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**RELATIONSHIP BETWEEN MINIMUM HABITAT
REQUIREMENTS AND ANNUAL REPRODUCTIVE RATES
IN FOREST BREEDING BIRDS**

By

Melissa D. Vance

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

Department of Biology

Carleton University

Ottawa, Ontario

January 2002

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Relationship between minimum habitat requirements and annual
reproductive rates in forest breeding birds

Submitted by
Melissa D. Vance

in partial fulfillment of the requirements
for the degree of Masters of Science

Chair, Department of Biology
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Carleton University

ABSTRACT

A major challenge facing conservation biologists and wildlife managers is to predict how fauna will respond to habitat loss. Different species require different amounts of habitat for population persistence, and species' reproductive rates have been identified as one of the major factors affecting these habitat requirements. The purpose of this study was to test the prediction that species with higher reproductive rates require less habitat for population persistence than species with lower reproductive rates. I used 41 species of forest breeding birds to test for a relationship between the annual reproductive output, and the amount of forest cover at which each species has a 50% probability of presence in the landscape. To look at the presence of species over landscapes with varying amounts of forest cover I combined two large-scale independent data sets: the North American Breeding Bird Survey and the United States Geological Survey (USGS) Land Use and Land Cover (LULC) digital data. Species presence/absence information was determined over a 10-year window for 779 circular landscapes that surround each Breeding Bird Survey route in the central and eastern USA region. Annual reproductive rates were obtained from the literature.

There was a significant negative (inter-species) relationship between the estimated minimum habitat amount at which there was a 50% probability of presence in the landscape, and annual reproductive output ($F = 7.71$; $p = 0.008$; d.f. = 1, 39; $R^2 = 0.16$). This is the first direct test for a negative relationship between minimum habitat requirements and annual reproductive rates. Conservation implications are discussed with respect to the concern over neotropical migrant bird species declines in much of eastern North America.

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INTRODUCTION

Loss of habitat due to anthropogenic activities is the single biggest threat to the survival of many species, and to global biodiversity in general (Groombridge 1992, Ehrlich 1995, Lande 1998, Sih et al. 2000). The negative effects of habitat loss occur across ecosystems, affecting many different types of organisms: amphibians in north central USA wetlands (Lehtinen et al. 1999), beetles in Amazonian forests (Didham et al. 1998), butterflies in Swedish meadows (Bergman and Landin 2001), and small mammals in Californian scrub habitats (Soulé et al. 1992). There is special concern about the effects of habitat loss on forest birds that breed in the eastern United States and Canada, and winter in the neotropics (Robbins 1979, Whitcomb et al. 1981, Lynch and Whigham 1984, Freemark and Merriam 1986, Askins et al. 1987, Blake and Karr 1987, Robbins et al. 1989a, Terborgh 1989, Askins et al. 1990, Robinson and Wilcove 1994, Martin and Finch 1995, Flather and Sauer 1996). Many of these neotropical migrant birds are currently experiencing regional population declines throughout eastern North America (Robbins et al. 1989c, Robinson and Wilcove 1994).

The unprecedented rates of habitat destruction, and subsequent threat to species survival is of major concern to conservation biologists who are struggling to understand the effects of habitat loss, and to predict the effects of future landscape changes. Thus in order to make conservation efforts more proactive we must be able to predict the minimum amount of habitat that is necessary for population survival (Nee 1994, Doncaster et al. 1996, Fahrig 2001). This requires understanding the traits that make some species more sensitive to habitat loss than others (Pimm et al. 1988, McKinney 1997, Purvis et al. 2000).

Patch scale

Minimum habitat requirements have often been measured at the patch scale (Robbins 1979, Hayden et al. 1985, Robbins et al. 1989a, Wenny et al. 1993, Bright et al. 1994). Galli et al. (1976) and Forman et al. (1976) considered the minimum habitat amount to be the minimum size habitat patch in which a particular species was found, while Hinsley et al. (1995) considered it to be the minimum patch size in which a species breeds. However it has been recognized that one simple occurrence or breeding event in a patch does not indicate that the patch contains sufficient habitat for long-term population persistence. Calculations of minimum area requirements must be based on the amount of habitat necessary for population persistence (Hayden et al. 1985, Wenny et al. 1993). Diamond (1975, 1978) recognized this when he developed incidence functions in which the proportion of occurrence of a species is plotted against area, for a range of patch sizes, in order to obtain a measure of a species' minimum area requirements. Diamond (1978) considered the patch size for which a species has a 50% incidence, to be a good measurement of the amount of habitat required for population viability. Hayden et al. (1985), on the other hand, estimated the habitat area requirement for population persistence to be the patch size for which a species has an occurrence rate of 100%. The problem with using an occurrence rate of 100%, is that many species never reach this maximum occurrence, even in very large patches (Robbins et al. 1989a). Robbins et al. (1989a) thought that a conservative estimate of the minimum area required by a species to ensure population viability was the patch size at which the species was present at 50% of its maximum occurrence.

Landscape scale

Recently it has become recognized that species respond not only to within-patch characteristics, but also to habitat at a landscape scale (Askins et al. 1987, Turner 1989, Freemark and Collins 1989, Andrén 1994, Hinsley et al. 1995, Opdam et al. 1995, Weins 1995). Thus, instead of looking solely at the patch size as a measure of habitat amount, researchers are looking at the amount of habitat in landscapes of constant size and comparing species abundance or incidence across these landscapes (Flather and Sauer 1996, Findlay and Houlihan 1997, Drolet and Desrochers 1999, Jansson and Angelstam 1999, Trzcinski et al. 1999, Villard et al. 1999, Pope et al. 2000). Robbins et al. (1989a) extended their patch scale study of minimum habitat requirements to include what they called "isolation effects". This was essentially a landscape-scale measure of the amount of forest cover within 2 km of each bird census. Although they calculated minimum habitat requirements at the patch scale for several bird species, they never attempted to measure the minimum habitat requirements directly at the landscape scale. Their analysis, however, demonstrates the importance of looking beyond the patch scale.

Factors affecting minimum area requirements

The proportion of suitable habitat in a landscape necessary to maintain viable populations is not constant across species (Kareiva and Wennergren 1995, Bascompte and Solé 1996, Doncaster et al. 1996, Gibbs 1998, With and King 1999, Fahrig 2001, Flather et al. in prep). Modelling studies suggest that it depends on landscape factors such as the quality of the matrix or non-habitat portion of the landscape (Fahrig 2001) and the pattern (fragmentation) of habitat destruction (Dytham 1995, With and King 1999, Fahrig 2001), as well as species characteristics such as reproductive rate (Lande

1987, With and King 1999, Fahrig 2001), dispersal ability (Lande 1987, Dytham 1995, Hanski et al. 1996, With and King 1999), and rate of emigration (Fahrig 2001).

Minimum habitat requirements are predicted to increase with decreasing matrix quality, increasing habitat fragmentation, decreasing reproductive rate, decreasing dispersal ability, and increasing rate of emigration. Using a simulation model, Fahrig (2001) studied the relative effects of four factors that are thought to influence the amount of habitat required for population persistence at a landscape scale. She found that reproductive rate had the largest effect on the amount of habitat required for population persistence, followed by the rate of emigration, matrix quality, and habitat pattern respectively (Fahrig 2001). The results of With and King's (1999) model also showed that reproductive capacity had the largest effect on the amount of habitat required for population persistence.

Purpose

The objective of this study was to test the prediction that organisms with higher reproductive rates require less habitat for population persistence than do those with lower reproductive rates. I used 41 species of forest breeding birds to test for a relationship between the annual reproductive output of the bird species, and the amount of forest in the landscape at which the species have a 50% probability of presence over a 10-year window.

METHODS

Overview

I used data from the North American Breeding Bird Survey (BBS) to estimate the “proportion presence” of each of 41 forest bird species over a 10-year window, in circular landscapes that surround each BBS route. Proportion presence was calculated as the number of years a species was present, divided by the number of years the route was run over a 10-year window. To calculate the percent forest cover (coniferous, deciduous, and mixed forest) of the 779 circular landscapes (radius = 19.7 km) located in the central and eastern USA region, I used the United States Geological Survey (USGS) Land Use and Land Cover (LULC) digital data (U.S. Department of the Interior 1987) which were interpreted from high-altitude aerial photography taken between 1969 and 1985. I selected the landscapes that were within each species' geographical range using digital range maps (WILDSPACE™ 2001), and conducted the analysis on this subset. For each species, I plotted the proportion presence against the percent forest cover, and used nonparametric regression curves to smooth the data. I then used these smoothed curves to estimate the minimum habitat amount at which the species has a 50% probability of presence in the landscapes.

To estimate the annual reproductive output for each species, I multiplied the average clutch size by the number of broods produced per reproductive season, using values obtained from the literature. Finally, I used regression analysis to test for the predicted negative relationship between the minimum habitat required for a 50% probability of presence, and annual reproductive output.

Bird presence

The North American Breeding Bird Survey is a large-scale annual survey of more than 4,000 roadside routes, that are randomly distributed within a degree block of latitude and longitude, throughout the United States and southern Canada. Initiated in 1966, the BBS is used to monitor the distribution and status of North American breeding birds. Each route is 39.4 km long, with a total of 50 3-minute point-counts conducted at 0.8-km intervals. At each stop the observer records all birds heard at any distance, and seen within a 0.4-km radius.

I used BBS data (USGS Patuxent Wildlife Research Centre 2001) to determine the presence/absence of each species over a 10-year window, commencing with the year of the aerial photo for each landscape. Taking the species presence over a 10-year period was a compromise between allowing enough time for a species to respond to the landscape structure, and minimizing the amount of landscape change over that time period. A study by the United States Department of Agriculture (USDA), that looked at broad scale habitat trends, determined there was less than a 1% increase in forested land within the study area over a 10-year period, between 1982 and 1992 (Flather et al. 1999). Although the photo-year for many of the landscapes in this study was prior to 1982, Flather et al. (1999) showed, at least at the regional level, very little change in forest cover over a 10-year time period.

I considered a species present during a year if it was recorded on at least one of the 50 stops that year, then calculated the proportion presence in each landscape by dividing the number of years the species was present by the number of years the route was run over the 10-year window. I excluded routes from the analysis if they were not surveyed at least eight times in the 10-year window.

The BBS has strict guidelines for the conditions under which the routes are run. In most areas the routes are surveyed in early to mid-June under good weather conditions (high visibility with little or no rain and wind), and commence 30 minutes before sunrise. I excluded from the analysis those routes that did not meet these BBS guidelines.

This study focused on birds that require forest for breeding. I selected both interior and interior/edge forest species, as classified by Freemark and Collins (1989), and used the Birds of North America series (Poole and Gill 1992-ongoing) to select additional species not classified by Freemark and Collins (1989). Villard (1998) pointed out the lack evidence for classifying species as either interior or interior/edge, but because I combined these two categories this was not a problem.

I used an additional filter when selecting species to include in the analysis that required that they respond positively to increasing forest amount. This effectively excluded any species that may have been classified incorrectly by Freemark and Collins (1989). I removed both the species that showed a negative relationship between proportion presence and the amount of habitat, and the species that showed no relationship. These species included: Common Yellowthroat (*Geothlypis trichas*), Gray Catbird (*Dumetella carolinensis*), Northern Cardinal (*Cardinalis cardinalis*), Yellow-billed Cuckoo (*Coccyzus americanus*), and Yellow-shafted Flicker (*Colaptes auratus*).

I included species in the analysis if a substantial portion of their breeding range falls within the central and eastern USA region. Six forest birds, Carolina Chickadee (*Parus carolinensis*), Yellow-throated Warbler (*Dendroica dominica*), Blackburnian Warbler (*Dendroica fusca*), Black-throated Green Warbler (*Dendroica virens*), Black-and-white Warbler (*Mniotilta varia*), and Worm-eating Warbler (*Helmitheros vermivorus*), were excluded early in the analysis because range maps were not available

for these species. Raptors, fowl-like birds, and nocturnal species were also excluded, as the surveys are conducted during daylight hours and primarily use sound to identify species. For this reason, these birds are not surveyed very effectively with the Breeding Bird Survey methods (Robbins et al. 1989b, Kirk and Hyslop 1998). In the end, I selected a total of 41 forest species (Appendix A).

Reproductive output

I estimated the annual reproductive output for each of the 41 species by multiplying clutch size by the number of broods produced in a season. Ehrlich et al. (1988) was the primary source for this life history information as it is the most complete and recent publication that combines data from many different sources, and thus is meant to encompass the species' entire geographical range. When data for a certain species was missing or uncertain, I supplemented this information first with the Birds of North America series (Poole and Gill 1992-ongoing), followed by Harrison (1978) and Peck and James (1987) respectively (Appendix B).

Clutch size can vary both geographically and between individuals. Therefore I used the most common clutch size for each species. When the most common clutch size was given as a range in the number of eggs produced, I chose the mid-point of that range. This occasionally resulted in the clutch size not being a whole number (e.g. 3.5 eggs).

The number of broods produced in a season is not as well known as the clutch size, as it requires researchers to follow individual birds throughout the reproductive season. Within the geographical range of a species there can also be considerable variation in the number of broods produced, because the length of the reproductive season is longer in the southern portion of a species' range than it is in the north. For this

reason it may be common for a species to be double-brooded in the southern part of its range, and single-brooded in the north. Because I wanted to obtain a value that encompassed the entire range of a species, I averaged the number of broods produced to obtain a reasonable value for each species over their entire geographical range. If a species is single-brooded in the north and double-brooded in the south, I took the number of broods produced per season to be 1.5.

Ehrlich et al. (1988) occasionally states the number of broods produced per reproductive season followed by a question mark. In these situations, I supplemented this information with a second reference as stated above. Appendix B details the decisions I made in determining the number of broods produced per season for each species, as well as the reference that was used for this information.

Landscape data

The study area comprises central and eastern USA, and contains a total of 779 landscapes (Figure 1). Each point in Figure 1 represents a circular landscape with a radius of 19.7 km (area = 1200 km²), which is equal to half the length of a BBS route. Each circular landscape was centred on the mid-point of a BBS route to ensure that the landscapes contained the entire route.

The United States Geological Survey (USGS) Land Use and Land Cover (LULC) digital data (U.S. Department of the Interior 1987) were used to characterize the landscape structure surrounding each BBS route. The LULC data were interpreted from high-altitude aerial photography taken between 1969 and 1985, and they characterize land cover types such as forest cover, to a resolution of 200 meters (U.S. Department of the Interior 1987).

Appendix C shows the Anderson Level I and II classification system used for the LULC data. For this analysis, I used the more general Anderson Level I data because of some obvious photo-interpretation differences among states at the Level II classification (Anderson et al. 1976, Fitzpatrick-Lins 1980). See Anderson et al. (1976) for further details about the classification system used for the USGS land cover data.

I quantified the percent forest cover (coniferous, deciduous and mixed forest) in each landscape using Fragstats 2.0 (McGarigal and Marks 1994).

Data analysis

I used digital range maps to subset the BBS routes to be used in the analysis for each bird species. This was done by overlaying the species' range map (WILDSPACE™ 2001) on the centre location of the BBS routes using ArcView 3.2. and selecting the routes that fell within a species' geographical range. If the range of a species extended over the entire study area, all 779 landscapes were used in the analysis.

After selecting the routes within a species' geographical range, I plotted the proportion of years the species was present in the 10-year window against the amount of forest in the landscape surrounding each route. I repeated this for each of the 41 forest bird species.

Because BBS data are very noisy, I used a non-linear nonparametric regression to smooth the data. Non-linear regression was used instead of linear regression because when using non-linear methods it is not necessary to choose a model a priori, and this allows the data themselves to estimate the best regression surface (Cleveland 1979, Cleveland and Devlin 1988). I used a locally-weighted regression or LOESS, to smooth the dependent variable in a moving window fashion by fitting a local regression that was

weighted by the distance of the data points within a specified neighbourhood from a point x on the independent axis. Points close to x are given a large weight, and points farther from x are given a smaller weight (Cleveland 1979, Cleveland and Devlin 1988). To fit the LOESS curves, I used the default parameters in SAS which fits a local linear regression, uses a normal weight function, and selects the alpha value (window width) that minimizes the generalized cross-validation (GCV) mean squared error (SAS Institute 1990). This method was chosen as it offers a good compromise between goodness-of-fit to the data and the smoothness of the LOESS curve.

I used the smoothed regression curves to estimate the minimum habitat required for each species to have a 50% probability of presence in the landscape. Fifty percent presence was chosen, as this was considered a tendency towards occupancy. Figure 2 demonstrates how the minimum habitat amount was estimated from the regression curves, for four hypothetical species representing the four kinds of curves I encountered. A 'normal' curve is represented by curve A, where the estimation of the minimum habitat amount at which there is a 50% probability of presence in the landscape is a straightforward extrapolation from the graph. Curve B represents a species that always has a higher than 50% presence, regardless of the amount of habitat in the landscape. In this situation, the minimum habitat amount at which there is a 50% probability of presence was taken to be 1%. Curve D represents the opposite situation, where the species never reaches a 50% presence. In this case the minimum habitat amount was taken to be 99%. Curve C represents the situation in which there is more than one habitat amount where the species has a 50% presence. In this situation, the minimum habitat amount was taken to be the lowest amount of habitat in which the species has a 50% probability of presence in the landscape.

Finally, I used linear regression analysis in SAS (SAS Institute 1990) to test for an inter-species relationship between the minimum habitat required for a 50% probability of presence in the landscape, and annual reproductive output.

RESULTS

Annual reproductive output

The clutch size and number of broods produced per year, as well as the estimated annual reproductive output for the 41 forest bird species are shown in Table 1. The average clutch size ranged between 2.5 and 7 eggs (mean $\pm$ SE = 4.30 ± 0.14 eggs/clutch), while the average number of broods produced per year ranged from 1 to 2.5 (mean $\pm$ SE = 1.34 ± 0.06 broods/year). When the above two values were multiplied, the result was an average annual reproductive output that ranged between 2.5 and 9 eggs (mean $\pm$ SE = 5.71 ± 0.28 eggs/year). The Black-billed cuckoo produces the fewest eggs with an annual average of 2.5 eggs, while the Eastern Phoebe, Tufted Titmouse, and Yellow-rumped Warbler produce the most eggs averaging nine per year.

Landscape data

There was considerable variation in the amount of forest among the 779 landscapes, with forest cover ranging between 0.00% and 96.88% (mean $\pm$ SE = $43.10\% \pm 0.99\%$). Appendix D shows the percent forest cover in each of the 779 circular landscapes (radius = 19.7 km).

Data analysis

The number of landscapes used in the analysis of each species ranged between 143 and 779, depending on the geographic range of the species (see Table 1).

The relationship between the proportion presence over the 10-year window and the percent forest cover in the landscape is shown in Appendix E for each of the 41 forest

bird species. The LOESS smoothed curves are shown superimposed on the original scatterplot, and the minimum habitat amount at which there is a 50% probability of presence in the landscape is shown by the vertical line. The estimated minimum habitat amount required for a 50% probability of presence in the landscape is shown in Table 1 for each of the 41 species.

A simple linear regression indicated there was a significant negative (inter-species) relationship between the estimated minimum habitat amount at which there was a 50% probability of presence in the landscape, and annual reproductive output ($F = 7.71$; $p = 0.008$; d.f. = 1, 39; $R^2 = 0.16$) (Figure 3). This relationship was not driven by extreme data points or by the designation of 1% minimum habitat amount for those species that are always present in 50% of the years regardless of the amount of habitat in the landscape, and the designation of 99% minimum habitat amount for those species that are never present in 50% of the years. In fact the relationship was stronger when I removed these species from the analysis ($F = 8.79$; $p = 0.006$; d.f. = 1, 26; $R^2 = 0.25$).

DISCUSSION

This is the first empirical study that directly shows an inter-species relationship between minimum habitat requirements and annual reproductive output. The result is in agreement with the predictions from the modelling studies of Fahrig (2001) and With and King (1999): those species that have a lower reproductive output require more habitat than those species that have a higher reproductive output.

Within the field of ecology and conservation biology it has long been assumed that species with low reproductive rates require more habitat, and thus are more prone to extinction, than species with high reproductive rates. However there have been no direct empirical tests, and few indirect ones. Smith and Quin (1996) found that geographical range reductions of conilurine rodent species, which are undergoing high rates of extinction and decline in Australia, were less severe for those species that have higher annual reproductive rates. Diamond (1975) found that those species capable of surviving on smaller and more remote islands had longer breeding seasons and were capable of raising more broods per year than those species not found on these islands. In addition to these two studies, several anecdotal comparisons have been made between species with vast differences in reproductive abilities, such as comparing habitat requirements for large and small mammals (Peters 1983, Calder 1984). This study is unique because the cross-species comparison was limited to forest birds with comparatively similar body sizes, and where the variation in annual reproductive rate was relatively small. There was no significant relationship between either body size and annual reproductive rate ($F = 0.30$; $p = 0.59$; d.f. = 1, 39; $R^2 = 0.008$), or body size and the minimum habitat required for a 50% probability of presence in the landscape ($F = 0.06$; $p = 0.81$; d.f. = 1, 39; $R^2 =$

0.001). This makes the significant negative relationship between annual reproductive output and the minimum habitat required for a 50% probability of presence a particularly powerful test of the hypothesis.

The relationship between annual reproductive output and the minimum habitat required for a 50% probability of presence in the landscape is not a spurious one that is due to an underlying latitudinal trend in habitat amount. There is no significant relationship between percent forest cover and latitude ($F = 0.26$; $p = 0.61$; d.f. = 1, 777; $R^2 = 0.0003$).

Intuitively it has long been understood that smaller populations have a higher risk of extinction due to demographic stochasticity (Goodman 1987, Pimm et al. 1988, Raup 1991, Boyce 1992). It is also intuitive that landscapes with less habitat support smaller populations than landscapes with more habitat. Species with a higher reproductive potential are better able to survive in landscapes with less habitat because they can recover more quickly from low population numbers caused by environmental disturbance, disease, or predation. Species with a lower reproductive potential remain at low population levels longer, thus increasing their risk of extinction. An additional advantage for species with a higher reproductive output is that they produce more dispersers that are then able to colonize other areas in the landscape.

Modelling studies predict the existence of species-specific habitat extinction thresholds for population persistence, whereby a small reduction of habitat at the threshold results in a sharp drop in the probability of persistence (Lande 1987, Bascompte and Solé 1996, Pagel and Payne 1996, Bevers and Flather 1999, Hill and Caswell 1999, With and King 1999, Fahrig 2001). In this study I was unable to consistently locate the

extinction threshold for my species. Flather et al. (in prep.) illustrate the effect of immigration on species extinction thresholds. While landscapes in modelling studies are closed to immigration, in reality landscapes are open. Immigration into the landscapes serves to dampen the thresholds, thus making them very difficult to detect empirically (Flather et al. in prep.). To avoid the subjectivity of locating the habitat extinction thresholds for my species, I calculated the amount of habitat required for a 50% probability of presence in the landscape. I stress that the minimum habitat requirements measured in this study are not absolute minimum habitat requirements, but rather relative requirements that allowed a cross-species comparison.

The relationship between minimum habitat requirements and annual reproductive output found here (Figure 3) is particularly significant because the estimates of habitat and reproductive output contained many sources of error. First, the estimated annual reproductive rate was averaged to encompass a species' entire range, yet for some species there is considerable geographic variation within the study area in terms of the number of eggs produced per year (Ricklefs 1973). This is especially true for species that are single-brooded in the northern part of their range, and double-brooded in the southern part of their range (Ehrlich et al. 1988). Second, "habitat" was measured as any forest (coniferous, deciduous, and mixed forest), which was a very coarse measure of the true amount of breeding habitat for each species. Species have different microhabitat requirements, and thus the true amount of breeding habitat within each landscape may be overestimated for some species. For example, the Prothonotary Warbler, Louisiana Waterthrush, and Northern Waterthrush build their nests near standing or running water, while woodpeckers and other cavity nesting species require standing dead trees for

breeding and thus early seral stage forest (which would have few, if any, standing dead trees) is not actually breeding habitat for them (Poole and Gill 1992-ongoing).

Differences in species detectability may also have been a source of extraneous variation in my study (Boulinier et al. 1998), although I minimized this problem by excluding species that are known to be sampled poorly by the BBS (e.g. nocturnal species, raptors).

The methodology of the Breeding Bird Survey itself is another potential source of unexplained variation. Because the BBS is a roadside survey there is a potential for bias in the types of habitats found next to roads (Bart et al. 1995, Keller and Scallan 1999). In their study in Maryland and Ohio, Keller and Scallan (1999) found that forest was underrepresented in the habitat along roads. This may have resulted in an underestimation of the true proportion presence in the landscape over the 10-year window. However, as all the species in this study are forest birds, this bias should have been consistent across species. Another criticism with the reliability of BBS data, is differences in observer quality (Sauer et al. 1994, Kendall et al. 1996). BBS observers differ in their ability to count birds, and thus there may be differences between observers in the estimation of species abundance (Sauer et al. 1994, Kendall et al. 1996). These differences in observer quality should be minimized in this study because I used only presence/absence data, not abundance, for each route. Despite the inherent biases with BBS data, it remains a very valuable source of information for the status of North American birds at a continental scale.

Conservation implications

A major challenge facing conservation biologists and wildlife managers is to predict how fauna will respond to habitat loss. Different species require different

amounts of habitat for population persistence, and it is imperative that we identify the factors that affect these habitat requirements. This study shows a clear negative relationship between a forest bird species' reproductive rate and the amount of habitat required for a certain probability of presence in the landscape. This result gives empirical evidence to the long-held belief that species with low reproductive potential are more prone to extinction due to habitat loss than species with high reproductive potential.

Neotropical migrants have received special attention with respect to the effects of forest loss and fragmentation on species survival (Robbins 1979, Whitcomb et al. 1981, Lynch and Whigham 1984, Freemark and Merriam 1986, Askins et al. 1987, Blake and Karr 1987, Freemark and Collins 1989, Robbins et al. 1989a, 1989c, Terborgh 1989, Robinson and Wilcove 1994, Flather and Sauer 1996). These species have a relatively short breeding season compared to short-distance migrants and resident species, and this often precludes them from raising multiple broods per season (Whitcomb et al. 1981, Robbins et al. 1989c). This makes neotropical migrants more vulnerable to the effects of predation and nest parasitism which have been shown to increase with habitat loss and fragmentation in the central and eastern USA region (Brittingham and Temple 1983, Wilcove 1985, Donovan et al. 1995, Robinson et al. 1995). Until landscape-scale minimum habitat requirements needed to maintain viable populations can be measured empirically, it will be necessary to maintain large tracts of forest throughout the breeding range to ensure population survival of all species.

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Table 1. Clutch size, number of broods, annual reproductive output, minimum habitat required for a 50% probability of presence, and the number of landscapes used in the analysis for each of 41 forest breeding birds. Details of how the annual reproductive output was calculated are given in the methods section, as well as Appendix B. Minimum habitat amounts (% forest) were estimated from the graphs in Appendix E.

Species	Clutch Size ^a	Number of Broods	Reproductive Output (Clutch Size X No. Broods)	Minimum Habitat Amount	Number of Landscapes
Black-billed Cuckoo	2.5	1 ^c	2.5	99	669
Red-bellied Woodpecker	4.5	1.75 ^a	7.9	3	611
Yellow-bellied Sapsucker	5.5	1 ^a	5.5	89	230
Downy Woodpecker	4.5	1 ^{a,c}	4.5	1	779
Hairy Woodpecker	4	1 ^a	4	95	779
Pileated Woodpecker	4	1 ^a	4	73.5	710
Olive-sided Flycatcher	3	1 ^b	3	99	230
Eastern Wood-Pewee	3	1 ^a	3	1	774
Acadian Flycatcher	3	2 ^a	6	53	625
Eastern Phoebe	4.5	2 ^a	9	15	732
Great Crested Flycatcher	5	1 ^a	5	1	779
Blue Jay	4.5	1.75 ^a	7.9	1	779
Black-capped Chickadee	7	1 ^{a,b}	7	5.5	429
Tufted Titmouse	6	1.5 ^a	9	1	678
White-breasted Nuthatch	6.5	1 ^{a,b}	6.5	58	767
Brown Creeper	5.5	1 ^d	5.5	99	272
Blue-gray Gnatcatcher	4.5	1.5 ^a	6.75	47.5	715
Veery	4	1.5 ^{a,b}	6	26.5	313
Hermit Thrush	4	2 ^{a,b}	8	74.5	208
Wood Thrush	3.5	2 ^a	7	10	743
White-eyed Vireo	4	1.5 ^a	6	20	556
Yellow-throated Vireo	4	1 ^b	4	74	736
Red-eyed Vireo	4	1.5 ^c	6	9	779
Blue-headed Vireo	4	1.5 ^a	6	82.5	428
Northern Parula	4.5	1.5 ^b	6.75	99	523
Black-throated Blue Warbler	4	1.5 ^b	6	90.5	160
Yellow-rumped Warbler	4.5	2 ^a	9	68	143
Pine Warbler	4	1 ^b	4	77.5	479
Cerulean Warbler	4	1 ^b	4	99	500
American Redstart	4	1 ^b	4	62.5	693
Ovenbird	4.5	1.5 ^a	6.75	38	657
Northern Waterthrush	4.5	1 ^b	4.5	99	244
Louisiana Waterthrush	5	1 ^b	5	99	616
Kentucky Warbler	4.5	1 ^b	4.5	66.5	464
Prothonotary Warbler	5	1.5 ^a	7.5	99	628
Hooded Warbler	3.5	1 ^a	3.5	78.5	477

Table 1 continued...

Species	Clutch Size ^a	Number of Broods	Reproductive Output (Clutch Size X No. Broods)	Minimum Habitat Amount	Number of Landscapes
Canada Warbler	4	1 ^b	4	92.5	351
Summer Tanager	4	1.5 ^b	6	19	377
Scarlet Tanager	4	1 ^a	4	26.5	645
Rose-breasted Grosbeak	4	1.5 ^a	6	2.5	523
Eastern Towhee	3.5	2.5 ^a	8.75	8	723

^a Ehrlich et al. 1988^b Poole and Gill 1992- ongoing^c Harrison 1978^d Peck and James 1987

Figure 1. Study area in central and eastern USA, showing the location of the 779 circular landscapes. Each landscape has a radius of 19.7 km and is centred on a Breeding Bird Survey route, so that the landscape contains the entire route. The location of the Breeding Bird Survey route within each landscape is shown in gray. Black areas represent forest, and white areas include all other habitat types.

Figure 2. Nonparametric regression curves for four hypothetical species, from which I estimated the minimum habitat (forest) amount at which there was a 50% probability of presence in the landscape over a 10-year window. Curve A: A 'normal' graph of proportion presence versus percent forest cover. Minimum habitat amount was estimated to be 9%. Curve B: The presence over the 10-year window never dropped to 50%, and thus the minimum habitat amount was taken to be 1%. Curve C: 50% presence in the landscape occurs at more than one habitat amount. I took the minimum habitat to be the lowest amount of habitat at which the species was present in 50% of the years (18.5%). Curve D: The presence never reached 50%, and therefore the minimum habitat amount was estimated at 99%.

Figure 3. Relationship between the minimum habitat required for a 50% probability of presence in the landscape, and the annual reproductive output of forest breeding birds ($n=41$). The hollow dots represent both the common species and the rare species for which minimum habitat requirements were estimated to be 1% and 99% respectively (see Figure 2).

Appendix A. Common names, scientific names, and AOU codes for the 41 forest bird species used in the present analysis.

Common Name	Scientific Name	AOU Code
Black-billed Cuckoo	<i>Coccyzus erythrophthalmus</i>	BBCU
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	RBWO
Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>	YBSA
Downy Woodpecker	<i>Picoides pubescens</i>	DOWO
Hairy Woodpecker	<i>Picoides villosus</i>	HAWO
Pileated Woodpecker	<i>Dryocopus pileatus</i>	PIWO
Olive-sided Flycatcher	<i>Contopus borealis</i>	OSFL
Eastern Wood-Pewee	<i>Contopus virens</i>	EAWP
Acadian Flycatcher	<i>Empidonax virescens</i>	ACFL
Eastern Phoebe	<i>Sayornis phoebe</i>	EAPH
Great Crested Flycatcher	<i>Myiarchus crinitus</i>	GCFL
Blue Jay	<i>Cyanocitta cristata</i>	BLJA
Black-capped Chickadee	<i>Parus atricapillus</i>	BCCH
Tufted Titmouse	<i>Parus bicolor</i>	TUTI
White-breasted Nuthatch	<i>Sitta carolinensis</i>	WBNU
Brown Creeper	<i>Certhia americana</i>	BRCR
Blue-gray Gnatcatcher	<i>Polioptila caerulea</i>	BGGN
Veery	<i>Catharus fuscescens</i>	VEER
Hermit Thrush	<i>Catharus guttatus</i>	HETH
Wood Thrush	<i>Hylocichla mustelina</i>	WOTH
White-eyed Vireo	<i>Vireo griseus</i>	WEVI
Yellow-throated Vireo	<i>Vireo flavifrons</i>	YTVI
Red-eyed Vireo	<i>Vireo olivaceus</i>	REVI
Blue-headed Vireo	<i>Vireo solitarius</i>	BHVI
Northern Parula	<i>Parula americana</i>	NOPA
Black-throated Blue Warbler	<i>Dendroica caerulescens</i>	BTBW
Yellow-rumped Warbler	<i>Dendroica coronata</i>	YRWA
Pine Warbler	<i>Dendroica pinus</i>	PIWA
Cerulean Warbler	<i>Dendroica cerulea</i>	CERW
American Redstart	<i>Setophaga ruticilla</i>	AMRE
Ovenbird	<i>Seiurus aurocapillus</i>	OVEN
Northern Waterthrush	<i>Seiurus noveboracensis</i>	NOWA
Louisiana Waterthrush	<i>Seiurus motacilla</i>	LOWA
Kentucky Warbler	<i>Oporornis formosus</i>	KEWA
Prothonotary Warbler	<i>Protonotaria citrea</i>	PROW
Hooded Warbler	<i>Wilsonia citrina</i>	HOWA
Canada Warbler	<i>Wilsonia canadensis</i>	CAWA
Summer Tanager	<i>Piranga rubra</i>	SUTA
Scarlet Tanager	<i>Piranga olivacea</i>	SCTA
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	RBGR
Eastern Towhee	<i>Pipilo erythrophthalmus</i>	EATO

Appendix B. A list of the decisions I made when calculating the number of broods produced per reproductive season for each species. The original quotes from the references are given, as well as the interpretation of those quotes. When the primary source (Ehrlich et al. 1988) was uncertain (shown by a question mark) about the number of broods produced, I consulted a second source.

Species	Quote	Interpretation
Black-billed Cuckoo	? ^a //1 brood ^c	1 brood
Red-bellied Woodpecker	1 brood in north, 2-3 in south ^a	1.75 broods
Yellow-bellied Sapsucker	1 brood ^a	1 brood
Downy Woodpecker	1 brood in north, 2? in south ^a //1 brood ^c	1 brood
Hairy Woodpecker	1 brood ^a	1 brood
Pileated Woodpecker	1 brood ^a	1 brood
Olive-sided Flycatcher	? ^a //1 brood ^b	1 brood
Eastern Wood-Pewee	1 brood ^a	1 brood
Acadian Flycatcher	2 broods ^a	2 broods
Eastern Phoebe	2 broods ^a	2 broods
Great Crested Flycatcher	Usually 1 brood ^a	1 brood
Blue Jay	1 brood in north, 2-3 in south ^a	1.75 broods
Black-capped Chickadee	1? brood ^a //Usually 1 brood, 2 rare ^b	1 brood
Tufted Titmouse	1 brood, 2 in south ^a	1.5 broods
White-breasted Nuthatch	1? brood ^a //No 2 nd broods observed ^b	1 brood
Brown Creeper	? ^a //1 brood ^d	1 brood
Blue-gray Gnatcatcher	1 brood, 2 in far south ^a	1.5 broods
Veery	1 brood, 2? in south ^a //1 brood, some suggestion of 2 ^b	1.5 broods
Hermit Thrush	2 broods 3? in south ^a //sometimes 2 broods ^b	2 broods
Wood Thrush	Often 2 broods ^a	2 broods
White-eyed Vireo	1 brood in north, 2 in south ^a	1.5 broods
Yellow-throated Vireo	? ^a //1 brood, 2 is rare if at all ^b	1 brood
Red-eyed Vireo	? ^a // Occasionally 2 broods ^c	1.5 broods
Blue-headed Vireo	Occasionally 2 broods ^a	1.5 broods
Northern Parula	? ^a //2 broods reported in south ^b	1.5 broods
Black-throated Blue Warbler	? ^a //1 brood, occasionally 2 ^b	1.5 broods
Yellow-rumped Warbler	Often 2 broods ^a	2 broods
Pine Warbler	? ^a // No direct evidence of 2 nd brood ^b	1 brood
Cerulean Warbler	? ^a //Usually 1 brood ^b	1 brood
American Redstart	? ^a //1 brood ^b	1 brood
Ovenbird	Occasionally 2 broods ^a	1.5 broods
Northern Waterthrush	? ^a //No indication of 2 nd brood ^b	1 brood
Louisiana Waterthrush	? ^a //1 brood ^b	1 brood
Kentucky Warbler	? ^a //1 brood, 2 rare ^b	1 brood
Prothonotary Warbler	1 brood in north, 2 in south ^a	1.5 broods
Hooded Warbler	Usually 1 brood ^a	1 brood

Appendix B continued...

Species	Quote	Interpretation
Canada Warbler	? ^a //1 brood ^b	1 brood
Summer Tanager	? ^a //Unknown proportion lay 2 broods ^b	1.5 broods
Scarlet Tanager	1 brood ^a	1 brood
Rose-breasted Grosbeak	1 or 2 broods ^a	1.5 broods
Eastern Towhee	2 broods, occasionally 3 in south ^a	2.5 broods

^a Ehrlich et al. 1988

^b Poole and Gill 1992- ongoing

^c Harrison 1978

^d Peck and James 1987

Appendix C. The United States Geological Survey Land Use and Land Cover classification system.

Anderson Level I	Anderson Level II
1 Urban or Built-up Land	11 Residential 12 Commercial and Services 13 Industrial 14 Transportation, Communications, and Utilities 15 Industrial and Commercial Complexes 16 Mixed Urban or Built-up Land 17 Other Urban or Built-up Land
2 Agricultural Land	21 Cropland and Pasture 22 Orchards, Groves, Vineyards, Nurseries, and Ornamental Horticultural Areas 23 Confined Feeding Operations 24 Other Agricultural Land
3 Rangeland	31 Herbaceous Rangeland 32 Shrub and Brush Rangeland 33 Mixed Rangeland
4 Forest Land	41 Deciduous Forest Land 42 Evergreen Forest Land 43 Mixed Forest Land
5 Water	51 Streams and Canals 52 Lakes 53 Reservoirs 54 Bays and Estuaries
5 Wetland	61 Forested Wetland 62 Nonforested Wetland
7 Barren Land	71 Dry Salt Flats 72 Beaches 73 Sandy Areas other than Beaches 74 Bare Exposed Rock 75 Strip Mines, Quarries, and Gravel Pits 76 Transitional Areas 77 Mixed Barren Land

Appendix C continued...

Anderson Level I	Anderson Level II
8 Tundra	81 Shrub and Brush Tundra
	82 Herbaceous Tundra
	83 Bare Ground Tundra
	84 Wet Tundra
	85 Mixed Tundra
9 Perennial Snow or Ice	91 Perennial Snowfields
	92 Glaciers

Appendix D. Total amount of forest (%) in each of the 779 circular landscapes (radius = 19.7 km) in the central and eastern USA region. Each landscape corresponds to a North American Breeding Bird Survey route, and is identified by both a state code and a route number. The location of each BBS route can be found on the BBS website (USGS Patuxent Wildlife Research Center 2001).

State	Route No.	% Forest Cover	State	Route No.	% Forest Cover
IA	33	0.00	IA	6	2.32
IL	15	0.10	OH	13	2.39
KS	28	0.15	IL	2	2.42
IL	34	0.26	OH	32	2.45
IL	31	0.27	WI	63	2.54
IN	14	0.33	IN	11	2.66
NE	3	0.33	IL	11	2.69
OH	7	0.36	IA	30	2.72
KS	14	0.46	OH	6	2.98
TX	77	0.46	IL	6	3.01
IN	15	0.49	NE	12	3.06
IL	12	0.53	IL	16	3.12
IA	5	0.54	WI	70	3.36
KS	15	0.73	WI	46	3.44
IL	32	0.83	KS	2	3.46
TX	76	0.85	NE	13	3.48
IN	20	0.88	FL	22	3.49
IA	4	0.96	OH	65	3.55
OH	8	1.06	IN	8	3.57
OH	27	1.06	MO	30	3.59
IL	47	1.07	IA	20	3.73
IN	10	1.09	IL	40	3.76
IA	16	1.14	AR	17	3.82
IL	29	1.29	FL	30	3.93
IN	17	1.29	FL	16	4.03
TX	67	1.35	FL	27	4.24
WI	66	1.37	IL	43	4.24
KS	29	1.38	IL	4	4.46
NE	2	1.46	IL	24	4.55
IA	9	1.47	IN	7	4.75
FL	24	1.49	KY	2	4.88
IN	16	1.49	IL	7	5.02
IL	30	1.54	NE	1	5.11
OH	33	1.60	IL	18	5.13
IA	34	1.70	KS	1	5.13
NE	24	1.73	IA	10	5.20
IA	21	1.85	OH	34	5.24
IA	27	1.89	FL	20	5.41
MO	32	2.28	IL	8	5.51

Appendix D continued...

State	Route No.	% Forest Cover	State	Route No.	% Forest Cover
IL	17	5.65	IL	3	8.56
WI	67	5.67	PA	84	8.57
IL	28	5.74	KY	23	8.59
AR	2	5.75	IL	38	8.69
IA	8	5.77	MI	22	8.73
MO	24	5.83	MI	58	8.86
NY	65	5.97	IL	1	8.98
KS	13	6.04	WI	58	9.01
IA	7	6.06	IN	9	9.06
OH	61	6.06	KY	12	9.16
WI	9	6.08	MO	16	9.16
WI	62	6.21	MD	36	9.23
MI	54	6.40	FL	26	9.28
MI	72	6.42	TX	64	9.32
IL	58	6.45	IL	36	9.99
IA	28	6.50	KS	27	10.15
MI	73	6.56	MD	9	10.26
OK	23	6.60	IL	19	10.33
MN	8	6.70	IL	54	10.52
FL	23	6.73	WI	47	10.61
OH	41	6.84	OK	24	11.01
IN	12	6.86	WI	69	11.01
IL	45	6.91	MI	20	11.10
IN	19	7.02	MI	51	11.15
IL	10	7.10	MI	35	11.16
IN	13	7.29	IL	37	11.18
MI	66	7.36	IN	29	11.25
IL	26	7.37	MO	1	11.27
MN	41	7.51	TN	12	11.29
IL	5	7.52	IL	22	11.32
OH	60	7.65	WI	56	11.35
MN	15	7.80	FL	39	11.43
TX	66	7.80	NY	66	11.54
IA	29	7.84	IL	9	11.67
IL	23	7.88	MI	49	11.91
MI	56	7.89	MO	29	11.91
IL	20	8.00	IL	25	12.20
MN	50	8.12	PA	75	12.28
KS	26	8.38	MO	27	12.43
IA	17	8.39	TX	62	12.45
KS	105	8.44	IL	64	12.62
IN	3	8.47	AR	16	12.77
IN	2	8.52	MN	2	12.83

Appendix D continued...

State	Route No.	% Forest Cover	State	Route No.	% Forest Cover
MI	36	13.12	VA	46	18.76
TX	65	13.32	NY	54	18.85
MD	6	13.33	KY	26	19.00
TN	11	13.38	PA	78	19.06
MD	37	13.56	MD	15	19.11
WI	64	13.60	NY	40	19.11
MI	39	13.62	IN	21	19.38
NY	67	13.75	IA	2	19.44
OH	57	13.89	TN	1	19.46
TN	2	14.27	NJ	10	19.51
MO	7	14.38	IN	22	19.52
IL	53	14.51	KY	44	19.75
OH	59	14.99	AR	10	19.80
MN	27	15.27	KY	38	19.85
KY	40	15.48	WI	10	19.87
MO	22	15.48	MD	40	20.64
IL	46	15.54	MD	23	20.65
AR	18	15.74	VA	48	20.94
IL	48	15.74	TN	4	21.21
MN	49	15.75	DE	3	21.38
OH	21	15.89	AR	8	21.50
IL	59	15.95	MD	17	21.54
IN	42	15.96	MD	10	21.70
MD	14	16.11	MD	11	21.72
KY	6	16.14	MD	12	21.72
AR	25	16.34	MD	35	21.78
TN	5	16.46	MD	13	22.05
MD	43	16.56	WV	51	22.39
IA	3	16.59	TN	20	22.66
OH	16	16.79	MD	19	22.79
WI	31	16.91	MD	21	23.00
IL	50	16.98	NY	2	23.02
AL	40	17.04	OH	18	23.27
NJ	2	17.19	PA	4	23.34
DE	1	17.32	OK	5	23.47
IN	33	17.37	MN	7	23.57
PA	96	17.69	VA	2	23.57
KY	3	17.71	MO	28	23.84
WI	39	17.83	KY	32	23.99
KY	7	18.04	WI	36	24.36
MI	32	18.23	NY	47	24.57
NJ	12	18.54	MD	42	24.64
PA	93	18.76	IL	60	24.90

Appendix D continued...

State	Route No.	% Forest Cover	State	Route No.	% Forest Cover
MD	34	24.95	AL	9	31.04
OH	43	24.98	WI	54	31.08
OK	16	25.07	GA	25	31.21
IL	63	25.28	TN	22	31.27
LA	1	25.35	TN	41	31.50
MS	4	25.37	OK	17	31.62
MD	16	25.47	OK	14	31.84
KY	137	25.64	GA	10	31.96
NJ	20	25.66	PA	36	32.30
IL	61	25.67	MD	7	32.43
WI	40	25.91	WI	44	32.44
GA	54	26.68	NY	53	32.51
PA	95	26.86	AR	29	32.60
OK	7	26.89	PA	70	32.67
MD	41	27.02	MO	19	32.70
MD	33	27.03	NY	1	32.70
MO	34	27.22	TN	24	32.75
MO	14	27.30	PA	76	32.89
AR	19	27.31	KY	30	32.98
DE	4	27.35	MD	48	33.03
NY	55	27.47	WI	53	33.06
WI	18	27.74	MD	44	33.23
MD	24	28.10	IL	39	33.47
MD	20	28.35	KY	25	33.56
TN	8	28.38	MD	27	33.96
PA	87	29.14	MD	22	34.03
WI	45	29.17	MD	39	34.29
WI	57	29.21	NC	6	34.36
MD	32	29.24	MO	23	34.46
WI	12	29.45	TN	21	34.60
PA	81	29.54	MI	37	34.68
WI	14	29.65	MA	1	34.79
AL	2	29.69	MD	8	34.88
NY	58	29.75	MS	11	35.16
MD	18	29.89	TN	19	35.31
OH	17	29.93	WI	55	35.32
PA	1	30.27	MO	21	35.34
MD	38	30.36	AR	24	35.51
NY	70	30.44	TN	40	35.56
MI	21	30.46	WI	38	35.64
AL	6	30.58	NY	96	35.74
OH	81	30.94	NY	95	35.83
NY	91	30.95	OK	26	35.90

Appendix D continued...

State	Route No.	% Forest Cover	State	Route No.	% Forest Cover
MN	28	35.91	GA	33	42.71
NC	13	35.99	MO	13	42.87
MI	42	36.00	MD	46	42.92
NC	2	36.12	KY	4	42.93
TN	33	36.87	NJ	13	42.98
GA	28	36.91	GA	7	43.05
WI	43	37.31	PA	38	43.24
TN	37	37.49	MD	45	43.29
VA	29	37.67	TN	38	43.36
GA	34	37.72	KY	24	43.74
MS	12	37.83	TX	59	43.92
NC	10	38.05	NY	63	44.20
WI	42	38.28	GA	56	44.28
PA	46	38.73	FL	9	44.32
AL	31	38.81	GA	14	44.38
KY	39	38.87	KY	41	44.42
MD	26	39.07	KY	21	44.48
TN	17	39.31	WI	11	44.69
OK	125	39.35	NY	52	44.70
TN	3	39.48	TX	58	44.77
WI	51	39.68	NC	9	44.91
SC	10	39.72	MD	47	45.02
MN	23	40.05	WI	41	45.03
TN	23	40.11	SC	4	45.05
CT	10	40.15	NY	74	45.10
AR	6	40.20	TN	26	45.12
NY	69	40.31	MN	22	45.16
MO	5	40.50	NY	10	45.30
DE	6	40.55	NJ	5	45.31
MN	31	41.15	OH	49	45.41
CT	6	41.55	MI	41	45.45
AL	26	41.61	VA	4	45.54
NC	16	41.67	NY	11	45.57
WI	50	41.77	WI	34	45.63
AL	1	42.03	DE	7	45.72
OK	3	42.04	WI	32	45.80
NJ	11	42.05	KY	27	45.82
NY	61	42.05	MD	25	45.86
IN	36	42.08	MN	1	46.01
IN	40	42.33	SC	6	46.29
OH	51	42.36	TN	27	46.42
NY	57	42.53	MD	30	46.44
PA	47	42.60	NY	15	46.73

Appendix D continued...

State	Route No.	% Forest Cover	State	Route No.	% Forest Cover
FL	15	46.78	MD	28	53.39
IN	26	47.03	TN	6	53.49
ME	5	47.23	NC	23	53.63
NY	8	47.28	MN	26	53.72
NY	6	47.35	ME	1	53.93
WI	17	47.44	WI	52	53.93
MD	29	47.47	NJ	19	54.12
GA	17	47.64	VA	42	54.17
MI	16	47.64	OH	56	54.28
MD	31	47.72	AL	8	54.36
KY	34	47.73	NY	59	54.37
VA	30	48.42	MI	31	54.50
SC	9	48.52	FL	11	54.57
IL	62	48.71	MN	36	54.57
NY	12	48.80	AR	7	54.65
TN	36	49.17	TN	9	54.89
NY	26	49.23	PA	88	55.35
NY	16	49.31	MO	6	55.73
AL	5	49.44	TN	10	55.74
VT	21	49.48	OH	86	55.86
AL	22	49.50	MO	20	55.93
FL	18	49.58	OK	11	56.18
PA	35	50.37	AL	24	56.40
OH	73	50.38	WI	5	56.61
TN	25	50.46	VA	6	56.89
WI	19	50.55	GA	22	57.03
CT	15	51.04	MO	4	57.17
TN	14	51.05	TN	15	57.21
WI	24	51.24	MN	25	57.40
NC	25	51.36	NY	38	57.42
GA	44	51.38	VA	41	57.55
AR	22	51.42	FL	6	57.57
PA	83	51.51	PA	54	57.87
AR	4	51.75	TX	45	58.13
MN	37	51.85	TN	13	58.16
GA	24	52.15	MA	6	58.21
MA	7	52.40	PA	49	58.29
WI	35	52.65	NY	43	58.31
FL	38	52.71	NJ	14	58.36
FL	14	52.84	NY	9	58.42
MS	8	53.02	NY	30	58.47
TN	7	53.12	TN	16	58.50
NY	41	53.23	GA	6	58.53

Appendix D continued...

State	Route No.	% Forest Cover	State	Route No.	% Forest Cover
OH	82	58.84	NY	13	64.76
MO	2	59.12	AR	26	64.83
CT	11	59.34	MA	16	64.88
CT	13	59.39	AL	27	64.96
NC	12	59.40	WI	16	64.96
IN	39	59.43	WI	25	65.16
VA	7	59.56	PA	85	65.19
NY	72	59.60	NY	36	65.21
FL	21	59.72	PA	11	65.45
VA	24	60.09	PA	90	65.49
AL	44	60.15	ME	22	65.56
SC	8	60.20	WI	23	65.85
CT	2	60.34	MN	38	65.88
CT	16	60.39	NY	46	65.89
FL	10	60.46	RI	4	66.02
MS	18	60.60	MA	3	66.09
MS	21	60.61	MA	14	66.14
NH	4	60.74	MO	3	66.20
AR	21	61.20	CT	8	66.27
MI	17	61.30	NY	17	66.35
AL	37	61.36	VA	22	66.40
MA	13	61.36	MO	18	66.58
NY	123	61.50	WI	20	66.63
WI	21	61.62	SC	18	66.73
AL	32	61.69	PA	67	66.76
MI	18	61.73	FL	37	66.81
MI	48	62.11	AR	5	66.86
ME	28	62.48	OK	2	66.86
NH	2	62.48	WV	40	66.90
MA	22	62.55	VT	2	66.93
NY	31	63.12	WI	6	67.42
OH	76	63.14	ME	42	67.63
PA	24	63.23	PA	39	67.68
NY	45	63.52	VA	18	67.69
WI	1	63.55	FL	1	67.71
WI	26	63.58	AR	27	67.84
ME	4	63.68	GA	26	67.86
PA	58	64.09	SC	2	67.87
LA	27	64.20	MI	45	68.00
VA	8	64.29	CT	12	68.32
MA	15	64.36	PA	22	68.33
NY	75	64.45	WI	22	68.80
NY	33	64.48	CT	9	68.93

Appendix D continued...

State	Route No.	% Forest Cover	State	Route No.	% Forest Cover
WV	37	69.16	AL	4	73.33
VT	8	69.28	AL	15	73.78
MD	3	69.56	PA	43	73.80
GA	9	69.68	PA	25	73.94
AL	25	69.81	PA	41	73.94
CT	1	69.89	MD	2	74.12
CT	3	69.90	VT	15	74.20
WI	7	70.01	RI	1	74.35
PA	40	70.40	PA	27	74.42
PA	91	70.51	TN	18	74.52
PA	69	70.54	AL	13	74.54
GA	45	70.66	AL	36	74.54
TN	39	70.67	AR	14	74.68
WI	8	70.92	GA	38	75.20
ME	15	71.01	GA	47	75.20
VT	17	71.02	NH	10	75.22
PA	64	71.21	CT	14	75.35
WV	1	71.29	TN	34	75.39
MD	1	71.37	WI	2	75.54
OH	88	71.38	WI	15	75.73
VA	19	71.42	PA	21	75.82
MA	20	71.43	AR	3	75.93
CT	7	71.47	AR	28	76.06
NC	15	71.49	CT	5	76.08
VT	10	71.60	MI	60	76.12
WV	38	71.61	MN	32	76.25
VT	18	71.64	NH	8	76.25
PA	44	71.95	ME	45	76.31
NC	24	71.96	WV	44	76.34
VA	21	72.21	MO	10	76.43
NY	111	72.30	VA	20	76.50
PA	57	72.36	AL	34	76.74
NY	78	72.37	WV	33	76.92
GA	20	72.53	WV	41	77.17
WV	53	72.55	VA	25	77.19
FL	19	72.64	GA	32	77.23
PA	66	72.76	MS	24	77.25
NY	102	72.80	AL	19	77.28
PA	92	72.88	VA	28	77.32
LA	16	72.93	ME	3	77.38
MA	21	72.99	MI	61	77.54
GA	36	73.04	VA	23	77.58
TX	57	73.13	MN	34	77.59

Appendix D continued...

State	Route No.	% Forest Cover	State	Route No.	% Forest Cover
TX	44	77.64	AR	20	82.09
NY	14	77.67	MI	46	82.54
TX	33	77.76	VT	4	83.00
WI	37	77.81	WV	46	83.00
TN	42	77.82	NH	1	83.18
AL	29	77.85	NH	3	83.23
MO	11	77.98	FL	3	83.32
AL	12	78.07	ME	9	83.32
KY	145	78.13	PA	12	83.41
KY	46	78.54	VA	14	83.63
MO	8	78.55	NH	5	84.00
WV	19	78.60	WV	31	84.09
WV	48	78.70	TN	32	84.39
WI	29	78.70	MS	2	84.43
VT	12	78.84	AL	39	84.49
AL	16	78.88	PA	37	84.57
GA	37	78.95	VA	3	85.02
TN	31	79.01	AL	23	85.16
GA	46	79.54	MD	4	85.33
MO	9	79.60	NH	23	85.35
NH	9	79.67	NH	12	85.56
PA	32	79.69	NH	13	85.57
WI	28	79.72	AL	35	86.26
MA	17	79.82	AL	20	86.44
GA	31	79.87	NH	15	86.52
WV	50	79.91	AL	17	86.77
TN	29	80.20	WV	32	87.12
AR	15	80.23	WI	4	87.23
NY	199	80.26	PA	13	87.26
ME	18	80.44	NH	20	87.32
IN	23	80.53	NY	114	87.45
MD	5	80.67	NH	14	87.52
NH	7	80.89	MN	33	87.62
AL	14	81.08	AL	43	87.75
NY	73	81.18	NH	18	88.22
TN	35	81.34	AR	12	88.57
AR	11	81.46	AR	23	88.80
GA	15	81.46	WV	23	89.46
AR	13	81.69	NY	100	89.47
WV	49	81.72	NH	22	90.07
WI	3	81.88	NY	83	91.09
MA	18	82.06	PA	6	91.13
NH	6	82.06	NY	81	91.46

Appendix D continued...

State	Route No.	% Forest Cover	State	Route No.	% Forest Cover
TX	32	91.46	OK	1	94.68
NH	11	92.04	NY	106	94.71
NY	85	92.67	NH	17	94.76
WV	22	92.88	NH	19	95.00
PA	16	94.12	NY	84	95.39
VA	13	94.20	PA	10	96.88
PA	14	94.67			

Appendix E. Relationship between the proportion presence over the 10-year window and the percent forest cover in the landscape, with corresponding LOESS smoothed curves superimposed. The minimum habitat amount at which there is a 50% probability of presence in the landscape is shown by the vertical line. See Appendix A for the species four-letter AOU codes.

Appendix E continued...

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