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**THE EFFECTS OF FOREST LOSS AND FRAGMENTATION ON THE DISTRIBUTION OF
FOREST BREEDING BIRDS**

by

M. Kurtis Trzcinski, B. Sc.

A thesis submitted to
the Faculty of Graduate Studies and Research
in partial fulfilment of
the requirements for the degree of

Master of Science

Department of Biology
Carleton University
Ottawa, Ontario
6 November 1995

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"The effects of forest loss and fragmentation on the
distribution of forest breeding birds"

submitted by

M. KURTIS TRZCINSKI, B.Sc.

in partial fulfilment of the requirements
for the degree of Master of Science

Chair, Department of Biology

Thesis Supervisor

Thesis Supervisor

Carleton University

to Stéphanie
and
to Maximilien, Gabrielle, and Ambroise

ABSTRACT

The objective of this study was to test the hypothesis that the negative effect of fragmentation on species survival increases with decreasing habitat amount. The independent effects of forest loss and fragmentation on the distribution of forest breeding birds were studied by sampling landscapes at the 10 km scale. For each landscape percent forest cover was measured, and a fragmentation index, independent of forest amount, was generated from the measures of mean forest patch size, forest patch number, and total forest edge. Presence of bird species in each of 94 sample landscapes was determined using Breeding Bird Atlas data. Responses of 13 bird species to forest loss and fragmentation were analysed using logistic regression. The hypothesis predicted a negative interaction effect of forest amount and fragmentation on bird distribution. All significant responses to forest loss were negative. Responses to forest fragmentation were variable. There was no interaction in species responses to forest loss and fragmentation. I conclude that 1) forest loss has a negative effect on forest bird species richness, 2) there is no evidence for consistent negative effects of forest fragmentation *per se* on bird species presence, 3) the relative effect of forest loss is greater than that of forest fragmentation, and 4) there was no evidence to support the hypothesis that the effect of fragmentation on species survival increases with decreasing habitat amount.

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INTRODUCTION

Many studies have concluded that habitat loss and fragmentation have important effects on species survival (e.g. Elton 1949, Huffaker 1958, MacArthur and Wilson 1963, Levins 1970, Levin 1976, Wiens 1976, Southwood 1977, Merriam 1984, Wilcox and Murphy 1985, Fahrig and Merriam 1985, McLellen et al. 1986, Kareiva 1987, Quinn and Robinson 1987, Pulliam 1988, Wiens 1989, Lord and Norton 1990, Harris and Silva-Lopez 1992, Hobbs 1993, Hobbs et al. 1993, Villard et al. 1995). Habitat fragmentation can affect gene flow, predation, parasitism, habitat selection, competition, individual movement, and the abundance and distribution of species. Often, habitat fragmentation is viewed as the most serious threat to species survival and biological diversity (Wilcox and Murphy 1985, Wilcove et al. 1986, Noss 1991, Harris and Silva-Lopez 1992).

Since the process of habitat fragmentation usually occurs simultaneously with habitat loss, the term 'habitat fragmentation' has often included both habitat loss and fragmentation *per se*. Fragmentation is the breaking apart or separation into smaller pieces (Oxford English Dictionary 1971, Lord and Norton 1990, Harris and Silva-Lopez 1992). Habitat loss is the reduction in the proportion of habitat in a landscape. Notice that habitat loss and fragmentation are defined in spatial units termed landscapes. The importance of separating the effects of habitat loss and fragmentation is based on the hypothesis that they have independent biological impacts (Haila and Hanski 1984, Kareiva 1987, Quinn and Robinson 1987, Robinson and Quinn 1988, Irlandi 1994, Irlandi et al. 1995).

To understand the effect of habitat fragmentation, the effect of habitat loss should be controlled (Haila and Hanski 1984, Kareiva 1987, Quinn and Robinson 1987, Robinson and Quinn 1988, Irlandi 1994, Irlandi et al. 1995). Habitat fragmentation is usually considered to have a negative effect on population survival (Wilcox and Murphy 1985, Wilcove et al. 1986, Burkey 1989, Herben et al. 1991, Perry and Gonzalez-Andujar 1993, Adler and Nuernberger 1994). Explanations for the negative impact of fragmentation are that it increases the mortality of individuals moving between patches, reduces recolonization rates of empty patches, and reduces local population sizes making them more susceptible to extinction. There is also some evidence that habitat fragmentation can have a positive effect on population survival by 1) desynchronising the dynamics of local populations and 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).

When is habitat fragmentation important in influencing population survival? The current belief seems to be that habitat fragmentation is always relevant (Wilcox and Murphy 1985, Wilcove et al. 1986, Harris and Silva-Lopez 1992). This belief leads to the notion that that conservation efforts aimed at reducing the degree of fragmentation are always essential (Wilcox and Murphy 1985, Noss 1991). The efforts and resources of researchers and conservationists can be better focused by identifying when habitat fragmentation is unlikely to affect species survival (Kareiva 1990, Levin 1992, Fahrig submitted). A few studies suggest that habitat fragmentation has a negative effect on population survival only at low levels of habitat amount (see Figure 7 in McLellen et al.

1986, Andren 1994, Fahrig submitted). These studies use different approaches but make similar general predictions. McLellen et al. (1986) used a deterministic equilibrium model. Andren (1994) reviewed empirical studies, and Fahrig (submitted) used a spatially explicit, individual based, simulation model. They predict that fragmentation has the strongest effect when habitat amount is low (less than 20 % cover). The implications of this prediction are twofold. At high amounts of habitat it is unnecessary to 1) measure the degree of fragmentation and 2) use spatially explicit models. This study tests the hypothesis that the effect of habitat fragmentation increases with a decrease in habitat amount. The test of this hypothesis also produces interesting results on the separate effects of habitat loss and fragmentation, and on their relative impacts on species survival.

Habitat loss and fragmentation occur in a landscape over time. A study of a single landscape over time will inevitably confound the effects of habitat loss and fragmentation. It is only by comparing many landscapes over a large spatial domain that the effects of habitat loss and fragmentation can be separated. The landscape pattern at a given time results from the processes of forest loss and fragmentation, and each landscape sampled in this study represents one possible outcome. This approach allowed me to test for the separate effects of habitat loss and fragmentation on species survival while retaining the ability to evaluate their relative impacts and test for their interaction.

METHODS

I tested this hypothesis and its generality using Universal Transverse Mercator (UTM) squares as sample units of landscapes of an arbitrary scale (10 km) altered by a range of forest loss and fragmentation. Since this hypothesis depends on theoretical studies that model the dynamics of populations in a system of habitat / non-habitat, landscape composition was defined as forest / non-forest. I selected species for which the assumption that forest represented habitat was reasonable.

Study Region

The study region is in southern and eastern Ontario, and southern Quebec ($n = 94$, see Figure 1). The study region 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 characterised 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). Study sites were located in regions of medium to high levels of agricultural activity. Sites were not selected in the central portion of the study region because forest structure and composition as well as the bird species assemblage differ from the rest of the study region (Rowe 1977, Wilken et al. 1993, Taylor and Smith 1987) due to differences in geology. The central part of the study region is composed of Precambrian rock known as the Canadian Shield (Thureston et al. 1992). This area consists of hard rocks such as granites and gneisses. The rest of the study region is made up of softer substrates consisting of limestone, sandstone, dolostone, and shale (Thureston et al. 1992, Globensky 1987). Sites

were selected to represent large variation in habitat fragmentation, and habitat amount from around 5 % forest cover to around 50 % forest cover. Sites from the two areas were pooled into one analysis because I expected a similar response of a species to habitat loss and fragmentation between the two areas. To check this assumption I excluded the study sites from the north-east part of the study region and reanalysed the data. There were no major changes in the results that would affect the conclusions of this study.

Parameter estimation

To test the hypothesis stated in the introduction, population survival, habitat amount, and degree of fragmentation were measured in each sample landscape. The presence / absence of forest breeding birds was used as a surrogate for population survival. Percent forest cover estimated the amount of habitat in a sample landscape. The degree of habitat fragmentation was estimated by combining three indices of fragmentation into one variable using principal components analysis. The estimates of population survival, habitat loss, and habitat fragmentation are explained below.

Population Survival

The presence / absence of forest breeding birds was used as a surrogate for population survival. Breeding Bird Atlas data (BBA), were used to determine the presence / absence of a species for each 10 km X 10 km UTM square (Cadman et al. 1987, Gauthier and Aubry 1995). The BBA data for Ontario were collected between 1981-1985, and BBA data for Quebec were collected between 1984-1989. If there was any evidence of a species breeding in a sample landscape at the time of census, I assumed that a population was present.

Forest breeding birds were chosen for study because 1) forest habitat within the study region exists in a wide range of habitat amount and fragmentation 2) forest represents a general habitat type for a definable group of birds, and 3) forest and non-forest can be identified with a relatively high level of precision using remote sensing. Species were selected for analysis out of a pool of 78 forest birds (Freemark and Collins 1989). Freemark and Collins (1989) classified the habitat use of forest birds as interior, interior / edge, and edge species by both collecting data and reviewing literature (Whitcomb et al. 1981, Blake and Karr, 1984, 1987, Hayden et al. 1985, Freemark and Merriam 1986, Askins et al. 1987). There was little disagreement in the classification of birds among studies. The only species in this study where there was some disagreement in classification was the Black-billed Cuckoo (see Appendix A for scientific names). The criteria for bird species selection in this study were that 1) the range of the species included all of the study region (Cadman et al. 1987, Gauthier and Aubry 1995) 2) it bred in both forest interior and edge (Freemark and Collins 1989), and 3) there was sufficient variation in its presence (present and absent in at least 10 % of the sites). Twenty-four species met the first two criteria, and 13 species met all three criteria (Appendix A).

Forest amount

Percent forest cover estimates the amount of habitat for forest breeding birds in a sample landscape. Large scale aerial photography (1:50,000) collected during the time of census or the closest point in time before the census was used to define forest and non-forest patch types for each sampled landscape (National Air Photo Library). Forest and non-forest were traced from the air photos, tracings were digitised, and percent forest cover was estimated using SPANS GIS (1993).

Forest fragmentation

To test the relative effects of habitat loss and fragmentation and their interaction a single measure of the degree of fragmentation was needed. Changing the degree of habitat fragmentation affects a group of landscape variables -- mean patch size, patch number, and the total amount of edge. I measured mean forest patch size, forest patch number and the total amount of forest edge for each sample landscape using SPANS GIS (1993) (means, variances and frequency distributions for each variable are in Appendix B). Forest patch number and total amount of forest edge were calculated within the 10 km X 10 km UTM square. The calculation of mean forest patch size included patches which extended outside the 10 km X 10 km UTM square boundary. The three indices of forest fragmentation were correlated with each other (Table 1). Mean forest patch size and total edge correlated positively with forest cover ($p < 0.0001$, Table 1). I used principal components analysis to summarise the information in mean forest patch size, forest patch number and the total amount of forest edge into an index of the degree of forest fragmentation (SAS 1990, Proc PRINCOMP). The first two principal components explained 94% of the variation (see Table 2 for loadings). The first principal component explained 52% of the variation and was most highly correlated with mean forest patch size and total forest edge. The first principal component also correlated highly with percent forest cover ($R^2 = 0.88$, Figure 2). The second principal component explained 42% of the variation and was mostly made up of patch number. The second principal component was uncorrelated with forest cover ($R^2 = 0.03$, Figure 3). If the direction of the loadings are examined, one observes that as the second principal component increases mean forest

patch size decreases, forest patch number increases and total forest edge increases (Table 2). Thus, increasing the second principal component is interpreted as increasing forest fragmentation. The second principal component, corrected for its slight correlation with forest cover, was used as an index of forest fragmentation that is independent of forest cover.

Figure 4 shows the utility of the forest fragmentation index in studying the effects of the independent processes of forest loss and fragmentation on landscape structure in four sample landscapes. The effects of forest loss and fragmentation are confounded in studies which conclude that landscape 'd' in Figure 4 is more fragmented than landscape 'a'. While this conclusion is true, landscape 'd' also has less forest.

Analyses

To test for the effects of forest loss and fragmentation, their relative impacts, and their interaction the data were analysed using logistic regression (SAS 1990, Proc LOGISTIC). The response of each species provides an independent test of the hypotheses. Therefore, each species was analysed separately.

To assess the response of the species assemblage to forest loss and fragmentation, bird species richness was analysed using multiple regression (SAS 1990, Proc GLM). Species richness was the number of species present in a landscape from a total of 24 species that met the species selection criteria 1 and 2 (Appendix A).

The presence of a species within a landscape might be influenced by its presence or absence in surrounding landscapes. Spatial autocorrelation was used to measure the degree of spatial dependence in the species richness values (R package, Legendre and

Vaudor 1991). Eight distance classes were used and the Moran coefficient was calculated for each class (Moran 1950). A Bonferroni correction for multiple tests was calculated ($\alpha = 0.006$). There was significant spatial autocorrelation in bird species richness for the distance class 10-30 km (Table 3, Legendre and Fortin 1989). It is interesting to note that the first distance class, which tests if there is autocorrelation in contiguous squares, was not significant. The spatial dependence in bird species richness indicates that species respond to pattern at scales between 10 and 30 km.

RESULTS

Forest cover positively affected the presence of all 13 species studied except for the Blue-gray Gnatcatcher. In six of these cases the response was statistically significant at $\alpha = 0.05$ (Table 4). Species richness increased with forest cover ($p < 0.0001$, Table 5, Figure 16).

The effect of fragmentation varied for the 13 species studied. Of the five species that responded significantly to fragmentation, the probability of presence decreased for three species (Yellow-bellied Sapsucker, Purple Finch, and Northern Flicker) and increased for two species (Rufous-sided Towhee, and Blue-gray Gnatcatcher) with increasing fragmentation (Table 4). No significant relationship was found between species richness and forest fragmentation (Table 5).

The relative impacts of forest cover and fragmentation were determined by comparing the amount of deviance each variable explained (χ^2 values in Table 6). There was not a consistent tendency for either forest cover or forest fragmentation to have a greater impact on species presence. However, forest cover had a greater impact than forest fragmentation on species richness (SS values in Table 5).

The effect of forest fragmentation on the probability of presence of a species did not change with increasing forest cover (see interaction terms in Table 4). Although the Black-billed Cuckoo showed a significant interaction between forest cover and fragmentation, the main effects of forest cover and fragmentation were not significant. The lack of significant interaction terms indicates that there is no evidence for a threshold of 20

% cover below which the degree of fragmentation becomes increasingly important in determining species survival. There was no interaction between the effects of forest cover and forest fragmentation on species richness (Table 5).

DISCUSSION

The separate effects of forest loss and fragmentation

Twelve of 13 species studied responded positively to forest cover. Six of the 13 bird species studied had significant positive responses. Species richness increased as forest cover increased. These results indicate that increasing forest cover positively affects species richness, but that the tolerance and sensitivity to forest cover at this spatial scale is species specific (Table 4, Figures 5, 7, 9, 11, 12, 13).

Species did not respond consistently to forest fragmentation independent of forest amount. Five of the 13 species studied had significant responses to forest fragmentation. The Yellow-bellied Sapsucker, Purple Finch, and the Northern Flicker responded negatively, and the Rufous sided-Towhee, and Blue-gray Gnatcatcher responded positively (Table 4). Species varied in tolerance and sensitivity to forest fragmentation (Figures 6, 8, 10, 14, 15). Other studies also have concluded that species response to fragmentation is variable (Villard and Taylor 1994, Margules et al. 1994, Henein 1995). No significant relationship between species richness and forest fragmentation was found (Table 5). This result supports the conclusions of Margules et al. (1994) and Robinson et al. (1992) that generalisations about species responses to fragmentation *per se* are not possible.

Most studies predict that habitat fragmentation reduces population survival (Wilcox and Murphy 1985, Wilcove et al. 1986, McLellen et al. 1986, Burkey 1989, Herben et al. 1991, Noss 1991, Harris and Silva-Lopez 1992, Perry and Gonzalez-Andujar

1993, Adler and Nuernberger 1994, Fahrig submitted). Possible explanations for the discrepancy between this prediction and the results of this study are 1) assumptions in theoretical models control the relationship 2) habitat fragmentation is correlated with other measures of landscape pattern, and 3) species interactions strongly influence the effect of fragmentation.

Most theoretical studies predict that habitat fragmentation negatively affects population survival (McLellen et al. 1986, Burkey 1989, Herben et al. 1991, Perry and Gonzalez-Andujar 1993, Adler and Nuernberger 1994). Fahrig's (submitted) theoretical study found that there are five conditions which must be met to find a negative effect of fragmentation: 1) the between-generation movement distance of the organism is neither very short nor very long relative to the distances between breeding patches, 2) the breeding habitat of the organism covers less than 20 % of the landscape, 3) the habitat is not ephemeral on a time scale similar to the generation time of the organism, 4) the organism has low dispersal rates, and 5) the mortality rate in non-breeding habitat is much higher than in breeding habitat. Other models predicting a negative effect of fragmentation explicitly and implicitly assume these conditions (McLellen et al. 1986, Burkey 1989, Herben et al. 1991, Perry and Gonzalez-Andujar 1993, Adler and Nuernberger 1994). Most are not spatially explicit (except Adler and Nuernberger 1994); therefore, they assume that organisms either move the right distance and arrive at a new patch or they die. They either do not include spatio-temporal destruction and regeneration of habitat (McLellen et al. 1986, Burkey 1989, Adler and Nuernberger 1994), if they do, landscape change has an effect on time scales longer than the generation time (Herben et

al. 1991, Perry and Gonzalez-Andujar 1993). Some of the models (McLellen et al. 1986, Herben et al. 1991, Perry and Gonzalez-Andujar 1993) assume low dispersal rates. All the models assume that mortality is always higher when moving between habitat patches than within patches. Therefore, these models meet the conditions for finding an effect of fragmentation. In my study, can not evaluate whether the landscape pattern and the birds response to this pattern meet the above conditions, because I did not measure these variables, nor could I find them in the literature. However, it is possible that one or more of these conditions / assumptions do not hold for most of the species in this study, resulting in a general lack of significant effects of fragmentation.

Why do these models predict a consistent *negative* effect of habitat fragmentation and not a variable response as was found in this study? This prediction could depend on assumptions of mortality. As fragmentation increases, habitat patch size decreases and total habitat edge increases (Fahrig submitted, Table 2), causing more individuals to move into non-habitat (Stamps et al. 1987). If there are more individuals in non-habitat and the model assumes higher mortality in non-habitat, a larger proportion of the population dies, and population survival decreases with increasing fragmentation. Few empirical studies have shown higher mortality rates in non-habitat (Van Vuren and Armitage 1994). Wegner (1995) studied a small mammal (*Peromyscus leucopus*) and found high turnover rates in habitat patches and large spatial scale of movement. Based on these results he suggests that movement may not be harmful (Wegner 1995). Even if the assumption of higher mortality in non-habitat is correct, individuals may avoid non-habitat and use corridors or spend little time in non-habitat and moving through it quickly (Merriam and

Lanoue 1990). The result of such behaviour might be that even though the probability of mortality in non-habitat may be higher, the actual proportion of the population dying in non-habitat will be small. Relaxing the model assumption of higher mortality in non-breeding habitat may eliminate the negative effect of fragmentation in most models, but relaxing this assumption may prove necessary to find conditions in which fragmentation positively affects population survival.

Species may respond positively to forest fragmentation because it is *negatively* correlated with forest isolation. This relationship is evident by examining Figure 4. Forest fragmentation *per se* is not a measure of forest isolation, rather, it is a measure of the degree of forest subdivision (see Introduction). The negative effect of habitat isolation has been the major focus of studies of 'habitat fragmentation'. However, habitat fragmentation and habitat isolation measure different ecological patterns and likely influence different demographic processes. Habitat fragmentation divides habitat into many patches of smaller size and consequently divides the population into many local populations of smaller size. At low levels of habitat amount, each local population will be more likely to go extinct because of random demographic or environmental events (Fahrig and Merriam 1994). Habitat isolation influences landscape connectivity (the probability of an individual moving from one patch to any other patch in the landscape) (Merriam 1984, Fahrig and Merriam 1985, Fahrig and Paloheimo 1988, Henein and Merriam 1990, Taylor et al. 1993, Henein 1995). Therefore, a positive response to fragmentation could really be due to a stronger negative response to isolation. These examples demonstrate the need to separate the effect of habitat isolation from habitat loss and fragmentation. Note,

however, that it is not possible to separate their effects without allowing either patch size or landscape dimension to vary (Harrison and Fahrig 1995).

Models that predicts a negative effect of habitat fragmentation on species survival often do not include species interactions. If one begins with the assumption that species have evolved in a heterogeneous environment (Southwood 1977), and that a species has co-evolved with its natural enemies, fragmentation of the heterogeneous environment could decouple species interactions creating spatio-temporal refugia for the prey (Huffaker 1958, Levin 1976, Kareiva 1987, Roland 1993). This explanation suggests a dichotomy in species responses to habitat fragmentation. Species that have not evolved under strong species interactions will be negatively affected by habitat fragmentation. Fragmentation will divide the population into smaller local populations making species survival more dependent on movement. Species that have evolved under strong species interactions could respond positively or negatively depending on whether the movement or searching behaviour of natural enemies is inhibited or facilitated by habitat fragmentation. In the case of Kareiva's (1987) study, the movement of predators was inhibited by fragmentation. In the case of many birds, fragmentation has negative effects by facilitating the searching behaviour of nest predators and parasites, and by increasing their landscape population size (Robinson et al. 1995, Andren 1992).

The relative impacts of habitat loss and fragmentation

The notion that habitat fragmentation has a separate and unique impact on species, has been shown in studies that controlled for habitat amount (Irlandi 1994, Irlandi et al. 1995). These studies draw attention to the separate influence of habitat fragmentation,

but can not compare the relative magnitudes of the effects of habitat fragmentation and habitat loss. This study is the first to compare the separate responses of species to forest loss and fragmentation. There was not a consistent tendency across species for either forest cover or forest fragmentation to have a greater impact on species presence (Table 6), but forest cover had a much larger effect on species richness than forest fragmentation (Table 5).

An interaction between habitat loss and fragmentation?

My analyses do not demonstrate the hypothesised negative interaction in the effects of habitat amount and fragmentation on species survival (McLellen et al. 1986, Andren 1994, Fahrig submitted). Since these theoretical studies predict a negative effect of fragmentation, only those species that responded positively to forest amount and negatively to forest fragmentation can be used to test this hypothesis. These are the Yellow-bellied Sapsucker, Purple Finch, and Northern Flicker (Table 4). There was no significant interaction effect of forest cover and fragmentation on the probability of presence for these species. Therefore, there is no evidence for the hypothesised threshold of 20 % forest cover below which the degree of fragmentation becomes increasingly important in determining species survival.

Effects of scale and heterogeneity

Theoretical studies predict the effects of habitat loss, fragmentation and their interaction at different scales (McLellen et al. 1986, Andren 1994, Fahrig submitted). McLellen et al. (1986), and Andren (1994) predict the effects of habitat loss and

fragmentation at the patch scale, whereas, Fahrig (submitted) predicts the effects at the landscape scale. This study was conducted at the landscape scale. Therefore, I can not reject the hypothesis that fragmentation has the strongest effect when forest amount is low (less than 20 % cover) at smaller (the patch) or larger scales.

There is some evidence that forest loss and fragmentation increase the scale of individual movement (Wiggett and Boag 1989, Wegner and Merriam 1990, Taylor 1994, Matthysen et al. 1995, Taylor and Merriam 1995, Henein 1995, Wegner 1995), and that some species can better adapt to landscape changes than others (Margules et al. 1994, Taylor 1994, Matthysen et al. 1995, Taylor and Merriam 1995, Henein 1995, Wegner 1995). It is possible that the species that have significant responses to forest loss and fragmentation in this study are those species that are most sensitive to landscape change, and can not adapt.

The amount of heterogeneity measured could also influence the results of this study. Studies have shown that increasing the heterogeneity measured from simply habitat / non-habitat patches to breeding patches, foraging patches, refuge patches, and matrix patches can increase our understanding of species survival (Kotliar and Wiens 1990, Henein and Merriam 1990, Kadmon 1993, Webb and Thomas 1994, Henein 1995). Using just two patch types (forest / non-forest) I was able to partially predict the distribution of 8 of the 13 species studied, based on forest amount and fragmentation. The method developed in this study could be extended to measure the fragmentation of any patch type. I do not know whether an increase in the level of heterogeneity measured would have produced better predictive power.

Conclusion

The amount of habitat and its degree of fragmentation define important elements of landscape pattern. The separation of the effects of habitat loss and fragmentation is critical to understanding species survival. Habitat amount and fragmentation probably alter individual behaviour and population dynamics differently. In this study I found that species responded negatively to forest loss, but no general response to forest fragmentation was found across species. Forest loss affects species richness more than forest fragmentation. There is no evidence for the hypothesised threshold of 20 % forest cover below which the degree of fragmentation becomes increasingly important in determining species survival. Conservationists' primary focus should be on increasing habitat amount, and not on decreasing fragmentation *per se*. This recommendation is made not because fragmentation is unimportant, but rather, because no general predictions can be made about the effects of fragmentation.

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Table 1. Pearson product-moment correlation coefficients indicating the correlation between three indices of forest fragmentation and forest cover. All relationships are significant at $p \leq 0.0001$ except the relationship between patch number and cover which is not significant at $p \leq 0.05$.

	Mean patch size	Patch number	Total edge	Cover
Mean patch size	1.00	-0.37	0.54	0.83
Patch number		1.00	0.30	0.003
Total edge			1.00	0.84
Cover				1.00

Table 2. Principal component loadings for the three indices of forest fragmentation. PC 1 explained 52 % and PC 2 explained 42 % of the variation.

	PC 1	PC 2
Mean patch size	0.74	-0.23
Patch number	-0.15	0.85
Total edge	0.65	0.47

Table 3. A test for spatial independence in species richness in 10 km sample landscapes using the Moran coefficient (R package, Legendre and Vaudor 1991). $\alpha = 0.006$, calculated using the Bonferroni correction, was used to reject the null hypothesis of spatial independence. The upper limit of a distance class was included in the class, whereas lower limits were not. $P > 1$ is reported for positive and $p < 1$ for negative coefficients.

Distance Class	Moran Coef. (I)	$p > 1$
		$p < 1$
0 - 10	0.186	0.05
10 - 30	0.238	0.001
30 - 50	-0.063	0.19
50 - 100	-0.052	0.06
100 - 160	-0.015	0.42
160 - 230	-0.051	0.09
230 - 310	0.052	0.04
> 310	-0.068	0.17

Table 4. Logistic regression coefficients for percent forest cover, index of fragmentation, and their interaction in each of 13 stepwise logistic regressions using the log likelihood statistic in SAS (1990) (n=94). Level of significance is indicated by *'s, and the coefficients in small type are not significant.

Species	Cover	Fragmentation	Interaction
Yellow-bellied Sapsucker	0.125 ***	-0.314 *	-0.011
Rufous-sided Towhee	0.043 *	0.995 *	-0.028
Purple Finch	0.118 ***	-1.232 **	0.028
Sharp-shinned Hawk	0.055 **	0.244	-0.013
Red-shouldered Hawk	0.064 *	-0.540	0.024
Yellow-throated Vireo	0.036 *	0.973	-0.031
Northern Flicker	0.062	-1.975 **	0.054
Blue-gray Gnatcatcher	-0.012	0.649 **	-0.007
Black-billed Cuckoo	0.020	1.385	-0.061 **
Yellow-billed Cuckoo	0.014	0.447	-0.022
Ruffed Grouse	0.068	-0.408	0.006
Downy Woodpecker	0.149	0.564	-0.075
Eastern Phoebe	0.029	0.853	-0.026

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

Table 5. The effect of forest cover, fragmentation and their interaction on species richness.

Variable	df	Type I SS	F value	p > F	Coefficient
Model	3	133.73	10.01	0.0001	
Cover	1	117.05	26.30	0.0001	0.09
Fragmentation	1	7.95	1.79	0.18	
Interaction	1	8.73	1.96	0.16	
Error	90	400.62			

Table 6. The partial deviances and p-values for percent forest cover, index of fragmentation, and their interaction in each of 13 stepwise logistic regressions using the log likelihood statistic in SAS (1990) (n=94). All terms were included in the model. P-values are only given if $p < 0.05$.

Species	<u>Cover</u>		<u>Fragmentation</u>		<u>Interaction</u>	
	χ^2	$p > \chi^2$	χ^2	$p > \chi^2$	χ^2	$p > \chi^2$
Yellow-bellied Sapsucker	20.045	0.0001	4.192	0.041	0.159	
Rufous-sided Towhee	5.893	0.015	5.883	0.015	1.714	
Purple Finch	19.298	0.0001	8.234	0.004	1.083	
Sharp-shinned Hawk	8.121	0.004	0.339		0.116	
Red-shouldered Hawk	5.504	0.019	1.197		0.351	
Yellow-throated Vireo	4.015	0.045	3.351		2.742	
Northern Flicker	3.348		7.401	0.006	1.378	
Blue-gray Gnatcatcher	0.486		8.759	0.003	0.197	
Black-billed Cuckoo	0.664		2.529		8.347	0.004
Yellow-billed Cuckoo	1.05		1.241		0.369	
Ruffed Grouse	3.038		1.238		0.023	
Downy Woodpecker	2.075		0.500		0.743	
Eastern Phoebe	2.203		2.785		0.873	

Figure 1. The distribution of landscapes sampled by 10 km X 10 km UTM squares.

Figure 2. The relationship between the first principal component and percent forest cover
(n=94, $R^2 = 0.88$).

Figure 3. The relationship between the second principal component and percent forest cover ($n=94$, $R^2 = 0.03$).

Figure 4. Forest loss and fragmentation in four sample landscapes. Landscape a: percent 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.

Figure 5. The effect of percent forest cover on the probability of presence of the Yellow-bellied Sapsucker. X's represent bird presence or absence at a site (n=94). The '■'s represent the proportion of presences in each interval, and the bars indicate the 95 % confidence interval.

Figure 6. The effect of the forest fragmentation index on the probability of presence of the Yellow-bellied Sapsucker. The degree of forest fragmentation increases from negative to positive. X's represent bird presence or absence at a site (n=94). The '■'s represent the proportion of presences in each interval, and the bars indicate the 95 % confidence interval.

Figure 7. The effect of percent forest cover on the probability of presence of the Rufous-sided Towhee. X's represent bird presence or absence at a site (n=94). The '■'s represent the proportion of presences in each interval, and the bars indicate the 95 % confidence interval.

Figure 8. The effect of the forest fragmentation index on the probability of presence of the Rufous-sided Towhee. The degree of forest fragmentation increases from negative to positive. X's represent bird presence or absence at a site (n=94). The '■'s represent the proportion of presences in each interval, and the bars indicate the 95 % confidence interval.

Figure 9. The effect of percent forest cover on the probability of presence of the Purple Finch. X's represent bird presence or absence at a site (n=94). The '■'s represent the proportion of presences in each interval, and the bars indicate the 95 % confidence interval.

Figure 10. The effect of the forest fragmentation index on the probability of presence of the Purple Finch. The degree of forest fragmentation increases from negative to positive. X's represent bird presence or absence at a site (n=94). The '■'s represent the proportion of presences in each interval, and the bars indicate the 95 % confidence interval.

Figure 11. The effect of percent forest cover on the probability of presence of the Sharp-shinned Hawk. X's represent bird presence or absence at a site (n=94). The '■'s represent the proportion of presences in each interval, and the bars indicate the 95 % confidence interval.

Figure 12. The effect of percent forest cover on the probability of presence of the Red-shoulder Hawk. X's represent bird presence or absence at a site (n=94). The '■'s represent the proportion of presences in each interval, and the bars indicate the 95% confidence interval.

Figure 13. The effect of percent forest cover on the probability of presence of the Yellow-throated Vireo. X's represent bird presence or absence at a site (n=94). The '■'s represent the proportion of presences in each interval, and the bars indicate the 95 % confidence interval.

Figure 14. The effect of the forest fragmentation index on the probability of presence of the Northern Flicker. The degree of forest fragmentation increases from negative to positive. X's represent bird presence or absence at a site (n=94). The '■'s represent the proportion of presences in each interval, and the bars indicate the 95 % confidence interval.

Figure 15. The effect of the forest fragmentation index on the probability of presence of the Blue-gray Gnatcatcher. The degree of forest fragmentation increases from negative to positive. X's represent bird presence or absence at a site (n=94). The '■'s represent the proportion of presences in each interval, and the bars indicate the 95 % confidence interval.

Figure 16. The relationship between percent forest cover and species richness (Type III SS, multiple regression results: $R^2 = 0.25$, $F = 20.33$, $p \leq 0.0001$).

Appendix A: 24 bird species out of a pool of 78 species (Freemark and Collins 1989)

met criterion 1 - that their large scale range included the study region (see Fig. 1), and criterion 2 - they breed in forest interior and edge. A subset of 13 species met criterion 3 - present or absent in at least 10 % of the sites. Species meeting criteria 1-3 were used in the analysis of a species response to forest loss and fragmentation (13 species). All species meeting criteria 1 and 2 were used in the analysis of the response of the assemblage to habitat loss and fragmentation (24 species).

Species	Met Criteria 1 and 2	Met Criteria 1-3
Sharp-shinned Hawk <i>Accipiter striatus</i>	x	x
Red-shouldered Hawk <i>Buteo lineatus</i>	x	x
Ruffed Grouse <i>Bonasa umbellus</i>	x	x
Black-billed Cuckoo <i>Coccyzus erythrophthalmus</i>	x	x
Yellow-billed Cuckoo <i>Coccyzus americanus</i>	x	x
Yellow-bellied Sapsucker <i>Sphyrapicus varius</i>	x	x
Downy Woodpecker <i>Picoides pubescens</i>	x	x
Northern Flicker <i>Colaptes auratus</i>	x	x
Eastern Phoebe <i>Sayornis phoebe</i>	x	x
Blue-gray Gnatcatcher <i>Poliophtila caerulea</i>	x	x

Appendix A. (cont.)

Species	Met Criteria 1 and 2	Met Criteria 1-3
Yellow-throated Vireo <i>Vireo flavifrons</i>	x	x
Rufous-sided Towhee <i>Pipilo erythrophthalmus</i>	x	x
Purple Finch <i>Carpodacus purpureus</i>	x	x
Wild Turkey <i>Meleagris gallopavo</i>	x	
Red-bellied Woodpecker <i>Melanerpes carolinus</i>	x	
Eastern Wood-Pewee <i>Contopus virens</i>	x	
Great Crested Flycatcher <i>Myiarchus crinitus</i>	x	
Blue Jay <i>Cyanocitta cristata</i>	x	
Black-capped Chickadee <i>Parus atricapillus</i>	x	
Wood Thrush <i>Hylocichla mustelina</i>	x	
Gray Catbird <i>Dumetella carolinensis</i>	x	
Red-eyed Vireo <i>Vireo olivaceus</i>	x	
Common Yellowthroat <i>Geothlypis trichas</i>	x	
Rose-breasted Grosbeak <i>Pheucticus ludovicianus</i>	x	

Appendix B. Means, variances and frequency distributions for mean forest patch size, forest patch number, and total forest edge for landscapes sampled in 10 km X 10 km UTM squares.

Variable	Mean	Variance
Mean patch size (km ²)	0.281	0.059
Patch number	91.000	897.074
Total edge (km)	202.690	8080.780

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