Importance of patch scale vs landscape scale on selected forest birds

Michelle Lee, Lenore Fahrig, Kathryn Freemark and David J. Currie

Lee, M., Fahrig, L., Freemark, K. and Currie, D. J. 2002. Importance of patch scale vs landscape scale on selected forest birds. – Oikos 96: 110–118.

The management and protection of natural areas have primarily occurred in isolation from surrounding land management. The structure of surrounding land cover, however, may be important to the abundance and reproductive success of birds within a habitat patch. We investigated the relative importance of forest patch area, within patch habitat and surrounding landscape forest cover on the abundance of three Neotropical migrant bird species thought to be area-sensitive (ovenbird [*Seiurus aurocapillus*], wood thrush [*Hylocichla mustelina*] and red-eyed vireo [*Vireo olivaceus*]), and on pairing success of the ovenbird. We selected 31 isolated forest patches of differing sizes, and three 80-ha plots in continuous forest each centered within non-overlapping 200-ha landscapes, such that patch area and landscape forest cover were uncorrelated among landscapes. Each study plot was surveyed to estimate abundances of territorial males and ovenbird pairing success. Landscape forest cover ($p < 0.05$) explained the most variation in ovenbird abundance, while percent deciduous forest cover within patches ($p < 0.05$) and patch size ($p < 0.05$) explained the most variation in red-eyed vireo and wood thrush abundance, respectively. Patch size was a significant ($p < 0.05$) predictor of abundance for all three study species; however, density for all species decreased significantly ($p < 0.05$) with patch size. Ovenbird pairing success was higher in continuous forest plots than in forest patches ($p = 0.018$). This study's findings suggest that the relative importance of within patch characteristics, patch size and landscape forest cover varies for different bird species, and that conservation efforts would benefit from the inclusion of all three factors.

M. Lee and L. Fahrig (correspondence), Ottawa-Carleton Inst. of Biology, Carleton Univ., 1125 Colonel By Drive, Ottawa, ON, Canada K1S 5B6 (lfahrig@ccs.carleton.ca). – K. Freemark, Canadian Wildlife Service, Environment Canada, 100 Gamelin Blvd, Hull, QC, Canada K1A 0H3. – D. J. Currie, Ottawa-Carleton Inst. of Biology, Univ. of Ottawa, Box 450, Station A, Ottawa, ON, Canada K1N 6N5.

The apparent decline in many Neotropical migrant bird populations (see Askins et al. 1990 for review) has prompted a considerable amount of research into how to best manage remaining habitat. For forest dwelling migrant birds, existing research identifies forest patch size as an important predictor of bird species abundance (Freemark et al. 1995) and reproductive success (Gibbs and Faaborg 1990, Paton 1994, Huhta et al. 1998). Since abundance and reproductive success are critical to a species' vulnerability to extinction, conser-

vation managers have concentrated their efforts on preserving large tracts of remnant forest.

Variations in forest bird responses that are not accounted for by patch size have led researchers to look beyond patch boundaries for answers. Consequently, an emerging trend in conservation research is the consideration of landscape structure and configuration effects on bird populations (Freemark et al. 1995). Landscape structure and configuration surrounding a patch may affect the ease of movement between patches

(Fahrig and Merriam 1994), and rates of nest predation (Donovan et al. 1997) and parasitism (Saab 1999; but see Tewksbury et al. 1998).

Past research has focused on patch-scale processes, such as area and edge effects, which has led to the assumption that patch effects are more significant than other factors. However, while consideration of both patch and landscape effects is gaining support, the relative importance of these effects on bird populations is still largely unknown (but see Mazerolle and Villard 1999). In addition, due to the positive relationship between patch size and the proportion of forest cover in the landscape (Gustafson and Parker 1992), many studies may confound their effects (e.g. Gibbs and Faaborg 1990, Van Horn et al. 1995). As a result, landscape variables may be able to explain effects that have in the past been attributed to patch size. Alternatively, recently discovered landscape effects may be actually caused by the association of landscape characteristics with patch size.

In this paper we evaluate the independent effects of within-patch characteristics (local habitat), patch level characteristics (forest patch size) and landscape characteristics (proportion of forest cover in the landscape) on ovenbird (*Seiurus aurocapillus*), wood thrush (*Hylocichla mustelina*) and red-eyed vireo (*Vireo olivaceus*) abundance and on ovenbird pairing success.

Methods

Study species

The target species were selected because of their apparent sensitivity to both patch scale and landscape scale processes. Patch scale studies of the target species indi-

cate that they increase in population density or frequency with increased forest patch size (see review by Freemark et al. 1995). Although there is some evidence that the three species avoid habitat edges (summarized by Villard 1998), other research suggests that red-eyed vireos and wood thrush use both forest interior and forest edge (Freemark and Collins 1992).

Study site selection

The study area, located within 100 km of Ottawa, Ontario, Canada, is characterized by a scattered pattern of small forest patches imbedded in a primarily agricultural landscape. We selected 31 focal forest patches and three 80-ha continuous forest plots (hereafter also referred to as focal forest patches) centered within 200-ha landscapes (Fig. 1), such that patch size and forest cover in the surrounding landscape were not correlated (Fig. 2). Forest patches were relatively mature and dominated by sugar maple (*Acer saccharum*), white ash (*Fraxinus americana*), American basswood (*Tilia americana*), and ironwood (*Ostrya virginiana*), with a small occurrence of eastern white pine (*Pinus strobus*) and eastern hemlock (*Tsuga canadensis*). Focal forest patches were comprehensively surveyed for ovenbird, red-eyed vireo and wood thrush abundance and ovenbird pairing success.

A landscape size of 200 ha was deemed sufficiently large for study because ovenbirds and wood thrush interact with the surrounding landscape by foraging only occasionally outside of their 2-ha territories (Zach and Falls 1979, Holmes and Robinson 1988, Anders et al. 1998). Moreover, a summary of mark-recapture studies for European and North American long dis-

Fig. 1. Study region near Ottawa, Ontario. Thirty-four 200-ha, non-overlapping landscapes each encompassed a focal forest patch in which bird abundance, pairing success and habitat characteristics were surveyed.

3 0 3 Kilometers

Legend
- Landscapes
- Water
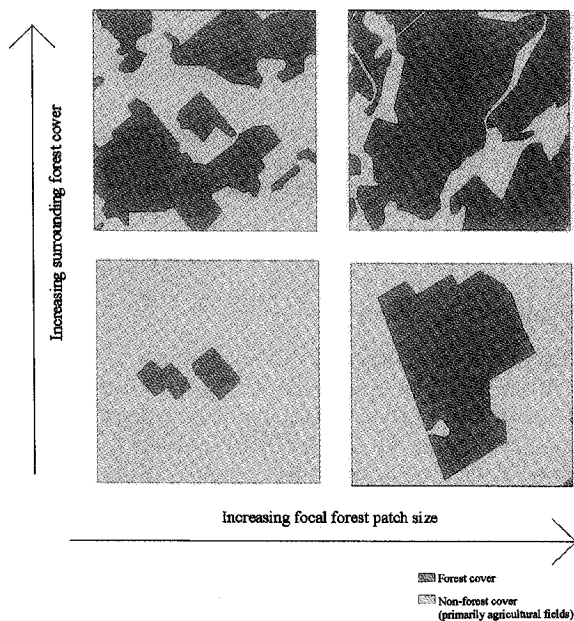- Roads
- Forest habitat
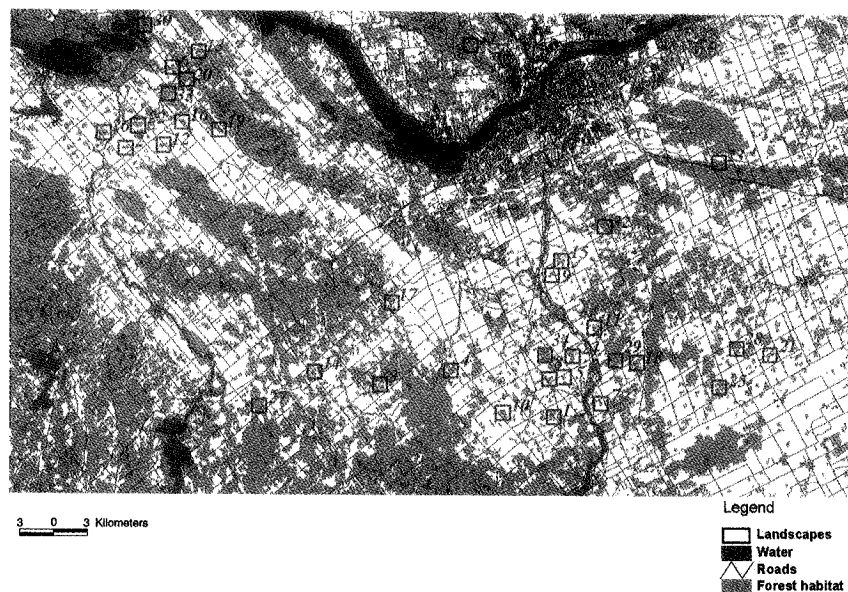
Fig. 2. Representation of landscape and patch selection. Study landscapes were selected to represent a range in percent forest cover surrounding the focal patch such that the two variables were uncorrelated.

tance migrants indicated that most marked individuals were recaptured within 200 m of their marked location, even after multiple breeding seasons (Villard 1991).

Focal patches were initially selected and characterized using 1:50000 aerial photographs taken in 1996 (National Air Photo Library of Canada). A spatial analysis program (Idrisi; Eastman 1997) and a 1991 satellite image of eastern Ontario (Russian MK-4; courtesy of The Ecosystem Management Section of Professional Services for Ontario Parks Canada, Dept of Canadian Heritage) were used to ensure that the 200-ha landscapes surrounding the patches did not overlap.

Focal patches were deciduous or mixed deciduous/coniferous forest types while landscapes were a mix of agricultural land (primarily hay and untended pasture) and forest cover (deciduous or mixed deciduous/coniferous forests). Of the 34 focal patches, 31 were isolated from other forest by paved roads or clearings of greater than 10 m. While this minimum distance may not have constituted a barrier to movement, it may have induced reluctance to move between patches in the target species. On average, patches were isolated from other forest by almost 60 m. Forest patch size and patch isolation were uncorrelated ($r = -0.005$).

Due to a shortage of naturally occurring landscapes characterized by both a large isolated forest patch (> 70 ha) and a large amount of surrounding forest cover (> 33%) in the study region, three of the focal patches were 80-ha forest plots within continuous forest to simulate the effect of a large forest patch embedded

in a high percent forest landscape. A forest was defined as continuous if its area exceeded 200 ha.

Areas of the focal patches ranged from 3 ha to 122.7 ha. The amount of surrounding forest covering each study landscape ranged from 0 to 46%, with 10 of the 34 landscapes containing over 33% forest cover. The range in surrounding forest cover was chosen to encompass the threshold of 30% identified by other studies as being significant for reducing patch area effects (Robbins et al. 1989, Freemark and Collins 1992, Andrén 1994).

A non-random selection of landscapes was necessary because patch size in random samples of real landscapes is expected to be correlated to the amount of surrounding forest cover. Because selection was subjective, landscapes do not necessarily reflect the true structure and configuration of the region. Others (e.g. Pearson 1993, McGarigal and McComb 1995, Trzcinski et al. 1999) have also used this pseudo-experimental approach to site selection.

Bird surveys

Abundance of territorial males

Focal forest patches and plots in each landscape were surveyed three times each between sunrise and 09:30 from 18 May to 15 July 1998 for territorial ovenbird, wood thrush and red-eyed vireo males. Patches were surveyed in their entirety by two field assistants who walked slowly and systematically throughout each forest patch. Efforts were made to equal survey time per hectare surveyed across all focal forests.

Surveys of the focal forest patches were conducted sequentially to stagger them throughout the field season. Two pairs of field assistants each surveyed all patches at least once to reduce sampling bias. Surveys were conducted after 18 May to minimize the chance that birds detected were only migrating through. An additional focal forest patch and landscape replaced patches in which none of the three study species was detected. Playbacks were used to verify absence of a target species, as well as to encourage singing in late mornings and poor weather.

Since recorded abundance tended to drop with rainy, windy or cold weather, we assumed that fluctuations in the number of recorded birds were due primarily to lower singing rates in poor weather. The maximum abundance value recorded across all three visits was therefore used as the best estimate of total male abundance in a given focal patch. In cases where the same total number of males was recorded on separate visits, the visit to be used for further analysis was randomly selected. The maximum abundance value for each forest patch was divided by the focal patch size to obtain an estimate of male density.

112

Ovenbird pairing success

Of the 34 focal forest patches, the 25 patches containing ovenbirds were surveyed to locate perches of territorial male ovenbirds and establish pairing status. Singing perches of male ovenbirds were flagged to approximate territory location and to facilitate finding the perch again on subsequent visits. Paired males sing less frequently than unpaired males (Hann 1937, Lein 1980, Gibbs 1988, Van Horn 1990), and therefore playbacks were used to encourage singing in paired males and increase the chance that singing perches of both paired and unpaired males would be found with equal likelihood.

The paired status of male ovenbirds was evaluated on three separate visits using singing rate and behavior as indicators of status. Playbacks were also used occasionally to elicit responses by female mates suspected to be within a territory. However, because playbacks could potentially interfere with singing rates and behavior of males, they were used only after singing rates and behavior were recorded.

A territorial male was considered paired if he met two of the following three criteria during a 20-min observation period: (1) low singing rate, (2) paired behavioral cues, and (3) tolerance of another ovenbird within 5 m. In the first 5 min of the 20-min evaluation, singing rates of territorial male ovenbirds were recorded. Field studies show that paired territorial males tend to sing six or fewer times in 5 min, while single males sing more frequently (Gibbs 1988, Gentry 1989, Van Horn 1990).

During the timing, and for an additional 10 min, behavioral and visual cues were observed to confirm ovenbird pairing status, such as food carrying, presence of a female, 'tsip' sounds made by a non-singing ovenbird (Lein 1980), or discovery of a nest. In the final 5 min, song playbacks were used to encourage a response from any female within the territory. When a discrepancy was found between the status as determined by singing rates and status as determined by behavior, the status based on behavioral observations was used.

Spotmapping was not used because focal forest patches were each visited only three times (International Bird Census Committee 1970, Bibby et al. 1992), and we did not want to exclude floaters (i.e. transient males) from our surveys. As a result, there is a risk that territorial ovenbird males may have been double counted while moving around within their territories. This risk was minimized in each visit by only flagging the singing perches if they were no less than 100 m from the next nearest singing perch, unless the songs originating from two close perches occurred simultaneously. Also, the low mean density of ovenbird territories in this study (eight ovenbirds per 100 ha) compared with reported average densities (14 per 100 ha – Whitcomb et al. 1981) facilitated the approximate delineation of ovenbird territories without spotmapping.

Vegetation surveys

Local habitat characteristics were considered to avoid spurious results that would arise if patch or landscape characteristics were correlated with within-patch variables. Habitat sampling plots in each focal forest patch were surveyed for specific habitat characteristics (Table 1) using a point-quarter method (Smith 1980) whereby each sampling plot was divided into quarters along the axes of a compass and one quadrant was surveyed.

Vegetation measurements were taken at both ovenbird territory and non-territory locations. This systematic sampling design was used to accommodate the design of a concurrent study that compared microhabitat differences in ovenbird territories and non-territories. While a random sampling design may have better characterized within-patch characteristics of focal forest patches, the systematic sampling scheme still provided an estimate of within-patch characteristics across a relatively even distribution of sampling points in space. A minimum of two point-quarter measurements was taken in very small focal patches and a maximum of six point-quarter measurements was taken in larger focal patches.

Table 1. Habitat characteristics measured in each of the 34 focal forest patches and their relative importance based on life history characteristics, for each species.

Habitat characteristics	Relative importance to target species		
	Ovenbird	Red-eyed vireo	Wood thrush
Tree diameter at breast height	moderate	moderate	moderate
Percent living ground cover	high	low	low
Leaf litter depth	high	low	low
Herb height	high	low	low
Shrub height	high	moderate	high
Canopy cover	high	high	high
Tree density	moderate	moderate	moderate
Tree height	low	high	high
Tree species richness	moderate	moderate	moderate
Percent deciduous species	high	high	high

Table 2. Summary statistics of bird abundance and density based on maximum number of territorial male detections per forest patch for ovenbird, wood thrush and red-eyed vireo. Standard deviations are indicated in brackets.

	Ovenbird	Wood thrush	Red-eyed vireo
Number of focal patches/plots in which species were detected (n = 34)	26	19	32
Total male abundance	117	48	115
Mean male abundance per patch	3.4 (3.3)	1.4 (1.6)	3.4 (2.7)
Mean density (no./ha)	0.12 (0.14)	0.04 (0.06)	0.14 (0.13)

Data analysis

The relationship between patch size and surrounding forest cover was tested using a Pearson's correlation (SAS Institute 1990).

Our null expectation for the effect of patch size on abundance was that abundance should increase in proportion to patch size, i.e. density should be constant with increasing patch size. We used abundance rather than density as the dependent variable in this study because of problems that arise when density is calculated as the ratio of abundance to patch area. Ratio variables have been shown to be statistically problematic (Jackson et al. 1990, Berges 1997). Also, since we were interested in the effects of patch area, we did not want to use a dependent variable that included area. If density remains constant with patch size, as predicted by our null hypothesis, then abundance must increase with patch size at a constant rate, and log(abundance) must increase with log(patch size) at a rate of 1:1.

Using a stepwise regression, we determined the variables that best predicted log(bird abundance) from log(patch size), surrounding forest cover, and selected habitat variables thought to be of high or moderate importance to the target species (Table 1). Since the regression identified patch size as a significant variable for all study species, the slope of the relationship between log (abundance) and log (patch size) was then compared to a line with a slope of one that shared the same mean point. We used this unconventional approach because we wanted to test whether the relationship between log(abundance) and log(patch size) was significantly different from one, rather than from zero.

To determine which predictor variables explained more variance in the abundance of each bird species, explained sums of squares for log(patch size) was calculated as the sum of the squared deviations (i.e. differences) of the predicted values of log(abundance) for a regression with only patch size in it, from the 1:1 line. The explained sums of squares for all other variables were taken from the ANOVA tables (SAS Institute 1990).

Pairing success
Ovenbird pairing success was evaluated with a logistic stepwise regression on the set of predictor variables used in the ovenbird abundance regression analysis.

The total number of territorial male ovenbirds detected in a focal forest patch was the number of 'trials', while the number of paired males was the number of 'successful events'. Pairing success ratios in the three continuous forests were also compared to pairing success ratios in the patches using a t-test for unequal variances to allow for comparisons between this paper and other studies.

Results

As designed (see Methods), focal forest patch area and surrounding forest cover were not correlated ($r = 0.117$, $p = 0.51$). Red-eyed vireo males were the most widespread (32 of 34 patches) while wood thrush males were present in the fewest patches (19 of the 34 patches) (Table 2). In all, 117 ovenbird, 115 red-eyed vireo, and 48 wood thrush territorial males were detected in focal forest patches across the 34 landscapes. Considerable variation existed in the numbers of birds detected per forest patch.

Species abundance

Log(ovenbird abundance) was best predicted by surrounding forest cover and log(patch size) ($F = 5.79$, $p = 0.02$). Results of the t-test revealed that the slope of the relationship between log(abundance) and log(patch size) was significantly less than one ($t = -3.55$,
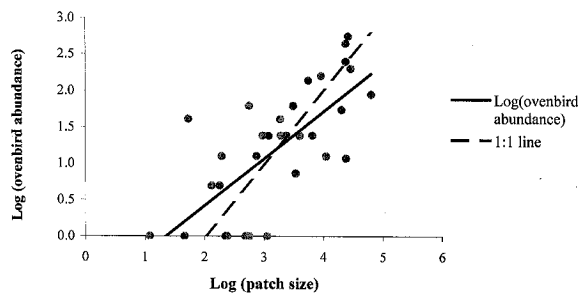
Fig. 3. Comparison of a line with a slope of one and a plot of log(ovenbird abundance) with increasing log(patch size). The slope of log(ovenbird abundance) was significantly less than one ($t = -3.55$, $p < 0.05$).
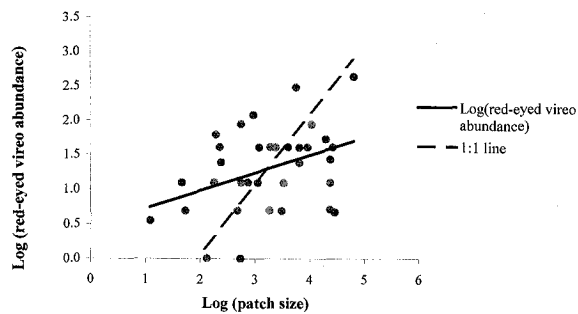
114

Fig. 4. Comparison of a line with a slope of one and a plot of log(red-eyed vireo abundance) with increasing log(patch size). The slope of log(red-eyed vireo abundance) was significantly less than one ($t = -6.38$, $p < 0.05$).

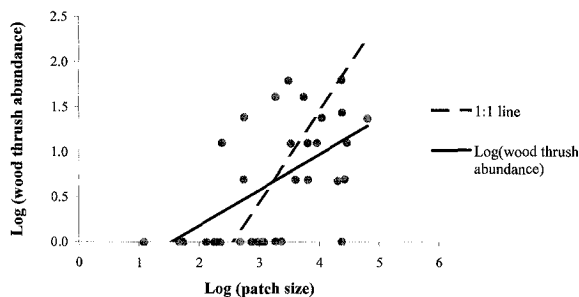Fig. 5. Comparison of a line with a slope of one and a plot of log(wood thrush abundance) with increasing log(patch size). The slope of log(wood thrush abundance) was significantly less than one ($t = -5.69$, $p < 0.05$).

$p < 0.05$) (Fig. 3), suggesting that ovenbird density was lower in large patches than in small ones. Surrounding forest cover (explained sums of squares = 29.3) explained a greater amount of variation in log(abundance) than did log(patch size) (explained sums of squares = 3.5).

The log of red-eyed vireo abundance was most closely related to the percent of deciduous trees and log(patch size) ($F = 8.6$, $p = 0.0063$). The slope of log(patch size) was again significantly less than one ($t = -6.38$, $p < 0.05$) (Fig. 4). The percent of deciduous trees explained more of the variance in log(red-eyed vireo abundance) (explained sums of squares = 32.5) than did log(patch size) (explained sums of squares = 15.5). Log(wood thrush abundance) was best predicted by only log(patch size), for which the slope was also significantly less than one ($t = -5.69$, $p < 0.05$) (Fig. 5).

Ovenbird pairing success

The logistic stepwise regression, relating the probability of pairing to habitat, patch and landscape variables, was not significant. The mean pairing success ratio, however, was significantly higher in the three extensive forests

than in the 22 forest patches in which ovenbirds were found ($t = 2.6$, $p = 0.04$).

Discussion

Patch or landscape scale: which matters more to forest birds?

Both surrounding forest cover and patch size were significant predictors of ovenbird abundance. Of the two, however, surrounding forest cover explained more variation in ovenbird abundance than did patch size. The greater importance of surrounding forest cover on ovenbird abundance contradicts previous reports that stress patch size or core area as the primary predictor of bird abundance (e.g. Freemark and Collins 1992, Burke 1998, Bender et al. 1998). Our results indicate that the effect of surrounding forest cover on ovenbird abundance is not the result of a correlation with forest patch size, because these two variables were uncorrelated in our study, by design.

In contrast to the results we report for ovenbirds, red-eyed vireo and wood thrush abundances were best predicted by percent deciduous forest cover within patches and patch size, respectively; surrounding forest was not significant for either species. Patch size was an important predictor for all three species.

Responses of species to landscape structure have been shown to be individualistic in this study and others (Pearson 1993, McGarigal and McComb 1995, Jokimäki and Huhta 1996, Saab 1999). Target species in this study each responded differently to surrounding forest cover despite their common area-sensitive classification and relatively similar habitat requirements. Others have found that certain avian groups (managed forest species, habitat generalists and edge species) were more affected by landscape features than were other groups (Jokimäki and Huhta 1996).

Differential responses between species or guilds may be due to differences in their life history traits. As ground nesters, ovenbirds may be more susceptible to predation-related mortality and brood failure (Gibbs and Faaborg 1990, Villard et al. 1993) that tend to be lower in highly forested landscapes (Donovan et al. 1997). Thus ovenbirds may experience either higher mortality in highly deforested landscapes, or they may have developed behavior required to avoid such high risk landscapes.

The ovenbird's interior forest species status suggests that is more sensitive to forest edge effects when compared to interior-edge species such as red-eyed vireos and wood thrush. A concurrent study using the same focal forest patches indicated that no ovenbird territories were located within 50 m of the forest boundary. Since edge effects may be moderated by landscape forest cover, ovenbirds may be more sensitive to landscape forest cover than the other target species.

Density and patch size

For all study species, log(abundance) increased at a significantly less than 1:1 rate with log(patch size). Therefore, for all species, density actually decreased with increasing patch size. This result is contrary to some studies that have found that the density of most interior forest bird species is positively related to patch size (e.g. Lynch and Whigham 1984, Askins et al. 1987). Note that this result is not likely explained by correlations between vegetation characteristics and patch area, because vegetation effects were accounted for in our stepwise regression. Of course, it remains possible that an unknown correlation between patch size and some unmeasured vegetation or habitat variable explains the patch size effect. The negative patch size effect also was not caused by decreasing sampling effort with increasing patch area, since effort per area was constant across all patches.

Using a similar statistical technique, Martin (1981) also found that total avian community abundance did not increase proportionally with patch size, leading to the conclusion that density was greater in smaller patches. Even when species that forage outside the patch boundaries were removed from the analysis, density remained constant with patch size. The applicability of Martin's (1981) findings to this study may be limited, since he studied avian communities in a very small patch size range (0.1–2.9 ha) and therefore the species detected were likely much less area-sensitive than those in this study.

A number of other studies have reported opposite results for forest interior bird species (Lynch and Whigham 1984, Askins et al. 1987, Blake and Karr 1987). In addition, metadata analyses by both Connor (2000) and Bender et al. (1998) found that as a group, bird density was positively correlated with patch size.

If useable habitat or resource availability increases proportionally with patch size, but the target species can supplement the habitat by foraging outside of small patches, an inflated abundance in small patches relative to resource abundance may occur.

Ovenbird pairing success

Ovenbird males were more often paired in plots within continuous forests than in forest patches, but pairing success within both patches and plots did not differ in relationship to landscape forest cover. No significant increase in pairing success occurred with increasing forest patch size, possibly because of an area threshold that was not encompassed by this study's range in patch sizes. A steeper slope for pairing success may have been noted if larger continuous forests were surveyed in this study.

The relationship between ovenbird pairing success in continuous plots vs forest patches in this study is similar to findings by others. Gibbs and Faaborg (1990) and Villard et al. (1993) found mean pairing success ratios to be around 80% for continuous forests (compared with 60% in this study), and between 23.5% and 58.6% for forest patches (compared with 30% in this study) (Villard et al. 1993).

Since nonbreeding females are assumed not to exist (e.g. Gibbs and Faaborg 1990, Villard et al. 1993), the high proportion of unmated males in all forests surveyed in this study suggests an uneven sex ratio. Effects outside of breeding habitat such as greater female overwintering or migration mortality may cause a biased sex ratio. Female ovenbirds overwinter in different locations and migrate at different times than males, and therefore they may be subjected to specific geographic or temporal stresses that males avoid. However, such external factors that reduce the female to male ratio only explain the existence of unpaired males in all forest patches; they do not account for the significant difference in the proportion of unpaired males between small patches and continuous forest.

Possible explanations for the greater proportion of unpaired males in forest patches compared with continuous forests include: (1) higher susceptibility of ground nesting female ovenbirds in patches to mortality related predation (Gibbs and Faaborg 1990), (2) direct female selection of high quality territories, which are more likely to occur in large forests, (3) selection by females of older males who, in turn exclude younger males from premium territories, which are more likely to occur in large forests, or (4) female selection of forests with higher male density (conspecific attraction) (Villard et al. 1993). The conspecific attraction hypothesis does not adequately explain the disparity in pairing success ratios among forest sizes in this study, since densities in extensive forests and patches were not significantly different.

Conservation implications

This study supports the hypothesis that the birds are affected differently and at different scales by habitat structure and configuration. Patch size had an important effect on all of our study species. For some species, however, surrounding forest cover may compensate for smaller patch sizes and therefore effective conservation must consider the amount of habitat in the whole landscape, not just forest patch size.

Two multi-landscape studies of forest birds (McGarigal and McComb 1995, Trzcinski et al. 1999) identified the total amount of forest in a landscape as the most significant predictor of abundance and distribution (respectively) of forest breeding birds in a landscape. Spatial pattern or fragmentation of the forest was of

secondary importance, where fragmentation implies a larger number of smaller patches (for the same total amount of forest). In these two studies, abundance of several forest birds actually increased with increasing forest fragmentation. This is consistent with our patch size effect and, again, indicates that habitat amount should be determined at the landscape scale rather than the patch scale.

Finally, the growing empirical evidence for the importance of surrounding landscape on forest bird communities (e.g. Hinsley et al. 1995, Sisk 1997, Saab 1999) lends support to the theory that forest reserves do not operate in isolation from the surrounding matrix; the structure and composition of a matrix surrounding a forest reserve affect the biological processes within.

References

Anders, A. D., Faaborg, J. and Thompson III, F. R. 1998. Postfledgling dispersal, habitat use and home-range size of juvenile wood thrushes. – Auk 115: 349–358.

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat – a review. – Oikos 71: 355–366.

Askins, R. A., Philbrick, M. J. and Sugeno, D. S. 1987. Relationship between the regional abundance of forest and the composition of forest bird communities. – Biol. Conserv. 39: 129–152.

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

Bender, D. J., Contreras, T. A. and Fahrig, L. 1998. Habitat loss and population decline: a meta-analysis of the patch size effect. – Ecology 79: 517–533.

Berges, J. A. 1997. Ratios, regression statistics, and "spurious" correlations. – Limnol. Oceanogr. 42: 1006–1007.

Bibby, C. J., Burgess, N. D. and Hill, D. A. 1992. Bird census techniques. – Academic Press, pp. 58, 66–84.

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

Burke, D. M. 1998. The relationship between forest fragmentation, food abundance, nest site, habitat and reproductive success of forest breeding birds. – Ph.D. thesis, Trent Univ., Peterborough, Canada.

Connor, E. F. 2000. Individuals-area relationship: the relationship between animal population density and area. – Ecology 81: 734–748.

Donovan, T. M., Jones, P. W., Annand, E. M. and Thompson III, F. R. 1997. Variation in local-scale edge effects: mechanisms and landscape context. – Ecology 78: 2064–2075.

Eastman, R. J. 1997. Idrisi for Windows: user's guide. Ver. 2.0. – Clark Univ., Worcester, MA.

Fahrig, L. and Merriam, G. 1994. Conservation of fragmented populations. – Conserv. Biol. 8: 50–59.

Freemark, K. E. and Collins, B. 1992. Landscape ecology of birds breeding in temperate forest fragments. – In: Hagan III, J. M. and Johnston, D. W. (eds), Ecology and conservation of Neotropical migrant landbirds. Smithsonian Inst. Press, Washington, DC, pp. 443–454.

Freemark, K. E., Dunning, J. B., Hejl, S. J. and Probst, J. R. 1995. A landscape ecology perspective for research conservation and management. – In: Martin, T. E. and Finch, D. M. (eds), Ecology and management of Neotropical migratory birds: a synthesis and review of critical issues. Oxford Univ. Press, pp. 381–427.

Gentry, R. 1989. Variable mating success of the ovenbird (*Seiurus aurocapillus*) within remnant forest tracts of central Missouri. – M.A. thesis, Univ. of Missouri, Columbia, MO.

Gibbs, J. P. 1988. Forest fragmentation, mating success, and the singing behavior of the ovenbird (*Seiurus aurocapillus*) and Kentucky Warbler (*Oporornis formosus*) in central Missouri. – M.A. thesis, Univ. of Missouri, Columbia, MO.

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

Gustafson, E. J. and Parker, G. R. 1992. Relationships between landcover proportion and indices of landscape spatial pattern. – Landscape Ecol. 7: 101–110.

Hann, H. W. 1937. Life history of the ovenbird in southern Michigan. – Wilson Bull. 44: 146–235.

Hinsley, S. A., Bellamy, P. E., Newton, I. and Sparks, T. H. 1995. Habitat and landscape factors influencing the presence of individual breeding bird species in woodland fragments. – J. Avian Biol. 26: 94–104.

Holmes, R. T. and Robinson, S. K. 1988. Spatial patterns, foraging tactics, and diets of ground-foraging birds in a northern hardwoods forest. – Wilson Bull. 100: 377–394.

Huhta, E., Jokimäki, J. and Rahko, P. 1998. Distribution and reproductive success of the Pied Flycatcher *Ficedula hypoleuca* in relation to forest patch size and vegetation characteristics: the effect of scale. – Ibis 140: 214–222.

International Bird Census Committee 1970. Recommendations for an international standard for a mapping method in bird census work. – Aud. Field Notes 24: 722–726.

Jackson, D. A., Harvey, H. H. and Somers, K. M. 1990. Ratios in aquatic sciences: statistical shortcomings with mean depth and the morphoedaphic index. – Can. J. Fish. Aquat. Sci. 47: 1788–1795.

Jokimäki, J. and Huhta, E. 1996. Effects of landscape matrix and habitat structure on a bird community in northern Finland: a multi-scale approach. – Ornis Fenn. 73: 97–113.

Lein, M. R. 1980. Display behavior of ovenbirds (*Seiurus aurocapillus*) I. Non-song vocalizations. – Wilson Bull. 92: 312–329.

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

Martin, T. E. 1981. Limitation in small habitat islands: chance or competition? – Auk 98: 715–734.

Mazerolle, M. J. and Villard, M.-A. 1999. Patch characteristics and landscape context as predictors of species presence and abundance: a review. – Ecoscience 6: 117–124.

McGarigal, K. and McComb, W. C. 1995. Relationships between landscape structure and breeding birds in the Oregon coast range. – Ecol. Monogr. 65: 235–260.

Paton, P. W. 1994. The effect of edge on avian nest success: how strong is the evidence? – Conserv. 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.

Robbins, C. S., Dawson, D. K. and Dowell, B. A. 1989. Habitat area requirements of breeding forest birds of the middle Atlantic states. – Wildl. Monogr. 103: 6–34.

Saab, V. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. – Ecol. Appl. 9: 135–151.

SAS Institute 1990. SAS/STAT user's guide, ver. 6, 4th ed. – SAS Institute Inc., Cary, NC.

Sisk, T. D. 1997. Bird assemblages in patchy woodlands – modeling the effects of edge and matrix habitats. – Ecol. Appl. 7: 1170–1180.

Smith, R. L. 1980. Ecology and field biology, 3rd ed. – Harper and Row, pp. 669–670.

Tewksbury, J. J., Hejl, S. J. and Martin, T. E. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. – Ecology 79: 2890–2903.

Trzcinski, M. K., Fahrig, L. and Merriam, G. 1999. Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. – Ecol. Appl. 9: 586–593.

Van Horn, M. A. 1990. The relationship between edge and the pairing success of the ovenbird (*Seiurus aurocapillus*). – M.Sc. thesis, Univ. of Missouri, Columbia, MO.

Van Horn, M. A., Gentry, R. M. and Faaborg, J. 1995. Patterns of ovenbird (*Seiurus aurocapillus*) pairing success in Missouri forest tracts. – Auk 112: 98–106.

Villard, M.-A. 1991. Spatio-temporal dynamics of forest bird patch populations in agricultural landscapes. – Ph.D. thesis, Carleton Univ., Ottawa.

Villard, M.-A. 1998. On forest-interior species, edge avoidance, area sensitivity, and dogmas in avian conservation. – Auk 115: 801–805.

Villard, M.-A., Martin, P. R. and Drummond, C. G. 1993. Habitat fragmentation and pairing success in the ovenbird (*Seiurus aurocapillus*). – Auk 110: 759–768.

Whitcomb, R. F., Robbins, C. S., Lynch, J. F. et al. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. – In: Burgess, R. L. and Sharpe, D. M. (eds), Island dynamics in man-dominated landscapes. Springer-Verlag, pp. 125–205.

Zach, R. and Falls, J. B. 1979. Foraging and territoriality of male ovenbirds (Aves: Parulidae) in a heterogeneous habitat. – J. Anim. Ecol. 48: 33–52.