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INDEPENDENT EFFECTS OF FOREST COVER AND FRAGMENTATION ON THE DISTRIBUTION OF FOREST BREEDING BIRDS

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Abstract. The aims of this study were (1) to determine the relative importance of the independent effects of forest cover and fragmentation on the distribution of forest breeding birds, and (2) to test the hypothesis that the negative effect of forest fragmentation on species distribution increases with decreasing forest cover, i.e., the negative interaction effect of forest cover and fragmentation on distribution. The independent effects of forest cover and forest fragmentation on the distribution of forest breeding birds were studied in 94 landscapes, 10 × 10 km each, ranging in forest cover from 2.5% to 55.8%. For each landscape, percent forest cover was measured, and a fragmentation index (independent of forest cover) was generated using PCA from the measures of mean forest patch size, number of forest patches, and total forest edge. Presence of 31 forest breeding bird species in each landscape was determined using Breeding Bird Atlas data. The effects of forest cover and forest fragmentation on species presence were analyzed using multiple logistic regression. All responses of individual species to forest cover were positive. Responses to forest fragmentation were weak and variable. There were only two species for which the interaction between cover and fragmentation was significant (one positive, one negative). We found no evidence for the hypothesized negative interaction effect between forest cover and forest fragmentation on species distribution. We conclude that (1) forest cover at the 10 × 10 km (Universal Transverse Mercator [UTM]) scale has a positive effect on the distribution of forest breeding birds, (2) forest fragmentation does not have a consistent negative effect on the distribution of forest breeding birds, (3) the effect of forest cover is greater than that of forest fragmentation, (4) responses to forest fragmentation are generally weak and highly variable among species, and (5) the effect of forest fragmentation on species distribution does not increase with decreasing forest cover. These results suggest that conservationists' primary focus should be on preventing a decrease in forest cover. They should not be misled by recent discussions of "fragmentation effects" to think that the negative effects of forest loss can somehow be countered by careful consideration of the spatial pattern of remaining forest. Our results indicate that they cannot.

Key words: *agricultural landscapes; bird distribution; Breeding Bird Atlas; forest cover; fragmentation; habitat loss; landscape pattern; multiple logistic regression; Ontario; Quebec; SPANS GIS; UTM squares.*

INTRODUCTION

Both habitat loss and fragmentation are usually thought to negatively affect species persistence (Wilcox and Murphy 1985, Wilcove et al. 1986, Burkey 1989, Herben et al. 1991, Noss 1991, Perry and Gonzalez-Andujar 1993, Adler and Nuernberger 1994). Explanations for the negative impact of fragmentation include increased mortality of individuals moving between patches, lower recolonization rates of empty patches, and reduced local population sizes resulting in increased susceptibility to extinction (Fahrig and Merriam 1994). There is also some evidence that habitat fragmentation can have a positive effect on regional population survival by (1) desynchronizing the dynamics of local populations, thereby spreading the risk of

extinction (den Boer 1981); and (2) providing temporal and spatial refugia for prey (Huffaker 1958, Levin 1976, Kareiva 1987, Roland 1993).

Because the effects of habitat amount and fragmentation are confounded in many studies, it is not clear which has the greater impact (Haila and Hanski 1984). Simulation results of Fahrig (1997, 1998) predict that the effects of habitat loss are much greater than the effects of habitat fragmentation on population extinction. To date, the only empirical test of the relative importance of habitat loss and fragmentation was conducted by McGarigal and McComb (1995), who compared the relative effects of forest cover and fragmentation on bird species abundances in late-seral forest in Oregon. They found that the effect of habitat amount was much greater than the effect of habitat pattern. However, their study was conducted in a predominantly forested area, and they urged comparison of their results with studies conducted in predominantly agricultural landscapes. The first objective of this study was

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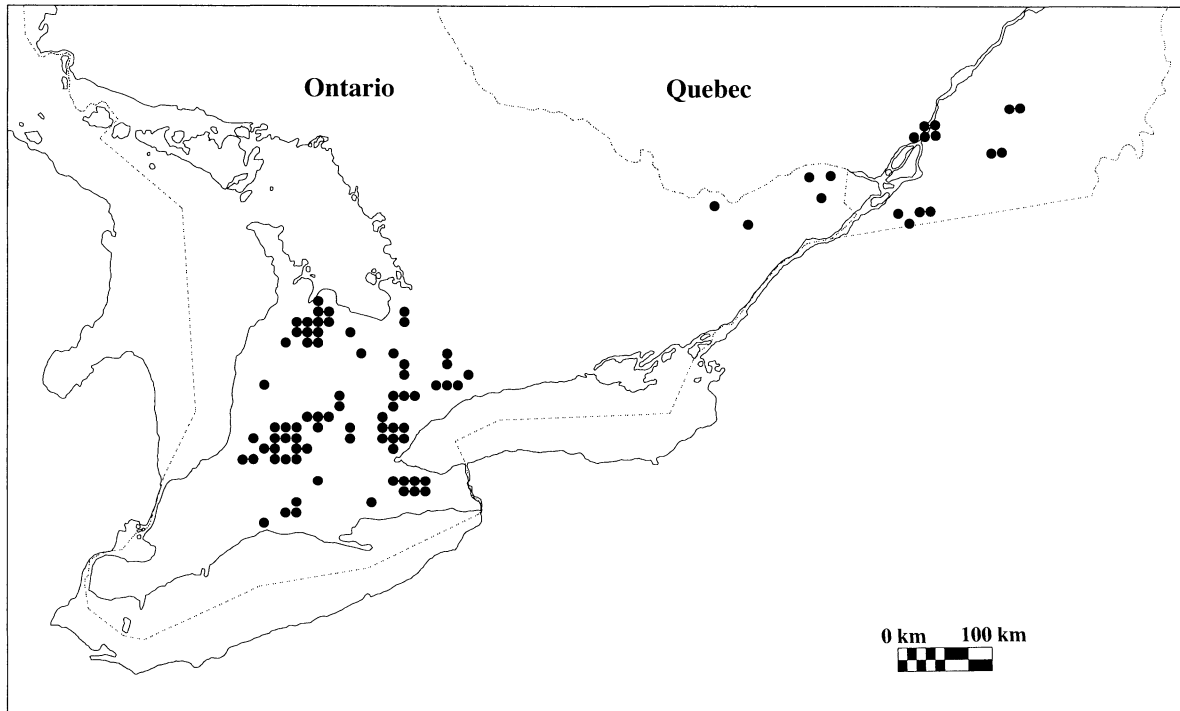


FIG. 1. Locations of 94 10 × 10 km landscapes.

to determine the relative importance of the independent effects of forest cover and forest fragmentation on the distribution of forest breeding birds in a predominantly agricultural area.

A few studies have suggested that fragmentation has the strongest effect when the amount of suitable habitat is low (McLellen et al. 1986, Andr n 1994, Fahrig 1998), and that habitat fragmentation has an insignificant effect at high amounts of habitat. In other words, they predict a negative interaction effect between habitat fragmentation and habitat amount. The implication of this prediction is that when suitable habitat is abundant, the degree of fragmentation does not affect population persistence. The second objective of this study was to test the hypothesis that the negative effect of forest fragmentation on species distribution increases with decreasing forest cover.

Forest loss and fragmentation occur in a landscape over time. If we begin with a completely forested landscape and gradually remove forest, fragmentation begins when the forest is broken into more than one patch. With further forest removal, fragmentation continues as the number of forest patches increases. At very low levels of forest cover, removal of whole forest patches will actually decrease forest fragmentation. Therefore, a study of a single landscape over time will inevitably confound the effects of forest cover and fragmentation. In this study, we compared many landscapes over a large spatial domain and a short time to separate the effects of forest cover and fragmentation. The landscape pattern at the time of study resulted from the

concurrent processes of forest loss and fragmentation, and each landscape sampled in this study represents one possible outcome. We quantified forest loss and fragmentation separately for each landscape, thus allowing us to test for the separate effects of forest cover and fragmentation on species distribution, while retaining the ability to evaluate their relative impacts and test for their interaction.

METHODS

Study area

The study area covered southern and eastern Ontario and southern Quebec, Canada, and is mostly contained in the Great Lakes–St. Lawrence forest region (Rowe 1977), also classified as the “mixed wood plain” (Wilken et al. 1993). The native vegetation is characterized by sugar maple (*Acer saccharum*), beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), red maple (*Acer rubrum*), basswood (*Tilia americana*), white ash (*Fraxinus americana*), red oak (*Quercus rubra*), eastern white pine (*Pinus strobus*), and eastern hemlock (*Tsuga canadensis*) (Rowe 1977). The region is predominantly agricultural, including features such as cultivated fields, pastures, roads, and buildings. Forested areas are typically on glacial drumlins or on the slopes of drainage valleys, on land rockier or steeper than adjacent cultivated fields.

We selected 94 landscapes, 10 × 10 km, ranging in forest cover from 2.5% to 55.8%, for the study (Fig. 1). These landscapes corresponded to Breeding Bird

Atlas Universal Transverse Mercator (UTM) blocks (Cadman et al. 1987, Gauthier and Aubry 1995). Landscapes were not randomly selected among all possible blocks, but were selected to (1) represent large variation in forest cover and forest fragmentation and (2) reduce the expected negative correlation between forest cover and fragmentation. The latter involved searching, in particular, for landscapes with poorly represented combinations of cover and fragmentation, i.e., landscapes with low cover but low fragmentation (a few fairly large patches in a predominantly open landscape), and landscapes with high cover but high fragmentation (many small patches in a predominantly forested landscape). Landscapes were not selected in the central portion of the study area because forest structure and composition, as well as the bird species assemblage, differed from the rest of the study region due to differences in geology (Rowe 1977, Taylor and Smith 1987). Forest was chosen for study because (1) forest within the study region exists in a wide range of cover and fragmentation, (2) forest includes habitat for a definable group of birds, and (3) forest and non-forest can be identified with a relatively high level of precision from aerial photographs.

Bird species presence/absence

Bird species that could potentially breed in the interior of a forest patch (both interior and interior/edge) were selected. Edge species were excluded because their potential breeding patches must be defined by excluding interior forest and incorporating their use of nonforest areas. Freemark and Collins (1989) classified the habitat use of 78 forest breeding birds as interior, interior/edge, and edge species by collecting data and reviewing the literature (Whitcomb et al. 1981, Blake and Karr 1984, Hayden et al. 1985, Freemark and Merriam 1986, Askins et al. 1987). Thirty-two species were classified as breeding in forest interior and 28 species were classified as breeding in both the forest interior and edge.

A species was included in the analyses relating bird species distribution (presence/absence) to forest cover and fragmentation only if it was present and absent in $\geq 10\%$ of the landscapes. This criterion was necessary because effects cannot be statistically tested on species that are very common or very rare. Thirty-one species met this criterion.

For the species whose ranges encompassed the entire study region, all of the 94 sampled landscapes were used to test the effects of forest cover and fragmentation. Ranges of three species (Rufous-sided Towhee, Yellow-throated Vireo, and Blue-gray Gnatcatcher) were limited to the southern portion of the study region (for scientific names, see *Results*, Table 3). For these species, only the 76 landscapes in southwestern Ontario were analyzed (Fig. 1). The Black-billed Cuckoo and the Pileated Woodpecker were the only species for which there was some disagreement in the classification

of habitat use (Freemark and Collins 1989). We retained them in our analysis.

Breeding Bird Atlas (BBA) data were used to estimate the presence/absence of a species for each of the 94 10×10 km UTM squares (Cadman et al. 1987, Gauthier and Aubry 1995). Although the scale of the landscape as determined by the BBA blocks was arbitrary, it was probably reasonable for many birds, because natal dispersal is typically on the order of 0.5–5 km (Villard 1991: Appendix 1). The BBA data for Ontario were collected between 1981 and 1985, and BBA data for Quebec were collected between 1984 and 1989. If there was any evidence of a species breeding in a sample landscape at the time of census (“possible,” “probable,” or “confirmed”), we assumed that the species was present. We assumed absence if a species was not detected as breeding in a UTM square. Therefore, “absence” does not necessarily mean that the species was absent from the block. Rather, it is an indication that the species was either absent or present in extremely low numbers (below detection limits). Note that BBA abundance estimates are extremely coarse and unlikely to provide qualitatively different information than the presence/absence data.

Forest cover

Large-scale aerial photography (1:50 000) conducted during the time of the Breeding Bird Atlas census, or at the nearest time to the census, was used to define forest and nonforest for each landscape (National Air Photo Library of Canada). The longest span between the time of aerial photography and the BBA census was 5 yr. Forest and nonforest were traced from the aerial photos, tracings were digitized (vector format), and percent forest cover was estimated using the program SPANS GIS (1993). The smallest forest patch size that we could measure using these techniques was 50×50 m (0.25 ha).

Forest fragmentation

To test the relative effects of forest cover, forest fragmentation, and their interaction effect, a single measure of the degree of fragmentation, independent of forest cover, was needed. Increasing the degree of forest fragmentation is expected to have the following simultaneous effects: mean patch size decreases, the number of patches in the landscape increases, and the total amount of edge in the landscape increases. We measured mean forest patch size, number of forest patches, and total amount of forest edge from the digitized map of each landscape, using the program SPANS GIS (1993). The number of forest patches and the total amount of forest edge were calculated within the 10×10 km UTM blocks. To avoid effects of patch truncation at edges on the calculation of mean forest patch size, we used the full sizes of patches that straddled the edges of the UTM block boundaries, i.e., we included the area outside the block for calculation of

TABLE 1. Pearson product-moment correlation coefficients indicating the correlation between three indices of forest fragmentation and forest cover.

Indices	No. patches	Total edge	Cover
Mean patch size	-0.37	0.54	0.83
No. patches		0.30	0.003
Total edge			0.84

Note: All relationships are significant at $P < 0.0001$ except for the relationship between patch number and cover, which is not significant at $\alpha = 0.05$.

patch size. Note that we did not measure distance between patches because it would not provide any additional information; interpatch distance is determined by amount of forest, patch number, and patch sizes (Fahrig 1992).

The three indices of forest fragmentation were correlated with each other (Table 1). Mean forest patch size and total forest edge were also correlated positively with forest cover (Table 1). To obtain a measure of forest fragmentation that was independent from forest cover, we used a correlation-based principal components analysis (PCA) of patch size, number, and edge (SAS 1990, Proc PRINCOMP). Nearly all of the measured information on forest pattern was contained in the first two principal components, which explained 94% of the variation (Table 2). The first principal component explained 52% of the variation and was essentially equivalent to a measure of percent forest cover ($r = 0.94, P < 0.0001$, Fig. 2). The second principal component explained 42% of the variation and was not significantly correlated with forest cover ($r = 0.18, P = 0.09$). As the second principal component increased, mean forest patch size decreased, the number of forest patches increased, and total forest edge increased (Table 2). Thus, the second principal component was a measure of forest fragmentation. We removed the (non-significant) correlation between the second principal component and forest cover by using simple linear regression. The residuals were used as a measure of forest fragmentation that was completely independent of forest cover.

Fig. 3 illustrates the independent measures of forest cover and fragmentation. The effects of forest cover and fragmentation are confounded in studies that conclude that landscape "d" in Fig. 3 is more fragmented than landscape "a." Although this conclusion is true, landscape "d" also contains less forest.

TABLE 2. Principal component loadings for the three indices of forest fragmentation.

Indices	PC 1	PC 2
Mean patch size	0.74	-0.23
No. patches	-0.15	0.85
Total edge	0.65	0.47

Note: PC 1 explained 52% and PC 2 explained 42% of the variation.

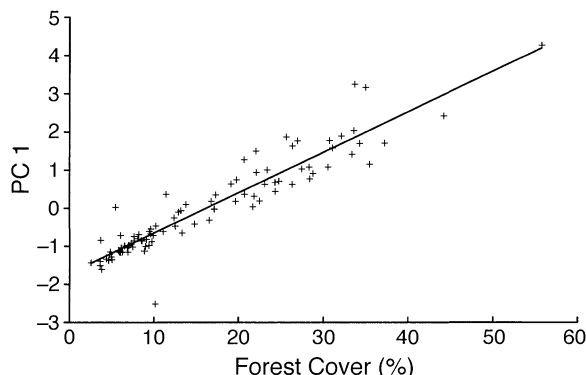


FIG. 2. Relationship between the first principal component and percent forest cover ($n = 94, r = 0.94, P < 0.0001$).

The effects of forest cover and forest fragmentation, their relative impacts, and their interaction effect on species distribution were assessed using multiple logistic regression analysis (SAS 1990, Proc LOGISTIC) for each of the species. Before analysis, the scales of forest cover and forest fragmentation were standardized so that the magnitude of the effects could be directly compared. We also conducted the analyses using PC1 as our measure of cover and PC2 as fragmentation. The results were qualitatively identical and are therefore not reported.

We checked for spatial autocorrelation in the predictor variables COVER and FRAG by performing Mantel tests using the RT program (Manly 1996). There was evidence for weak spatial autocorrelation ($P = 0.023$ and $P = 0.076$ for COVER and FRAG, respectively). Spatial autocorrelation causes a slight overestimate of the power of the logistic regression analyses, but it does not affect our final conclusions regarding the relative effects of COVER and FRAG.

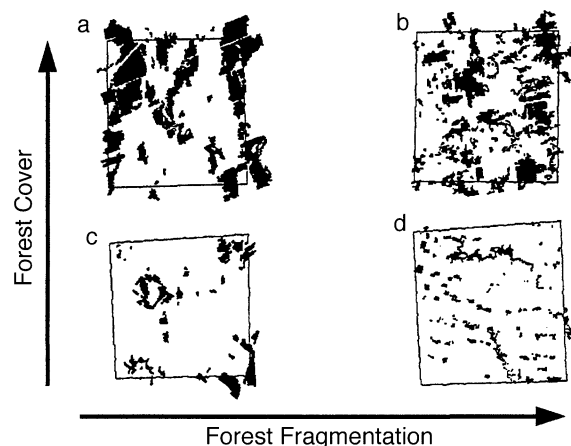


FIG. 3. Forest cover and forest fragmentation in four sample 10×10 km landscapes. Landscape a: percentage forest cover = 30.8, PC 2 = -1.56. Landscape b: percent forest cover = 28.4, PC 2 = 2.02. Landscape c: percent forest cover = 7.6, PC 2 = -1.54. Landscape d: percent forest cover = 7.51, PC 2 = 1.66.

TABLE 3. Multiple logistic regression coefficients for forest cover, forest fragmentation, and their interaction in each of 31 logistic regressions (SAS 1990) on bird species distribution data.

Species	Cover	Fragmentation	Interaction	Forest use‡
Sharp-shinned Hawk, <i>Accipiter striatus</i>	0.61**	0.04	-0.16	I/E
Cooper's Hawk, <i>Accipiter cooperii</i>	0.09	-0.06	0.08	I
Red-shouldered Hawk, <i>Buteo lineatus</i>	0.71*	-0.16	0.30	I/E
Broad-winged Hawk, <i>Buteo platypterus</i>	1.31***	-0.76	0.49	I
Ruffed Grouse, <i>Bonasa umbellus</i>	0.74	-0.35	0.07	I/E
Black-billed Cuckoo, <i>Coccyzus erythrophthalmus</i>	0.22	0.44	-0.75**	I/E
Yellow-billed Cuckoo, <i>Coccyzus americanus</i>	0.15	0.09	-0.28	I/E
Yellow-bellied Sapsucker, <i>Sphyrapicus varius</i>	1.38***	-0.55*	-0.14	I/E
Pileated Woodpecker, <i>Dryocopus pileatus</i>	0.83***	0.32	-0.22	I
Eastern Phoebe, <i>Sayornis phoebe</i>	0.32	0.47	-0.32	I/E
Red-breasted Nuthatch, <i>Sitta canadensis</i>	0.82**	-0.45	0.40	I
Brown Creeper, <i>Certhia americana</i>	0.54**	0.36	-0.11	I
Winter Wren, <i>Troglodytes troglodytes</i>	0.59*	-0.29	-0.28	I
Golden-crowned Kinglet, <i>Regulus satrapa</i>	0.88**	-0.18	0.32	I
Blue-gray Gnatcatcher†, <i>Poliophtila caerulea</i>	0.02	0.48	-0.04	I/E
Veery, <i>Catharus fuscescens</i>	1.75*	-0.68	-0.71	I
Hermit Thrush, <i>Catharus guttatus</i>	0.98*	-1.11*	0.63*	I
Yellow-throated Vireo†, <i>Vireo flavifrons</i>	0.58*	0.46	-0.28	I/E
Magnolia Warbler, <i>Dendroica magnolia</i>	0.93***	-0.29	0.03	I
Black-throated Blue Warbler, <i>Dendroica caerulescens</i>	0.82*	-0.22	0.21	I
Yellow-rumped Warbler, <i>Dendroica coronata</i>	1.45***	-0.85*	0.45	I
Black-throated Green Warbler, <i>Dendroica virens</i>	0.98***	0.02	0.09	I
Blackburnian Warbler, <i>Dendroica fusca</i>	1.17***	0.46	-0.33	I
Pine Warbler, <i>Dendroica pinus</i>	1.54***	-0.55	0.66	I
Black-and-white Warbler, <i>Mniotilta varia</i>	1.83***	-0.48	-0.45	I
American Redstart, <i>Setophaga ruticilla</i>	0.64*	0.00	-0.04	I
Northern Waterthrush, <i>Seiurus noveboracensis</i>	1.00***	0.22	-0.03	I
Canada Warbler, <i>Wilsonia canadensis</i>	0.58*	-0.10	0.04	I
Scarlet Tanager, <i>Piranga olivacea</i>	1.06***	0.52*	-0.13	I
Rufous-sided Towhee†, <i>Pipilo erythrophthalmus</i>	1.09**	0.65*	-0.49	I/E
Purple Finch, <i>Carpodacus purpureus</i>	1.30***	-0.87**	0.34	I/E

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, using log-likelihood statistics.

† $n = 76$ (southern Ontario); otherwise, $n = 94$.

‡ Forest use is based on Freemark and Collins (1989): I, interior; I/E, interior and edge.

RESULTS

The relationship between forest cover and the probability of presence was positive for all 31 species studied. For 25 of the 31 species, the response was statistically significant at $\alpha = 0.05$ (Table 3).

The effect of forest fragmentation differed among the species studied. For four species, the probability of presence decreased with increasing fragmentation (Yellow-bellied Sapsucker, Hermit Thrush, Yellow-rumped Warbler, and Purple Finch; Table 3). The probability of presence increased for two species (Scarlet Tanager and Rufous-sided Towhee; Table 3).

Forest cover explained a larger proportion of the deviance, and had a larger logistic regression coefficient than did forest fragmentation, in 24 of the 25 bird species that responded significantly to either effect (Table 3). Only the presence of the Hermit Thrush was predicted better by forest fragmentation.

For most species, the effect of forest fragmentation on the probability that a species would be present did not increase with decreasing forest cover (see the interaction terms in Table 3). Only the Black-billed Cuckoo and the Hermit Thrush showed a significant interaction (negative and positive, respectively) between forest cover and forest fragmentation.

DISCUSSION

Separate effects of forest cover and forest fragmentation

The presence of most forest breeding birds was strongly related to forest cover, although some species did not show a statistically significant response (Table 3). There was no general relationship between the presence of forest bird species and forest fragmentation (Table 3). Species responses to fragmentation varied in both direction and magnitude. Other studies of habitat fragmentation have concluded that the response to fragmentation is variable across species (Robinson et al. 1992, Aizen and Feinsinger 1994, Margules et al. 1994, Villard and Taylor 1994, Henein 1995). The definition used for habitat fragmentation often includes habitat loss (e.g., Wilcox and Murphy 1985, Wilcove et al. 1986, Herben et al. 1991, Noss 1991, Perry and Gonzalez-Andujar 1993). Based on our results, we suggest that the negative effects observed in these studies may be mainly due to habitat removal and not to habitat fragmentation.

Relative impacts of forest cover and forest fragmentation

The notion that habitat fragmentation has a separate and unique impact on species has been shown in ex-

perimental studies that controlled for habitat amount (Quinn and Robinson 1987, Robinson and Quinn 1988, Irlandi 1994, 1995). These studies focused attention on the separate influence of habitat fragmentation, but did not compare the relative magnitudes of the effects of habitat fragmentation and habitat amount.

McGarigal and McComb (1995) compared the relative effects of late-seral forest cover and fragmentation on bird species' abundances in Oregon. They studied 30 landscapes varying in late-seral forest cover from 0.7% to 100%. Similar to our results, they found that species' abundances were more strongly associated with habitat cover than with habitat configuration (i.e., fragmentation) indices that were statistically controlled for cover. McGarigal and McComb (1995) suggested that the lack of fragmentation effects might be because their study was conducted in predominantly forested landscapes; they urged comparison of their results with studies conducted in predominantly agricultural landscapes. Our study corroborates McGarigal and McComb's result in an agricultural region and supports the general prediction that habitat loss is more important than habitat fragmentation in affecting population survival (Fahrig 1997, 1998).

To date, these are the only two empirical studies to compare the independent effects of habitat loss and fragmentation. This is probably because data sets providing information on many species and spanning many landscapes are rare. It would be interesting to know whether the results would be different for taxa other than birds. In fact, some theoretical work (Fahrig 1998) suggests that the range of conditions under which fragmentation is likely to affect population survival is quite narrow and limited to the following: (1) the average between-generation movement distance of the organism is ~1–3 times the expected nearest distance between breeding sites; (2) the breeding habitat of the organism covers <20% of the landscape; (3) the habitat is not ephemeral; (4) the organism has high breeding-site fidelity; and (5) the mortality rate in the nonbreeding habitat areas is much higher than the mortality rate in breeding habitat areas. Note that the theory predicts that all of these conditions must hold for there to be an effect of breeding habitat fragmentation on population survival. Testing this hypothesis would require not only information on many species and spanning many landscapes, but also information on dispersal and survival in various sorts of habitat for each species.

An interaction between forest cover and forest fragmentation?

Our analyses do not support the hypothesized negative interaction between the effects of habitat amount and fragmentation on species distribution (McLellen et al. 1986, Andr n 1994, Fahrig 1998). Only the Black-billed Cuckoo and the Hermit Thrush showed significant interactions (negative and positive, respectively) between forest cover and forest fragmentation.

Effects of scale

Theoretical studies predict the effects of habitat amount, habitat fragmentation, and their interaction at different scales (McLellen et al. 1986, Andr n 1994, Fahrig 1997, 1998). McLellen et al. (1986) and Andr n (1994) predict the effects of habitat amount and fragmentation at the patch scale. Fahrig (1997) predicts the effects at the landscape scale, where the landscape consists of both breeding and nonbreeding habitat and each piece of breeding habitat is assumed to be sufficient to maintain at least one individual of the species under consideration. Our study was conducted at the landscape scale. Therefore, at smaller (e.g., patch) scales, we cannot reject the hypothesis that fragmentation has the strongest effect when forest cover is low. Hinsley et al. (1996) indirectly showed fragmentation effects on bird densities at the patch scale when habitat covered 1.9% and 3.2% of the landscape.

There is some evidence that habitat loss and fragmentation increase the scale of individual movement, and that some species can better adapt to landscape changes than others (Middleton and Merriam 1983, Wiggett and Boag 1989, Wegner and Merriam 1990, Margules et al. 1994, Henein 1995, Matthysen et al. 1995, Taylor and Merriam 1995, Wegner 1995). This type of adaptation to landscape change would reduce the negative effects of habitat loss and fragmentation. Redpath (1995) found that Tawny Owls (*Strix aluco*) have larger home range sizes in regions of low habitat cover. This response means that a Tawny Owl would experience functionally the same amount of habitat in regions of low habitat cover as those of high habitat cover. The ability to increase mobility in response to landscape change is probably a characteristic derived from the heterogeneous environment in which the organism evolved (Southwood 1977). Although the Tawny Owl is able to survive in regions of low habitat cover, increased movement and lower density may indicate that the population is near a threshold, beyond which the probability of population collapse increases rapidly (Lande 1988, Nee 1994). We suggest that the degree of adaptation to landscape change varies with species, and that some species are unable to adapt. We were unable to directly address species adaptations to landscape pattern, but we found that most species (25/31) were sensitive to forest cover. This result indicates that, despite possible adaptation to a reduction in forest cover, the distribution of many forest breeding birds will decrease. It is possible that those species too rare to be included in this study (e.g., Swainson's Thrush, *Catharus ustulatus*) are the most sensitive to landscape change and cannot adapt.

Other considerations

In this study, we did not have sufficient information to classify the forest in terms of its quality for the various bird species. Because it is unlikely that all for-

est represented suitable breeding habitat for all bird species, one might argue that forest cover is potentially a poor indicator of the amount of breeding habitat. In fact, if we had found little or no effect of forest cover on bird presence/absence, variation in habitat quality might have been a reasonable explanation. However, because we did find strong effects, it seems that our implicit assumption was reasonable, i.e., for each species, the amount of habitat is correlated with the amount of forest.

In both this study and that of McGarigal and McComb (1995), habitat fragmentation is measured using multivariate statistical methods. This begs the question of whether the concept of fragmentation is useful for managers. Both of these empirical studies, as well as theory (Fahrig 1997), suggest that the effects of fragmentation are negligible. Therefore, we suggest that managers should not try to measure fragmentation, but instead should focus on determining how much habitat is available and whether it is enough to support a population of the species of interest.

CONCLUSION

Habitat amount and habitat fragmentation define important elements of landscape pattern. Separation of the effects of habitat amount and habitat fragmentation is critical to understanding factors affecting population persistence. In this study, we found that species presence was positively correlated with forest cover, but no general response to forest fragmentation was found across species. Forest cover was a better predictor of the distribution of forest breeding birds than was forest fragmentation. There was no evidence from our study for the hypothesis that the degree of forest fragmentation has an increasingly negative effect on species distribution with decreasing forest cover. We conclude that conservationists' primary focus should be on preventing a decrease in forest cover. They should not be misled, by recent discussions of "fragmentation effects," to think that the negative effects of forest loss can somehow be countered by careful consideration of the spatial pattern of remaining forest. Results to date indicate that they cannot.

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LITERATURE CITED

- Adler, F. R., and B. Nuernberger. 1994. Persistence in patchy irregular landscapes. *Theoretical Population Biology* **45**:41–75.
- Aizen, M. A., and P. Feinsinger. 1994. Forest fragmentation, pollination, and plant reproduction in a chaco dry forest, Argentina. *Ecology* **75**:330–351.
- Andr n, 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., J. F. Lynch, and D. S. Sugen. 1987. Relationship between the regional abundance of forest and the composition of forest bird communities. *Biological Conservation* **39**:129–152.
- Blake, J. G., and J. R. Karr. 1984. Species composition of bird communities and the conservation benefit of large versus small forests. *Biological Conservation* **30**:173–187.
- Burkey, T. V. 1989. Extinction in nature reserves: the effect of fragmentation and the importance of migration between reserve fragments. *Oikos* **55**:75–81.
- Cadman, M. D., P. F. J. Eagles, and F. M. Helleiner. 1987. Atlas of the breeding birds of Ontario. University of Waterloo Press, Waterloo, Canada.
- den Boer, P. J. 1981. On the survival of populations in a heterogeneous and variable environment. *Oecologia* **50**:39–53.
- Fahrig, L. 1992. Relative importance of spatial and temporal scales in a patchy environment. *Theoretical Population Biology* **41**:300–314.
- . 1997. Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* **61**:603–610.
- . 1998. When does fragmentation of breeding habitat affect population survival? *Ecological Modelling* **105**:273–292.
- Fahrig, L., and G. Merriam. 1994. Conservation of fragmented populations. *Conservation Biology* **8**:50–59.
- Freemark, K., and B. Collins. 1989. Landscape ecology of birds breeding in temperate forest fragments. Pages 443–454 in J. M. Hagan, III and D. W. Johnston, editors. *Ecology and conservation of neotropical migrant landbirds*. Smithsonian Institution Press, Washington, D.C., USA.
- Freemark, K., and G. Merriam. 1986. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. *Biological Conservation* **36**:115–141.
- Gauthier, J., and Y. Aubry. 1995. The breeding birds of Quebec: atlas of the breeding birds of southern Quebec. Association quebecoise des groupes d'ornithologues; The Province of Quebec Society for the Protection of Birds; Canadian Wildlife Service, Quebec Region, Environment Canada, Canada.
- Haila, Y., and I. Hanski. 1984. Methodology for studying the effects of habitat fragmentation on land birds. *Annales Zoologici Fennici* **21**:393–397.
- Hayden, T. J., J. Faaborg, and R. L. Clawson. 1985. Estimates of minimum area requirements for Missouri forest birds. *Transactions of the Missouri Academy of Science* **19**:11–22.
- Henein, K. M. 1995. Predicting survival of woodland species in human altered landscapes. Dissertation. Carleton University, Ottawa, Canada.
- Herben, T., H. Rydin, and L. Soderstrom. 1991. Spore establishment probability and the persistence of the fugitive invading moss, *Orthodontium lineare*: a spatial simulation model. *Oikos* **60**:215–221.
- Hinsley, S. A., R. Pakeman, P. E. Bellamy, and I. Newton. 1996. Influences of habitat fragmentation on bird species distributions and regional population sizes. *Proceeding of the Royal Society of London B* **263**:307–313.
- Huffaker, C. B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia* **27**:243–283.
- Irlandi, E. A. 1994. Large- and small-scale effects of habitat structure on rates of predation: how percent coverage of seagrass affects rates of predation and siphon nipping on an infaunal bivalve. *Oecologia* **98**:176–183.
- . 1995. Landscape ecology and the marine environment: how spatial configuration of seagrass habitat influ-

- ences growth and survival of the bay scallop. *Oikos* **72**:307–313.
- Kareiva, P. 1987. Habitat fragmentation and the stability of predator–prey interactions. *Nature* **326**:388–390.
- Lande, R. 1988. Demographic models of the northern spotted owl (*Strix occidentalis caurina*). *Oecologia* **75**:601–607.
- Levin, S. A. 1976. Population dynamic models in heterogeneous environments. *Annual Review of Ecology and Systematics* **7**:287–310.
- Manly, B. F. G. 1996. RT version 2.0. Centre for Applications of Statistics and Mathematics. University of Otago, Dunedin, New Zealand.
- Margules, C. R., G. A. Milkovits, and G. T. Smith. 1994. Contrasting effects of habitat fragmentation on the scorpion *Cercophonius squama* and an amphipod. *Ecology* **75**:2033–2042.
- Matthysen, E., F. Adriaensen, and A. A. Dhondt. 1995. Dispersal distances of nuthatches, *Sitta europaea*, in a highly fragmented forest habitat. *Oikos* **72**:375–381.
- McGarigal, K., and W. C. McComb. 1995. Relationships between landscape structure and breeding birds in the Oregon coast range. *Ecological Monographs* **65**:235–260.
- McLellan, C. H., A. P. Dobson, D. S. Wilcove, and J. F. Lynch. 1986. Effects of forest fragmentation on new- and old-world bird communities: empirical observation and theoretical implications. Pages 305–313 in J. Verner, M. L. Morrison, and C. J. Ralph, editors. *Wildlife 2000*. University of Wisconsin Press, Madison, Wisconsin, USA.
- Middleton, J., and G. Merriam. 1983. Distribution of woodland species in farmland woods. *Journal of Applied Ecology* **20**:625–644.
- National Air Photo Library of Canada. Natural Resources Canada. Ottawa, Canada.
- Nee, S. 1994. How populations persist. *Nature* **367**:123–124.
- Noss, R. F. 1991. Landscape connectivity: Different functions at different scales. Pages 27–39 in W. E. Hudson, editor. *Landscape linkages and biodiversity*. Island Press, Washington, D.C., USA.
- Perry, J. N., and J. L. Gonzalez-Andujar. 1993. Dispersal in a metapopulation neighbourhood model of an annual plant with a seedbank. *Journal of Ecology* **81**:453–463.
- Quinn, J. F., and G. R. Robinson. 1987. The effects of experimental subdivision on flowering plant species diversity in a California annual grassland. *Journal of Ecology* **75**:837–856.
- Redpath, S. M. 1995. Habitat fragmentation and the individual: tawny owles *Srix aluco* in woodland patches. *Journal of Animal Ecology* **64**:652–661.
- Robinson, G. R., R. D. Holt, R. S. Gains, S. P. Hamburg, M. L. Johnson, H. S. Fitch, and E. A. Martinko. 1992. Diverse and contrasting effects of habitat fragmentation. *Science* **257**:524–526.
- Robinson, G. R., and J. F. Quinn. 1988. Extinction, turnover and species diversity in an experimentally fragmented California annual grassland. *Oecologia* **76**:71–82.
- Roland, J. 1993. Large-scale forest fragmentation increases the duration of tent caterpillar outbreak. *Oecologia* **93**:25–30.
- Rowe, J. S. 1977. Forest regions of Canada. Canadian Forestry Service Publication 1300, Ottawa, Canada.
- SAS. 1990. SAS/STAT users guide. Version 6.09, fourth edition, volume 2. SAS Institute, Cary, North Carolina, USA.
- Southwood, T. R. E. 1977. Habitat, the templet for ecological strategies? *Journal of Animal Ecology* **46**:337–365.
- SPANS GIS. 1993. Reference manual. Version 5.3, sixth edition. Intera Tydac Technologies, Nepean, Ontario, Canada.
- Taylor P. D., and G. Merriam. 1995. Wing morphology of a forest damselfly is related to landscape structure. *Oikos* **73**:43–48.
- Taylor P. D., and S. M. Smith. 1987. Multi-species clusters of birds in southern Ontario. Pages 576–580 in M. D. Cadman, P. F. J. Eagles, and F. M. Helleiner, editors. *Atlas of the breeding birds of Ontario*. University of Waterloo Press, Waterloo, Canada.
- Villard, M.-A. 1991. Spatio-temporal dynamics of forest bird patch populations in agricultural landscapes. Dissertation. Carleton University, Ottawa, Ontario, Canada.
- Villard, M.-A., and P. D. Taylor. 1994. Tolerance to habitat fragmentation influences the colonization of new habitat by forest birds. *Oecologia* **98**:393–401.
- Wegner, J. 1995. Habitat distribution, spatial dynamics and reproduction of a forest rodent (*Peromyscus leucopus*) in an agricultural landscape. Dissertation. Carleton University, Ottawa, Canada.
- Wegner, J., and G. Merriam. 1990. Use of spatial elements in a farmland mosaic by a woodland rodent. *Biological Conservation* **54**:263–276.
- Whitcomb, R. F., C. S. Robbins, J. F. Lynch, B. L. Whitcomb, M. K. Klimkiewicz, and D. Bystrak. 1981. Effects of forest fragmentation on the avifauna of the eastern deciduous forest. Pages 125–205 in R. L. Burgess, and D. M. Sharp, editors. *Forest island dynamics in man-dominated landscapes*. Springer-Verlag, New York, New York, USA.
- Wiggett, D. R., and D. A. Boag. 1989. Intercolony natal dispersal in the Columbian ground squirrel. *Canadian Journal of Zoology* **67**:42–50.
- Wilcove, D. S., C. H. McLellan, and A. P. Dobson. 1986. Habitat fragmentation in the temperate zone. Pages 237–256 in M. E. Soulé, editor. *Conservation biology*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Wilcox, B. A., and D. D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. *American Naturalist* **125**:879–887.
- Wilken, E. B., C. D. A. Rubec, and G. Ironside. 1993. Canada terrestrial ecoregions. State of the Environment Reporting. Environment Canada, Canada.