).

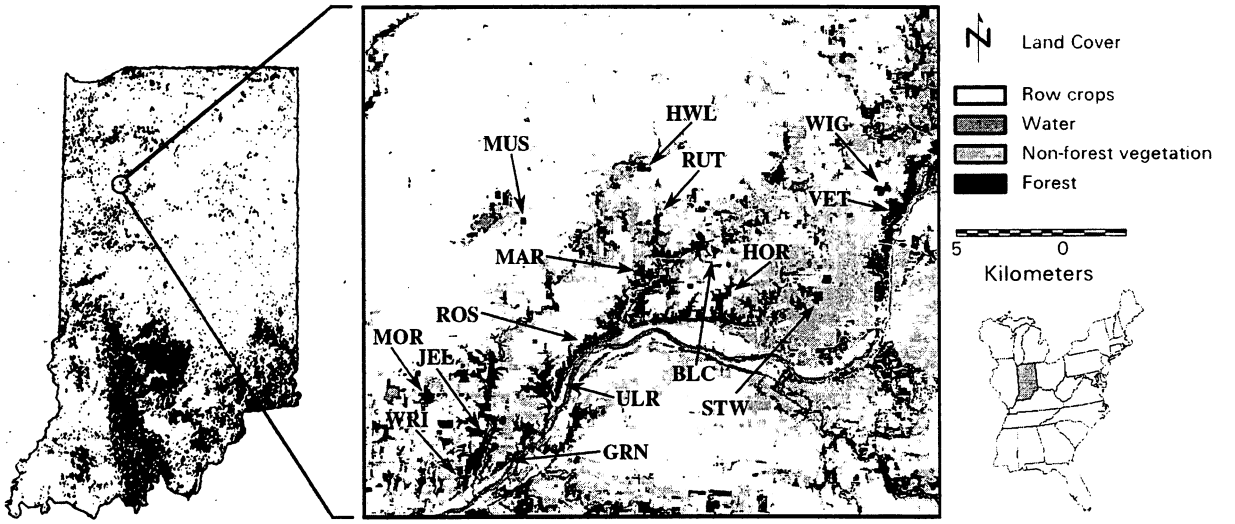

Figure 1. Landcover maps showing forested habitats of Indiana, and in more detail, the Indian-Pine Watershed in northern Indiana. The Indian-Pine Watershed map was derived from satellite imagery collected in April 1986. Regions depicted in black are forested (approximately 9% of the area). Non-forest vegetation (depicted in gray) includes winter wheat, golf courses, fallow fields and urban areas. Wood Thrushes were studied in the 15 study sites labeled on the map. The watershed comprises about 58,000 ha.

We derived all measures of abundance from the mean number of individuals detected during 6-min, 70-m radius point-count surveys (Hutto et al. 1986) conducted on fair-weather days from 05:30–09:30 in late-May through mid-June 1994 and 1995. Point-count surveys are standardized sampling techniques commonly used by researchers and wildlife managers to establish indices of bird abundance assuming equal detectability of birds among forest fragments. We established the maximum number of points within each fragment (range 4–8 points), such that survey points were approximately 150 m apart and at least 70 m from the nearest forest edge. We used this regular placement of survey points so that there was no overlap between points, and the area sampled by our surveys was completely within forested habitat. We surveyed each point three times during the breeding season, a seasonal effort that might be used by wildlife managers. We sampled six fragments in both 1994 and 1995, and used two-year means for these sites. We sampled the remaining sites in either 1994 or 1995 because of logistical constraints. We defined Neotropical migrants as species that breed in North America and migrate to the Caribbean, Mexico and southward for winter (as in DeGraaf and Rappole 1995). We modeled the abundance of four such species parasitized by cowbirds: wood thrushes, indigo buntings (*Passerina cyanea*), acadian flycatchers (*Empidonax virescens*), and red-eyed vireos (*Vireo olivaceus*).

We distinguished between male and female cowbirds using 'rattle' calls (Rothstein et al. 1988), and used the mean number of female cowbirds detected per point count as our measure of cowbird abundance. Cowbird hosts included all species known to accept cowbird eggs in Illinois (Robinson 1993), including 73% of the Neotropical migrants breeding in northern Indiana. We estimated reproductive success of wood thrushes in two ways: (1) the probability of raising at least one wood thrush fledgling per nesting attempt (Mayfield 1975), and (2) the mean number of wood thrush fledglings produced per nesting attempt (Fauth 2000).

Independent variables

We sampled vegetation within each fragment using methods modified from James and Shugart (1970). This sampling protocol is widely used by avian ecologists and wildlife managers to provide easily quantifiable estimates of vegetation metrics important to breeding birds. We used an area-dependent number of 10-m radius sampling points (at and between each point-count survey) at the study sites (range 8–17 points). Vegetation metrics are described in Table 2.

We derived landcover data for the Indian-Pine Watershed from a Landsat Thematic Mapper (TM) image (pixel width = 30 m) collected on April 12, 1986 using PC-ERDAS image-processing software (see Gustafson et al. 1994). We used supervised and

Table 1. Descriptions of the dependent variables used to model bird abundance and reproductive success of wood thrushes in a northern Indiana landscape.

Dependent variable	Description
Avian community[a]	
Neotropical migrant richness[b]	Total number of Neotropical migrant species (species richness) detected at each site.
Abundance of cowbird hosts	Mean number of detections per point count of all species that are parasitized by brown-headed cowbirds.
Abundance of cowbirds	Mean number of detections per point count of female cowbirds.
Abundance of indigo buntings, red-eyed vireos, and acadian flycatchers	Mean number of detections of each species per point count.
Wood thrushes[c]	
Abundance of wood thrushes	Mean number of wood thrushes detected per point count.
Nesting success of wood thrushes	Probability that a nesting attempt results in the production of at least one wood thrush fledgling. Based on Mayfield (1975).
Number of wood thrush fledglings	Mean number of wood thrush fledglings produced per nesting attempt.

[a] Based on 6-minute, 70 m-radius point-count surveys. Details in text and in Fauth (2000).
[b] A list of Neotropical migrant species recorded during point counts is in Fauth (1997).
[c] Details in Fauth (2000).

unsupervised classification techniques (Lillesand and Kieffer 1987) to assign the raster data to 5 classes: water, urban, forest, bare soil (mainly soybean and corn fields), and non-forest vegetation (consisting of shrubs, fallow fields, lawns, winter wheat, and scattered trees or shrubs). We assessed the accuracy of classification by comparing randomly selected points (1.03% of all points) on the classification map to 1:40,000 color-infrared aerial photos. The accuracy determined by this comparison was as follows: water-100.0%, urban-45.9%, forest-94.4%, bare soil-98.2%, and non-forest vegetation-95.7%; an overall accuracy of 95.3%. Although our accuracy in classifying urban landcover could be improved, its influence on our results is minimal because only 5% of the landscape contained components of the built environment. We classified forest patches as clusters of vertically or horizontally adjacent pixels (but not diagonally) as in other studies (e.g., Gardner et al. 1987; Gustafson et al. 1994), producing 3688 forest patches in the landscape. To reduce computation time, we eliminated all forest fragments < 0.45 ha (5 pixels) from the classification map before calculating the landscape metrics. This 'sieve' process served to eliminate the smallest fragments that were not used by wood thrushes (Fauth, unpubl. data) and reduced the number of fragments to 869, but did not affect the representation of openings within forest fragments. We used HISA (Gustafson and Parker 1994) and FRAGSTATS (McGarigal and Marks 1995) to measure the forest fragment and landscape metrics listed in Table 2. We did not examine all fragment and landscape metrics, but instead selected measurements that are often used by, or could be easily collected by wildlife managers and researchers interested in assessing the source-sink status of forest fragments (reviewed in Freemark et al. 1995). We used a scale in which to calculate landscape structure based on the extent of our northern-Indiana landscape. For example, we could not use the 10-km radius plots employed by Robinson et al. (1995) because nearly all the sites would have the same values for the landscape metrics.

Statistical analyses

We entered all independent variables (Table 2) into a stepwise regression analysis (SAS Institute 1995) to derive multivariate models that explained the variation observed in each of the dependent variables (Table 1). We used $\log_{10}$ and arcsin transformations as necessary so each variable met the assumptions of linear regression (Sokal and Rohlf 1981). The stepwise regression procedure is a modification of the forward-selection technique in that a variable added to the model in one step may be removed if it does not produce a significant F statistic in a later step. We used $P = 0.15$ as the significance level for entry into the model and $P = 0.10$ for retention, because we wanted to screen, but not eliminate the independent variables that explained some of the variation in the dependent variables and could be used as predictors in other midwestern U.S. landscapes. We did not include P-values

Table 2. Descriptions of the independent variables used to model bird abundance and reproductive success of wood thrushes in a northern Indiana landscape.

Independent variable	Description
Vegetation[a]	
Tree density	Mean number of trees per 10 m^2 (> 10 cm in diameter at 1.5 m from the ground).
Tree basal area	Mean basal area of trees at 1.5 m above ground (m^2/ha).
Forest heterogeneity	Standard error of the mean tree density. Used as an index of the uniformity of the tree distribution.
Subcanopy/canopy cover	Mean proportion of transects covered by vegetation. Based on 20 point surveys taken perpendicular to and at 1.5 m above ground along a randomly selected 20 m transect within each sampling point (James and Shugart 1970).
Ground cover	Mean proportion of transects covered with herbaceous vegetation. Based on 20 point surveys taken at a randomly selected 20 m transect on the ground within each sampling point (James and Shugart 1970).
Shrub/sapling density	Mean number of shrub and sapling stems per 10 m^2 (< 10 cm in diameter at 1.5 m above ground).
Proportion of oak/hickory	Proportion of the trees sampled that were oak (*Quercus*) or hickory (*Carya*). Used as a crude index of soil moisture in the forest: soil moisture tends to be lower in fragments containing high proportions of oak and hickory in this landscape.
Fragment[b]	
Area	Area (ha) of horizontally or vertically (not diagonally) connected pixels (30 m^2) representing a forest fragment.
Core area x	Area (ha) within a fragment greater than x from the boundary between the fragment under investigation and another landcover class, where x is either 60 m or 120 m (i.e., two separate measures). These measures are within the distance class with the highest level of parasitism by cowbirds reported by Temple and Cary (1988).
Proportion of Core x	Proportion of the fragment area considered as core area within the same x distances as above.
Perimeter	Total distance (m) measured along the outer-most pixels of a forest fragment.
Shape index	A measure of patch shape irregularity based on a square as a reference shape. Shape index = (0.25 * perimeter)/$\sqrt{\text{area}}$.
Edge density	The ratio of perimeter to area of a forest fragment (m/ha).
Landscape metrics[b]	
Proportion of forest within x km	Proportion of area within x radius of the fragment under investigation that is covered by forest, where x is either 0.9 and 3 km (i.e. two separate measures). These distances were selected among several possibilities because they were most strongly correlated with the dependent variables of interest and within the scale of our study.
Proportion of nonforest vegetation within x km	Proportion of area within x radius of the fragment under investigation that is covered by lawns, winter wheat, fallow fields, shrubs, or scattered trees using the same distances as above.
Proximity index within x km	An index to distinguish isolated fragments from those in a complex of patches: $P_x = \sum_{i=1}^{x} \frac{\text{area}i}{\text{distance}i}$, where area_i = the area of fragment i, distance_i = the distance between the fragment under investigation and fragment i, and x = the number of patches whose edges are within 0.9 or 3 km radius of the fragment under investigation. Small, isolated patches have low and large complexes of patches have high proximity values (Gustafson and Parker 1994).
Number of near neighbors	Number of fragments within 0.9 km of the fragment of interest.

[a]Modified from James and Shugart (1970). The number of sampling points was area-dependent and ranged from 8–17. Each sampling point was a 10 m-radius circular plot.
[b]Calculated using HISA (Gustafson and Parker 1994) and FRAGSTATS software (McGarigal and Marks 1995).

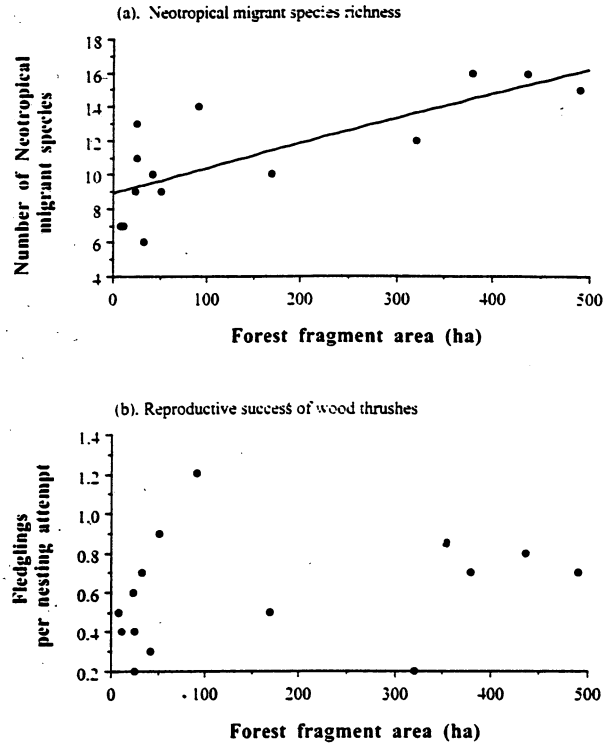

Figure 2. (a) Positive relationship between forest fragment area and the species richness of Neotropical migratory birds detected during point counts in northern Indiana, and (b) lack of a relationship between forest area and reproductive success of wood thrushes measured as number of fledglings produced per nesting attempt. Details about wood thrushes breeding in the Indian-Pine Watershed are found in Fauth (2000).

with our model results as we consider these analyses as exploratory rather than inferential (see James and McCulloch 1990).

Results

The stepwise regression models constructed for each of the dependent variables are described in Table 3. Model parameters included a small subset of the vegetation, fragment and landscape metrics entered into the stepwise regression analyses, and about half of the models consisted of a single variable. Landscape metrics most frequently incorporated into the models were measures of landcover composition within 0.9 km of the fragments (Table 3).

The species richness of Neotropical migrants within the study sites was positively related to fragment area (Table 3, Figure 2a). Models for the abundance of each Neotropical migrant species consisted of multiple variables at multiple spatial scales, and explained > 53% of the variance in abundance of each species (Table 3). The total abundance of cowbird hosts was modeled by the proportion of the fragment more than 60 m from a forest edge, edge density (ratio of perimeter to area of the fragment), and the proportion of forest cover within 0.9 km of the fragments (Table 3). Combined these variables accounted for 68% of the variation in cowbird-host abundance. The abundance of female cowbirds was modeled with a single variable: proportion of forest within 0.9 km of the study sites (Table 3). Nonetheless, this model explained less than 40% of the variation in cowbird abundance at the study sites. We produced a model that accounted for much of the variation in the abundance of wood thrushes based on vegetation and fragment metrics ($R^2 = 0.89$, Table 3). In contrast, fragment size was not a useful predictor of the reproductive success of wood thrushes ($R^2 < 0.07$, $P > 0.38$, Figure 2b). In fact, the model that best explained the variation in the reproductive success of wood thrushes ($R^2 \leq 0.30$) would not be useful to wildlife managers trying to predict potential source habitat in this landscape.

Discussion

Our ability to model the patterns of Neotropical migrant abundance and reproductive success required that the scale of the dependent variables matched the scale of our fragment and landscape metrics (Wiens 1994; Freemark et al. 1995; Gustafson 1998). Habitat selection by breeding Neotropical migrants involves a series of choices at hierarchical levels: territory, fragment, landscape and region (Wiens et al. 1987; Steele 1992; Probst and Weinrich 1993; Freemark et al. 1995). Population dynamics within landscapes containing fragmented forests could also influence habitat selection because of interspecific competition for preferred habitat (Layton and Thompson 1986, Probst and Hayes 1987, Hill 1988), altered dispersal patterns (Villard et al. 1995), conspecific attraction (Smith and Peacock 1990), or differential mortality rates among habitat patches (Gibbs and Faaborg 1990). Neotropical migrant populations in the midwestern U.S. show population dynamics consistent with the source-sink model of Pulliam (1988) at the level of a landscape (Villard et al. 1995) or within a larger geographic region (e.g., midwestern U.S.; Robinson et al. 1995; Brawn and Robinson 1996; Trine 1998). Until the

Table 3. Results of the stepwise regression procedures for predicting avian abundance and reproductive success of wood thrushes in 14 forest patches in a northern Indiana landscape. Variables required $P < 0.10$ to be retained in the model.

Dependent variable	Intercept	Model parameters	Estimate[a]	Adj. R^2	Model R^2
Avian community					
Neotropical migrant species richness	+3.34	Area	−4.26	0.62	0.62
Abundance of cowbird hosts	+23.4	Proportion core 60 m	−8.49	0.33	0.68
		Edge Density	−7.41	0.23	
		Proportion forest 0.9 km	+1.20	0.11	
Abundance of female cowbirds	+0.05	Proportion forest 0.9 km	+0.59	0.38	0.38
Abundance of indigo buntings	+1.31	Proportion forest 0.9 km	−1.20	0.59	0.94
		Proximity index 0.9 km	−0.12	0.12	
		Proportion oak/hickory	+0.67	0.19	
		Proportion ground cover	−0.43	0.04	
Abundance of red-eyed vireos	+0.73	Proportion nonforest 0.9 km	+1.35	0.28	0.53
		Shrub/sapling density	−0.09	0.25	
Abundance of acadian flycatchers	−0.34	Density of trees	+0.19	0.62	0.75
		Proportion of forest 0.9 km	+4.52	0.13	
Wood thrushes					
Abundance of wood thrushes	+8.44	Shrub/sapling stems	+0.09	0.55	0.89
		Proportion core 60 m	−3.65	0.20	
		Edge Density	−3.20	0.14	
Wood thrush nesting success	−0.02	Tree density	+0.70	0.30	0.30
Number of wood thrush fledglings per attempt	+1.17	Shrub/sapling stems	−0.07	0.26	0.26

[a]The sign of estimates in models with > 2 independent variables may not be the same as that of the correlation between the dependent and independent variables due to correlations among independent variables (Sokal and Rohlf 1981).

dispersal behavior of adults and juveniles is better understood, the appropriate scale at which to investigate possible source-sink dynamics and its consequences on habitat selection by Neotropical migrants will be difficult to ascertain. Given the imprecise information about dispersal and the impracticality of broad-scale experiments involving entire landscapes, we believe that using statistical procedures involving different vegetation, fragment and landscape metrics may be the only means of screening plausible predictors of Neotropical migrant abundance and reproductive success within agricultural landscapes of the midwestern U.S., and perhaps similar landscapes elsewhere in the breeding range. Moreover, the importance of predicting the location of remaining 'sources' for Neotropical migrants in such landscapes warrants our exploratory approach, particularly if management strategies can reduce or reverse the effect of large-scale sinks such as those in the midwestern U.S. (Robinson et al. 1995; Donovan et al. 1995; Brawn and Robinson 1996; Trine 1998; Fauth 2000).

Neotropical migrant richness and abundance

Species richness of forest-breeding Neotropical migrants was positively related to fragment size. This is consistent with several other studies conducted in landscapes with fragmented forests (e.g., Whitcomb et al. 1981; Ambuel and Temple 1983; Lynch and Whigham 1984; Blake and Karr 1987; Robbins et al. 1989). Large forests tend to support many forest-interior species (*sensu* Whitcomb et al. 1981) that are absent in smaller woodlots, possibly because of microclimatic or vegetation differences related to patch area (Freemark and Merriam 1986; Saunders et al. 1991) or their effect on food abundance (Burke and Nol 1998).

We also developed models that explained much of the variation in abundance of three Neotropical migrants: indigo buntings, acadian flycatchers, and

red-eyed vireos. These models incorporated vegetation metrics that could influence habitat selection by these species or correlate with such metrics (Table 3). In addition, all models contained landscape-level metrics, suggesting the importance of fragment pattern in the habitat selection of many Neotropical migrants. Fauth (1997) also suggested that habitat selection by some migrant birds during fall could be a result of both landscape-level (fragment isolation) and within-fragment (food resources) characteristics of forest patches in the same midwestern U.S. landscape. Similarly, Pearson (1993) found landscape variables that explained the variation in the abundance of wintering birds within forest openings.

Cowbird and cowbird-host abundance

The abundance of female cowbirds was modeled by the proportion of forest within 0.9 km of the study sites. Robinson et al. (1995) also showed that cowbird parasitism can be predicted on a landscape level using the same metric on a broader geographic scale (10 km). The extent of our landscape metrics was constrained by the dimensions of our study area; however, we were still able to explain a modest amount of variation in cowbird abundance. Cowbird abundance could also be influenced by host abundance within landscapes with fragmented forests (Robinson et al. 1999). We suggest that cowbird habitat choice is hierarchical within the scale of our study. Cowbirds may prefer locations within agricultural landscapes that contain a high proportion of forest habitats because of their apparent preference for forest-nesting rather than grassland-nesting host species (Hahn and Hatfield 1995), and then select territories with a high abundance of potential hosts. The fact that no vegetation measures contributed to the explanation of cowbird variance is consistent with Brittingham and Temple (1996) who found that, of 16 vegetation variables measured, only canopy closure was significantly different between sample plots containing parasitized and unparasitized acadian flycatcher nests.

Variation in the abundance of cowbird hosts was explained by a model that included two measures of edge-to-interior habitat within forest fragments and the proportion of forest within 0.9 km of the fragments. The model suggests that many cowbird hosts in this landscape prefer edge habitat, such as northern cardinals (*Cardinalis cardinalis*) and indigo buntings. Both of the edge-interior variables that were included in the model were highly correlated ($r = -0.96$, $P < 0.001$), but we used both variables in the model because we believe other agricultural landscapes will find a similar correlation between these two variables and the combined model produced reasonable predictive utility ($R^2 = 0.68$ vs. $R^2 < 0.33$ using only one of the variables: Table 3).

Wood thrush abundance and reproductive success

Variation in abundance of wood thrushes was modeled by vegetation and fragment-level variables. The abundance of wood thrushes within this landscape was also negatively related to fragment size (Fauth 2000). The measures of core area incorporated into the model were correlated with fragment size ($r > 0.53$; $P \leq 0.05$), so these parameters may reflect the apparent preference of wood thrushes to breed in smaller fragments of the midwestern U.S. (Donovan et al. 1995; Fauth 2000). The inclusion of shrub and sapling density in the model is consistent with the preference of wood thrushes to nest in dense pockets of shrubs and saplings within mesic forests.

Reproductive success of wood thrushes showed no relationship with any of our landscape variables. In fact, neither measure of the reproductive success of wood thrushes was explained adequately by our models ($R^2 \leq 0.30$). This is in strong contrast with the results of Hoover et al. (1995): more than 85% of the reproductive success of wood thrushes in a forested landscape of the eastern U.S. was explained by size of forest fragments. Brawn and Robinson (1996) also suggested that reproductive success of Neotropical migrants was not strongly related to patch size in agricultural landscapes of the midwestern U.S. In fact, Trine (1998) found that even the largest forest tracts in Illinois (1100–2200 ha) were sink habitats for wood thrushes. Our findings suggest that vegetation, fragment, or landscape predictors of the breeding success of wood thrushes, and perhaps other Neotropical migrants, will be difficult to find in agricultural landscapes of North America, and could require more extensive or fine-grained descriptions of vegetation composition and structure.

Limitations of the models

Wood thrushes share many characteristics with other forest-breeding Neotropical migrants, such as a short breeding season, relatively small clutch sizes and vulnerability to cowbird parasitism. Wood thrushes have been extensively studied because they nest in the

shrub-subcanopy layer and their nests are easily observed. In addition, general patterns of nest parasitism and predation observed for wood thrushes are similar to those reported for other Neotropical migrant species such as red-eyed vireos, acadian flycatchers, indigo buntings and ovenbirds (*Seiurus aurocapillus*; e.g., Robinson et al. 1995; Donovan et al. 1995). Nonetheless, wood thrushes may not be an ideal 'model' for all species of forest-breeding Neotropical migrants. In addition to their less-restrictive nesting habits, wood thrushes can successfully raise as many as three broods per season and produce both their own and cowbird offspring in each attempt (Donovan et al. 1995; Trine 1998; Fauth 2000). Smaller Neotropical migrants, such as red-eyed vireos, are less resistant to cowbird parasitism and as a result often have lower daily survival rates than wood thrushes (Robinson et al. 1995; Donovan et al. 1995). Conclusions about the 'quality' of breeding habitat based on the demography of wood thrushes must be carefully applied to other species of Neotropical migrants. Moreover, the ability to predict the location of high-quality breeding habitat may be possible for other species of Neotropical migrants, particularly those with more specific habitat requirements.

Our general conclusion that the reproductive success of Neotropical migrants cannot be easily modeled may be limited to agricultural landscapes in the breeding range of these birds. For example, Friesen et al. (1999) found generally high reproductive success for wood thrushes in an agricultural landscape in southwestern Ontario, Canada, but unlike more forested regions in eastern North America (e.g., Hoover et al. 1995), reproductive success was not related to fragment size. In agricultural landscapes throughout the range of these forest-breeding Neotropical migrants, the dynamics of nest predators and parasites appear complex and unpredictable, and may hamper efforts to identify the highest-quality breeding habitats based only vegetation and landscape metrics.

Finally, variation in reproductive success within sites (Holmes et al. 1986; Trine 1998; Fauth 2000), suggests that the production of models to identify 'high-quality' breeding habitat for Neotropical migrants could change periodically. Different forest patches may act as 'source' habitat during different breeding seasons, or as the landscape changes (i.e., forest tracts are lost). If our multivariate models or those produced by other researchers were successful in explaining the variation in reproductive success of wood thrushes, wildlife managers would still need to periodically 're-calibrate' the models based on new demographic data.

Conclusions

The statistical procedures we have employed do not permit inferences about the factors causing the patterns of Neotropical migrant abundance and reproductive success in the midwestern U.S. or in similar landscapes dominated by agriculture. We considered easily quantifiable variables that described the landscape at different spatial scales and could be useful in predicting source habitat for Neotropical migrants. Our goal was to collect the type and extent of data that might be used by wildlife managers trying to assess the population stability of forest-breeding Neotropical migrants in agricultural landscapes in North America. Our success was limited; we produced statistical models that accounted for the majority of variation in the abundance of wood thrushes and other Neotropical migrants, but could not construct models to explain the reproductive success of wood thrushes breeding in the midwestern U.S. In these agricultural landscapes, cowbirds and predators have saturated forest habitats, reduced the reproductive success of Neotropical migrants (Brawn and Robinson 1996), and could also affect habitat selection by adults (Roth and Johnson 1993, Villard et al. 1995). The reproductive success of Neotropical migrants in some midwestern U.S. landscapes shows interpatch variation consistent with landscape-level source-sink dynamics (Fauth 2000). Nonetheless, the results of our study suggest that locating remaining 'source' habitat within this region, and perhaps similar agricultural landscapes elsewhere, will require nothing less than extensive field work to document the demography of these birds and the factors influencing cowbird and predator distributions and behavior.

Acknowledgements

We thank the landowners who allowed us to work on their property: Blacks, Grenards, Howells, Janssens, Jewells, Ladds, Lewellens, Morgans, Mussers, Rutherfords, Ulrichs, Wiggins, and Wrights. P. Anderson, P. McDonald, and B. Thompson accommodated our research on Purdue University property. We thank Indiana Department of Natural Resources and Indiana Veterans' Home for permission to work in Veterans' Nature Preserve. P. Logan, and K. Kulow assisted

in data collection. R. Howard. J. Miller, S. Robinson, P. Waser and two anonymous reviewers provided helpful comments on earlier drafts of this manuscript. Funding for this research was provided by an Indiana Department of Natural Resources Special Projects Grant and the Purdue Research Foundation.

References

Ambuel. B. and Temple. S.A.. 1983. Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. Ecology 64: 1057–1068.

Askins. R.A.. Lynch. J.F. and Greenberg. R. 1990. Population declines in migratory birds in eastern North America. Current Ornithol 7: 1–57.

Blake. J.G.. and Karr. J.R. 1987. Breeding birds of isolated woodlots: area and habitat relationships. Ecology 68: 1724–1734.

Brawn. J.D. and Robinson. S.K. 1996. Source-sink population dynamics may complicate the interpretation of long-term census data. Ecology 77: 3–12.

Brittingham. M.C. and Temple. S.A. 1983. Have cowbirds caused forest songbirds to decline? Bioscience 33: 31–35.

Brittingham. M.C. and Temple. S.A. 1996. Vegetation around parasitized and unparasitized nests within deciduous forest. J. Field Ornithol. 67: 406–413.

Burke. D.M. and Nol. E. 1998. Influence of food abundance. nest-site habitat. and forest fragmentation on breeding Ovenbirds. Auk 115: 96–104.

DeGraaf. R.M. and Rappole. J.H. 1995. Neotropical Migratory Birds: Natural History. Distribution. and Population Change. Comstock Publishing Associates. Ithaca. NY.

Donovan. T.M.. Thompson III. F.R.. Faaborg. J. and Probst. J.R. 1995. Reproductive success of migratory birds in habitat sources and sinks. Cons. Biol. 9: 1380–1395.

Faaborg. J.. Brittingham. M.C.. Donovan. T.M. and Blake. J.G. 1995. Habitat fragmentation in the temperate zone. In Ecology and Management of Neotropical Migratory Birds: A Synthesis and Review of Critical Issues. pp. 357–380. Edited by T.E. Martin and D.M. Finch. Oxford University Press. New York.

Fauth. P.T. 1997. Effects of forest fragmentation on breeding and migrating birds in a midwestern landscape. Ph. D. thesis. Purdue University. West Lafayette. Indiana.

Fauth. P.T. 2000. Reproductive success of wood thrushes in forest fragments in northern Indiana. AUK 117: 194–204.

Flather. C.H. and Sauer. J.R. 1996. Using landscape ecology to test hypotheses about large-scale abundance patterns in migratory birds. Ecology 77: 28–35.

Freemark. K.E. and Merriam. H.G. 1986. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. Biol. Cons. 36: 115–141.

Freemark. K.E.. Dunning. J.B.. Hejl. S.J. and Probst. J.R. 1995. A landscape ecology perspective for research. conservation. and management. In Ecology and Management of Neotropical Migratory Birds: A Synthesis and Review of Critical Issues. pp. 381–427. Edited T.E. Martin and D.M. Finch. Oxford University Press. New York.

Friesen. L.. Cadman. M.D. and MacKay. R.J. 1999. Nesting success of Neotropical migrant songbirds in a highly fragmented landscape. Cons. Biol. 13: 338–346.

Gale. G.A.. Hanners. L.A. and Patton. S.R. 1997. Reproductive success of worm-eating warblers in a forested landscape. Cons. Biol. 11: 246–250.

Gardner. R.H.. Milne. B.T.. Turner. M.G. and O'Neill. R.V. 1987. Neutral models for the analysis of broad-scale landscape pattern. Landscape Ecol. 1: 19–28.

Gibbs. J.P. and Faaborg. J. 1990. Estimating the viability of ovenbird and Kentucky warbler populations in forest fragments. Cons. Biol. 4: 193–196.

Gustafson. E.J. 1998. Quantifying spatial pattern: What is the state of the art? Ecosystems 1: 143–156.

Gustafson. E.J. and Parker. G.R. 1994. Using an index of habitat patch proximity for landscape design. Landscape Urban Planning 29: 117–130.

Gustafson. E.J.. Parker. G.R. and Backs. S.E. 1994. Evaluating spatial pattern of wildlife habitat: A case study of the Wild Turkey (*Meleagris gallopavo*). Am. Midland Nat. 131: 24–33.

Hahn. D.C. and Hatfield. J.S. 1995. Parasitism at the landscape scale: cowbirds prefer forests. Cons. Biol. 9: 1415–1423.

Hill. G.E. 1988. Age. plumage brightness. territory quality. and reproductive success in the black-headed grosbeak. Condor 90: 379–388.

Holmes. R.T.. Sherry. T.W. and Sturges. F.W. 1986. Bird community dynamics in a temperate deciduous forest: Long-term trends at Hubbard Brook. Ecol. Monogr. 56: 201–220.

Hoover. J.P.. Brittingham. M.C. and Goodrich. L.J. 1995. Effects of forest patch size on nesting success of wood thrush. Auk 112: 146–155.

Hutto. R.L.. Pletschet. S.M. and Hendricks. T.P. 1986. A fixed-radius point-count method for nonbreeding and breeding season use. Auk 103: 593–602.

James. F.C. and Shugart. H.H. 1970. A quantitative method of habitat description. Audubon Field Notes 24: 727–736.

James. F.C. and McCulloch. C.E. 1990. Multivariate analysis in ecology and systematics: Panacea or Pandora's box? Annu. Rev. Ecol. Syst. 21: 129–166.

Layton. S.M. and Thompson. C.F. 1986. Site fidelity and habitat quality as determinants of settlement patterns in male painted buntings. Condor 88: 206–210.

Lillesand. T. M. and Kiefer. R.W. 1987. Remote Sensing and Image Interpretation. John Wiley and Sons. New York.

Lynch J.F. and Whigham. D.F. 1984. Effects of forest fragmentation on breeding bird communities in Maryland. USA. Biol. Cons. 28: 287–324.

Mayfield. H. 1975. Suggestions for calculating nest success. Wilson Bull. 87: 456–466.

McGarigal. K. and Marks. B.J. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. General Technical Report PNW-GTR-351. USDA Forest Service. Pacific Northwest Research Station. Portland. OR.

O'Neill. R.V.. Krummel. J.R.. Gardner. R.H.. Sugihara. G.. Jackson. B.. DeAngelis. D.L.. Milne. B.T.. Turner. M.G.. Zygmunt. B.. Christensen. S.W.. Dale. V.H. and Graham. R.L. 1988. Indices of landscape pattern. Landscape Ecol. 1: 153–162.

Paton. P.W.C. 1994. The effect of edge on avian nest success: How strong is the evidence? Cons. Biol. 8: 17–26.

Pearson. S.M. 1993. The spatial extent and relative influence of landscape-level factors on wintering bird populations. Landscape Ecol. 8: 3–18.

Porneluzi. P.. Bednarz. J.C.. Goodrich. L.J.. Zawada. N. and Hoover. J. 1993. Reproductive performance of territorial ovenbirds occupying forest fragments and a contiguous forest in Pennsylvania. Cons. Biol. 7: 618–622.

Probst, J.R. and Hayes, J.P. 1987. Paring success of Kirtland's warblers in marginal vs. suitable habitat. Auk 104: 234–241.

Probst, J.R. and Weinrich, J. 1993. Relating Kirtland's warbler population to changing landscape composition and structure. Landscape Ecol. 8: 257–271.

Pulliam, H.R. 1988. Sources, sinks and population regulation. Am. Nat. 132: 652–661.

Robbins, C.S., Dawson, D.K. and Dowell, B.A. 1989. Habitat area requirements of breeding forest birds of the Middle Atlantic States. Wildlife Monogr. 103: 1–34.

Robinson, S.K. 1993. Effects of forest fragmentation on migrant songbirds in the Shawnee National Forest. Report to the Illinois Department of Energy and Natural Resources. Springfield, Illinois.

Robinson, S.K., Hoover, J.P., Jack, R. and Herkert, J.R. 1999. Effects of tract size, habitat, cowbird density, and nesting stratum on cowbird parasitism levels. *In* Ecology and Management of Cowbirds. Edited by T. Cook, S.K. Robinson, S.I. Rothstein, S.G. Sealy and J.N.M. Smith. University of Texas Press, Austin, TX. In press.

Robinson, S.K., Thompson III, F.R., Donovan, T.M., Whitehead, D.R. and Faaborg, J. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267: 1987–1990.

Roth, R.R., and Johnson, R.K. 1993. Long-term dynamics of a wood thrush population breeding in a forest fragment. Auk 110: 37–48.

Rothstein, S.I., Yokel, D.A. and Fleischer, R.C. 1988. The agonistic and sexual functions of vocalizations of male brown-headed cowbirds, *Molothrus ater*. Animal Behav. 36: 73–86.

SAS Institute. 1995. SAS user's guide: statistics, version 6 ed. SAS Institute, Inc. Cary, NC.

Sauer, J.R., Hines, J.E., Gough, G., Thomas, I. and Peterjohn, B.G. 1997. The North American Breeding Bird Survey results and analysis. Version 96.4. Patuxent Wildlife Research Center, Laurel, Maryland.

Saunders, D.A., Hobbs, R.J. and Margules, C.R. 1991. Biological consequences of ecosystem fragmentation: A review. Cons. Biol. 5: 18–32.

Smith, A.T., and Peacock, M.M. 1990. Conspecific attraction and the determination of metapopulation colonization rates. Cons. Biol. 4: 320–323.

Sokal, R.R. and Rohlf, F.J. 1981. Biometery. 2nd edition. Freeman and Company, San Francisco, CA.

Steele, B.B. 1992. Habitat selection by breeding black-throated blue warblers at two spatial scales. Ornis Scandinavica 23: 33–42.

Temple, S.A. and J.R. Cary. 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. Cons. Biol. 2: 340–347.

Trine, C.L. 1998. Wood thrush population sinks and implications for the scale of regional conservation strategies. Cons. Biol. 12: 576–585.

Turner, S.J., O'Neill, R.V., Conley, W., Conley, M.R. and Humphries, H.C. 1991. Pattern and scale: Statistics for landscape ecology. *In* Quantitative Methods in Landscape Ecology. pp. 17–50. Edited by M.G. Turner and R.H. Gardner. Springer-Verlag, New York.

Villard, M.A., Merriam, G. and Maurer, B.A. 1995. Dynamics in subdivided populations of Neotropical migratory birds in a fragmented temperate forest. Ecology 76: 27–40.

Whitcomb, R.F., Robbins, C.S., Lynch, J.F., Whitcomb, B.L., Klimkiewicz, M.K. and Bystrak, D. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. *In* Forest Island Dynamics in Man-dominated Landscapes. pp. 125–205. Edited by R.L. Burgess and D.M. Sharpe. Springer-Verlag, New York.

Wiens, J.A. 1994. Habitat fragmentation: Island vs. landscape perspectives on bird conservation. Ibis 137: S97–S104.

Wiens, J.A., Rotenberry, J.T. and Van Horne, B. 1987. Habitat occupancy patterns of North American shrubsteppe birds: The effects of spatial scale. Oikos 48: 132–147.