

EFFECT OF REPRODUCTIVE RATE ON MINIMUM HABITAT REQUIREMENTS OF FOREST-BREEDING BIRDS

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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-amount 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. We 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, we combined two large-scale independent data sets: the North American Breeding Bird Survey and the U.S. 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 (interspecies) relationship between the estimated minimum habitat amount at which there was a 50% probability of presence in the landscape and annual reproductive output ($F_{1,39} = 7.71$, $P = 0.008$, $r^2 = 0.16$). This is the first direct test for a negative relationship between minimum habitat requirements and annual reproductive rates.

Key words: Breeding Bird Survey; deforestation; extinction threshold; forest-breeding birds; habitat amount; habitat loss; minimum area requirements; minimum habitat requirements; population persistence; reproductive rate.

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 wetlands of north-central USA (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 threats to species survival are 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 an understanding of those life-history 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

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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, whereas 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 it has been shown theoretically (Skellam 1951, Bevers and Flather 1999) and empirically (Robbins et al. 1989a) that many species never reach this maximum occurrence, even in very large patches. 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 rate.

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 1992, Andr  n 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). Some studies measure both patch size and what they term "isolation effects," which is essentially a landscape-scale measure of the amount of habitat within a specified area around a patch (Askins et al. 1987, Robbins et al. 1989a, Hinsley et al. 1995) and the resistance of the interpatch matrix to species movement (Ricketts 2001). These analyses demonstrate 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 Sol   1996, Doncaster et al. 1996, Gibbs 1998, With and King 1999, Fahrig 2001; C. H. Flather, M. Bevers, E. Cam, J. Nichols, and J. Sauer, *unpublished manuscript*). Modeling studies suggest that it depends on landscape factors such as the quality of the matrix or nonhabitat portion of the landscape (Fahrig 2001, Ricketts 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. We 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

We used data from the North American Breeding Bird Survey, BBS (USGS Patuxent Wildlife Research Center 2001), to estimate the "proportion presence" of each of 41 forest bird species over a 10-year window, commencing with the year of the aerial photo for each landscape, 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-yr window. To calculate the percent forest cover (coniferous, deciduous, and mixed forest) of the 779 landscapes located in the central and eastern USA (Fig. 1), we used the U.S. Geological Survey (USGS) Land Use and Land Cover (LULC) digital data (U.S. Department of the Interior 1987). Each point in Fig. 1 represents the centroid of a circular landscape with a radius of 19.7

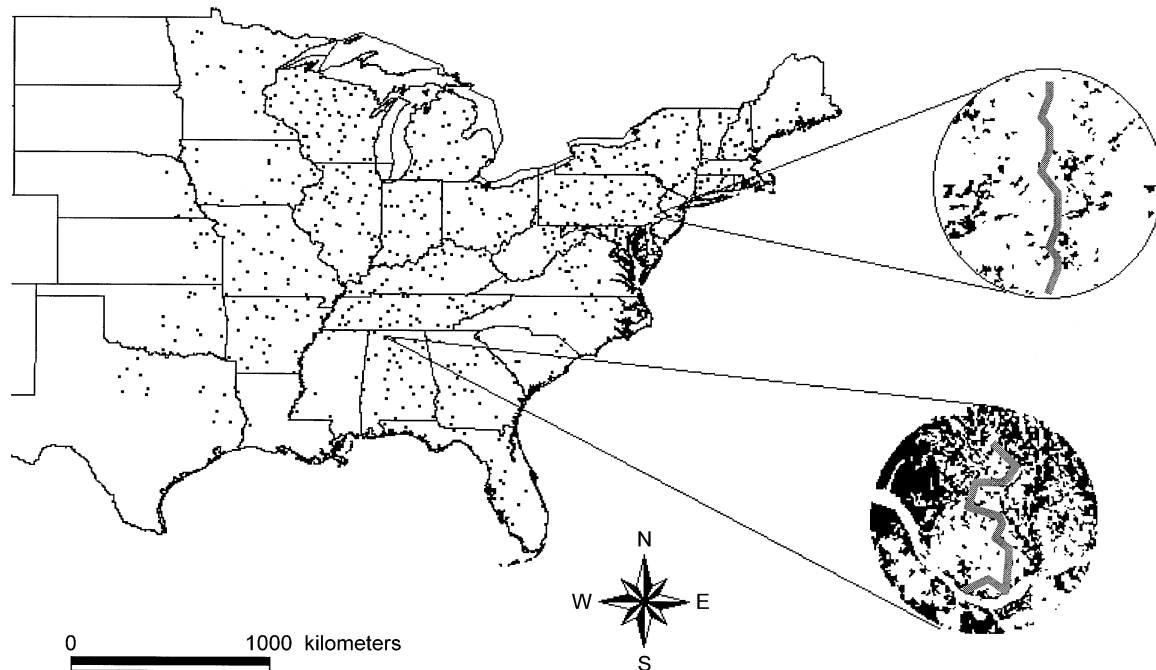


FIG. 1. Study area in central and eastern United States, showing the location of the 779 landscapes. Each landscape has a radius of 19.7 km and is centered on a Breeding Bird Survey route, so that the landscape contains the entire route. The location of the BBS route within each landscape is shown as a gray zigzag line. Black areas represent forest, and white areas include all other land cover types.

km (area $\sim 1200 \text{ km}^2$), which is equal to half the length of a BBS route. Each landscape was centered on the midpoint of a BBS route to ensure that the landscapes contained the entire route.

We 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, we plotted the proportion presence against the percent forest cover, and used non-parametric regression curves to smooth the data. These smoothed curves were then used 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, we multiplied the average clutch size by the number of broods produced per reproductive season, using values obtained from the literature. Finally, we 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 >4000 roadside routes that are randomly distributed within a one-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-min 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.

Taking the species presence over a 10-yr 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. We considered a species to be present during a year if it was recorded on at least one of the 50 stops that year, and we 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 min before sunrise. We excluded from the analysis those routes that did not meet these BBS guidelines.

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

An additional criterion that we used to select species for analysis was a positive response of proportional occurrence to increasing forest amount. A positive Pearson product-moment correlation ($P < 0.05$) between forest amount and proportional occurrence, estimated over the set of landscapes that fell within the species' range, was used to identify the set of birds qualifying for analysis. This effectively excluded any species that may have been classified incorrectly by Freemark and Collins (1992). The species excluded from our analysis included: Common Yellowthroat (*Geothlypis trichas*), Gray Catbird (*Dumetella carolinensis*), Northern Cardinal (*Cardinalis cardinalis*), Yellow-billed Cuckoo (*Coccyzus americanus*), and Yellow-shafted Flicker (*Colaptes auratus*).

We included species in the analysis if a substantial portion of their breeding range fell 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 digital range maps were not available for these species. Raptors, fowl-like birds, and nocturnal species were also excluded, because 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, we selected a total of 41 forest species (see the Appendix).

Reproductive output

Ehrlich et al. (1988) was the primary source for obtaining annual reproductive rates for each of the 41 species; 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 reproductive data for a certain species were missing or uncertain, we 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.

Clutch size can vary both geographically and between individuals. Because we were interested in interspecific comparisons of habitat occupancy patterns, we used the most common clutch size reported in the literature as representative of that species across its geographic range (or a good portion of its range). When the most common clutch size was given as a range in the number of eggs produced, we chose the midpoint of that range. This occasionally resulted in non-integer clutch size estimates (e.g., 3.5 eggs).

The number of broods produced in a season is not as well known as the clutch size, because 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 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 we wanted to obtain a value that encompassed the entire range of a species, we averaged the number of broods produced to obtain a reasonable value for each species over its entire geographical range. If a species is single-brooded in the north and double-brooded in the south, we 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, we supplemented this information with a second reference as stated previously. Further details on the decisions made in determining the number of broods produced per season for each species, as well as the references used for this information, can be found in Vance (2002).

Landscape data

The USGS LULC digital data (U.S. Department of the Interior 1987) were interpreted from high-altitude aerial photographs taken between 1969 and 1985, and they characterize land cover types (such as forest cover) to a resolution of 4 ha (200 × 200-m grid; U.S. Department of the Interior 1987). See Anderson et al. (1976) for further details about the classification system used for the USGS land cover data.

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

Data analysis

We 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 center 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, we plotted the proportion of years that the species was present in the 10-year window against the amount of forest in the landscape surrounding each route. We repeated this for each of the 41 forest bird species.

Because BBS data are very noisy, we used a nonlinear nonparametric regression to smooth the data. Nonlinear regression was used instead of linear regression because with nonlinear 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). We 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 neighborhood 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, we used the default parameters in SAS, which fits a local linear regression, uses a normal weight function, and selects the window width that minimizes the generalized cross-validation mean squared error (SAS Institute 1990). This method was chosen because it offers a good compromise between goodness of fit to the data and the smoothness of the LOESS curve.

We used the smoothed regression curves to estimate the minimum habitat required for each species to have a 50% probability of presence in the landscape. We chose 50% presence because this was considered a tendency toward occupancy. Fig. 2 demonstrates how the minimum habitat requirements were estimated from the LOESS-smoothed data for the four types of curves we encountered. A "normal" LOESS curve is represented by Fig. 2a, where the minimum habitat amount at which there was a 50% probability of presence in the landscape could be estimated directly from the graph. Fig. 2b represents a species that always had a presence >50%, 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%. Fig. 2c represents the opposite situation, in which the species never reaches a 50% presence. In this case, the minimum habitat amount was taken to be 99%. Fig. 2d 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, we used linear regression analysis in SAS (SAS Institute 1990) to test for an interspecies 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 the Appendix. The average clutch size ranged between 2.5 and 7 eggs (4.30 ± 0.14 eggs/clutch; all values are expressed as mean ± 1 SE), whereas the average number of broods produced per year ranged from 1 to 2.5 (1.34 ± 0.06 broods/yr). When these above two values were multiplied, the result was an average annual reproductive output that ranged between 2.5 and 9 eggs

(5.71 ± 0.28 eggs/yr). The Black-billed Cuckoo produces the fewest eggs, with an annual average of 2.5 eggs, whereas 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% (see Fig. 3).

Data analysis

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

The relationship between the proportion presence over the 10-yr window and the percent forest cover in the landscape is shown in Fig. 2 for four of the 41 forest bird species. The LOESS-smoothed curves are shown superimposed on the original scatterplot, and the vertical line shows the minimum habitat amount at which there is a 50% probability of presence in the landscape. The estimated minimum habitat amount required for a 50% probability of presence in the landscape is shown in the Appendix for each of the 41 species. See Vance (2002) for the remaining scatterplots and LOESS curves for the species not shown.

A simple linear regression indicated that there was a significant negative (interspecies) relationship between the estimated minimum habitat amount at which there was a 50% probability of presence in the landscape and annual reproductive output ($F_{1,39} = 7.71$, $P = 0.008$, $r^2 = 0.16$; Fig. 4). This relationship was not driven by extreme data points or by the designation of 1% minimum habitat requirements 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 requirements for those species that are never present in 50% of the years. In fact, the relationship was stronger when we removed these species from the analysis ($F_{1,26} = 8.79$, $P = 0.006$, $r^2 = 0.25$).

DISCUSSION

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

Within the fields 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

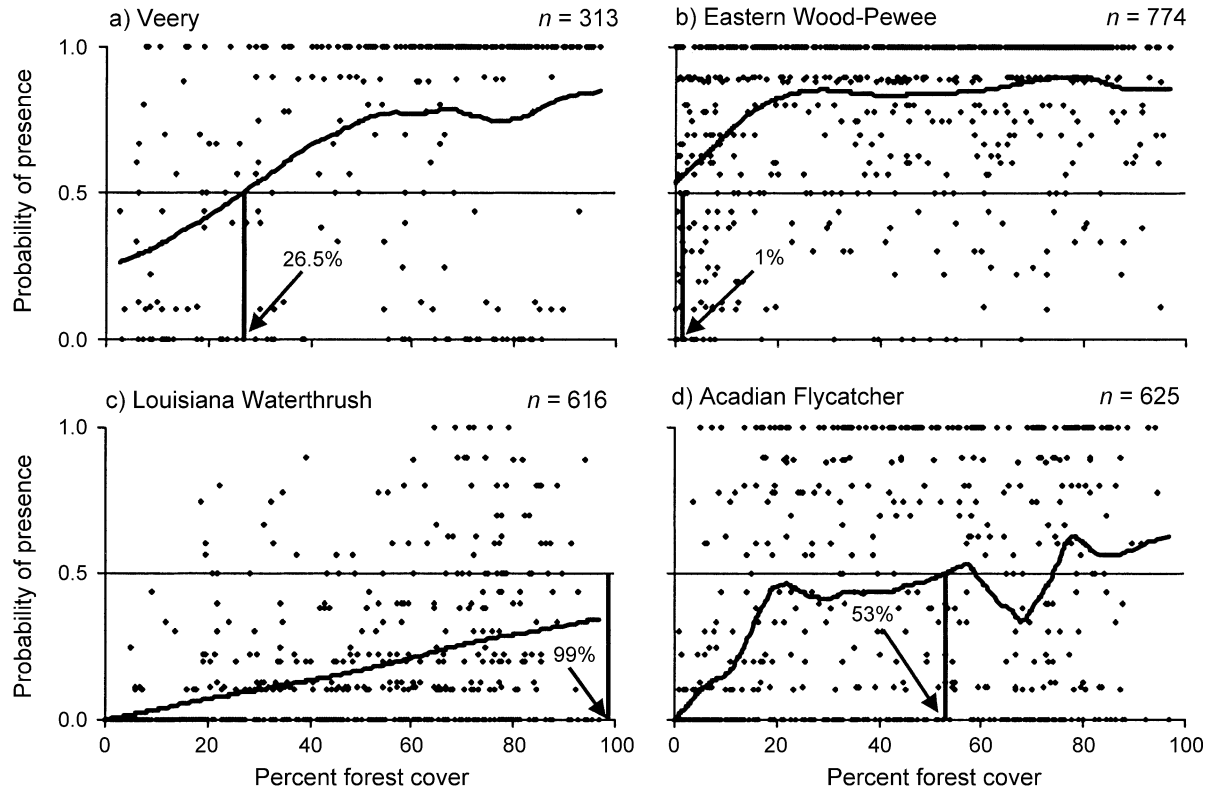


FIG. 2. Examples of each of the four types of LOESS curves observed with the 41 forest birds used in the analysis. Minimum habitat (forest) requirements at which there was a 50% probability of presence of the bird species in the landscape over a 10-yr window were estimated from these LOESS curves. The locations of the minimum habitat requirements along the axis of habitat amount (forest cover) are shown by the vertical bars. (a) The “normal” LOESS curve for which the minimum habitat requirement for a 50% probability of presence in the landscape could be estimated directly from the graph (22 species, with Veery as an example). (b) Species for which the probability of presence over the 10-yr window was always higher than 50% on the LOESS curve, as typified by Eastern Wood-Pewee. The minimum habitat amount for these species was determined to be 1% (5 species). (c) Species for which the probability of presence never reached 50% on the LOESS curve (e.g., Louisiana Waterthrush). The minimum habitat requirement for these species was estimated at 99% (8 species). (d) Species for which the 50% probability of presence in the landscape occurred at more than one habitat amount. We took the minimum habitat requirement to be the lowest amount of habitat at which the species was present in 50% of the years (6 species).

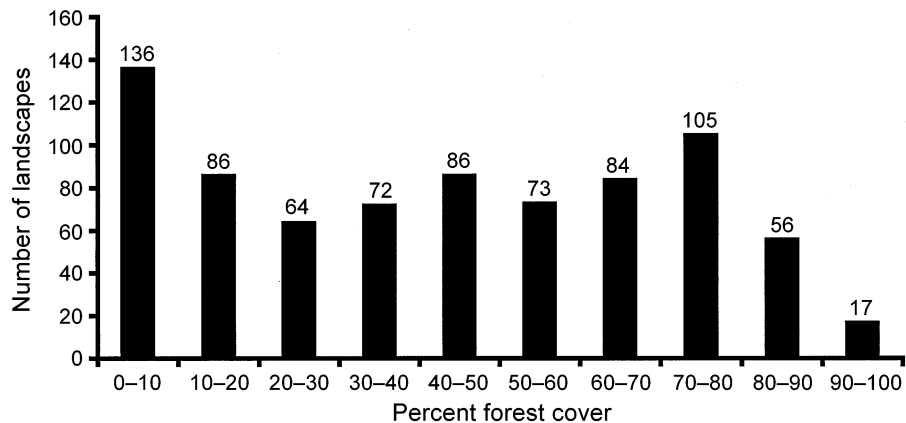
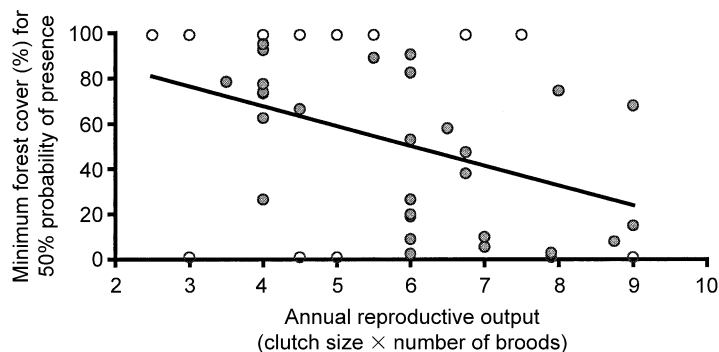


FIG. 3. Distribution of percent forest cover for the 779 landscapes used in the present analysis. The number of landscapes in each category is shown above the bar.

FIG. 4. Relationship between the minimum habitat required (percent forest cover) for a 50% probability of presence in the landscape, and the annual reproductive output of forest breeding birds ($n = 41$ species). The open circles represent both the common species and the rare species for which minimum habitat requirements were estimated to be 1% and 99%, respectively (see Fig. 2).



(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 (Dunning 1993) and the variation in annual reproductive rate was relatively small. Sutherland et al. (2000) found that body size scales with natal and breeding dispersal distance, such that dispersal distance increases with increasing body size. Because the birds in this study have fairly similar body sizes, they should be scaling to the landscape in a similar way.

We investigated the possibility that potential confounding covariates may have produced a spurious relationship between minimum habitat requirements and annual reproductive rates. These ancillary analyses suggest that this was not the case. There was no significant relationship between body size and annual reproductive rate ($F_{1,39} = 0.30$, $P = 0.59$, $r^2 = 0.008$), or between body size and the minimum habitat required for a 50% probability of presence in the landscape ($F_{1,39} = 0.06$, $P = 0.81$, $r^2 = 0.001$). Similarly, there was no significant difference in annual reproductive output between species restricted to forests (16 species) and species that are more generalist in their habitat use (25 species; $t = 1.12$, $df = 39$, $P = 0.27$). Therefore, although the amount of habitat required for a 50% probability of presence in the landscape may have been underestimated for generalist species, this could not have produced the observed relationship between annual reproductive output and minimum habitat requirements (although it probably added noise to the relationship).

The observed relationship also is not due to an underlying latitudinal trend in habitat amount. There was no significant relationship between percent forest cover and latitude ($F_{1,777} = 0.26$, $P = 0.61$, $r^2 = 0.0003$). Although we did observe a small positive relationship between altitude and forest cover, this did not produce a spurious relationship between reproductive output and minimum habitat requirements. This would occur if high-elevation study species had lower reproductive output than low-elevation species. In fact, the seven study species that prefer higher elevations (Black-throated Blue Warbler, Yellow-rumped Warbler, Olive-sided Flycatcher, Rose-breasted Grosbeak, Brown Creeper, Blue-headed Vireo, and Canada Warbler; Poole and Gill 1992–ongoing) had a mean annual reproductive rate of 5.64 ± 0.71 eggs/yr (see Appendix), whereas the six species that prefer lower elevations (Red-bellied Woodpecker, Yellow-throated Vireo, Pine Warbler, Kentucky Warbler, Prothonotary Warbler, and Hooded Warbler; Poole and Gill 1992–ongoing) had a mean annual reproductive rate of 5.23 ± 0.79 eggs/yr (see Appendix). The remaining 28 study species occur in both high- and low-altitude areas.

Finally, differences in species' detectability could potentially introduce bias into the results if species with low reproductive rates also had lower detection rates relative to species with high reproductive rates. We minimized this potential problem at the onset of this study by excluding species that are known to be sampled poorly by the BBS (e.g., nocturnal species, raptors). Furthermore, four of our study species were determined to have lower detection rates due to their secretive nature, quiet song, or less persistent singing (Brown Creeper, Black-billed Cuckoo, White-breasted Nuthatch, and Blue-gray Gnatcatcher; Poole and Gill 1992–ongoing). Those species had a mean annual reproductive rate of 5.31 ± 0.98 eggs/yr, which is not significantly lower than the mean annual reproductive rate of the remaining 37 study species (5.76 ± 0.29 eggs/yr) (see Appendix). Although this provides evidence, from a small subset of species, that behaviors leading to low detectability did not confound our inference, more subtle differences in detectability among

the remaining 37 species could still cause a spurious relationship if low-reproducing species had, on average, lower detection rates than high-reproducing species. A rigorous examination of this issue would require species-specific estimates of detectability on a route-by-route basis using a method similar to that reviewed in MacKenzie et al. (2002), which requires multiple visits to a BBS route over a relatively narrow temporal window.

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 (Pimm et al. 1988). 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.

Modeling 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). Although landscapes in modeling studies that show this sharp extinction threshold are closed to immigration, landscapes in reality are open. Pagel and Payne (1996) and Flather et al. (C. H. Flather, M. Bevers, E. Cam, J. Nichols, and J. Sauer, *unpublished manuscript*) illustrate the effect of immigration on species extinction thresholds. Their studies show that immigration into the landscape results in an underestimation of the amount of habitat required for population persistence (Pagel and Payne 1996; C. H. Flather et al. *unpublished manuscript*). Further, immigration serves to dampen the thresholds, which may make them difficult to detect empirically (C. H. Flather et al., *unpublished manuscript*). In this study, we were unable to consistently locate the extinction thresholds for our species. Thus, to avoid the subjectivity of locating these thresholds, we calculated the amount of habitat required for a 50% probability of presence in the landscape. We 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 (Fig. 4) 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 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 have been overestimated for some species. For example, the Prothonotary Warbler, Louisiana Waterthrush, and Northern Waterthrush build their nests near standing or running water and thus, not all forested areas may be used for breeding. In addition, woodpeckers and other cavity-nesting species require standing dead trees for breeding, so early-seral forest (which typically has few, if any, standing dead trees) may not qualify as breeding habitat for them (Poole and Gill 1992–ongoing). Similarly, habitat may be underestimated for more generalist species, such as the Black-capped Chickadee, that are able to use more open or residential areas for breeding in addition to forested areas (Poole and Gill 1992–ongoing). Differences in species detectability may also have been a source of extraneous variation in this study (Boulinier et al. 1998). We minimized this potential problem by excluding species that are poorly sampled by the BBS. One way to lessen the detectability issue would be to repeat the analysis at the species level by looking at geographic variation in annual reproductive rates and minimum habitat requirements, and testing to see if the negative relationship still holds.

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-yr 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 the difference 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 we used presence/absence data, not abundance, for each route. Despite the inherent biases with data, the BBS remains a very valuable source of information

for the status of North American birds at a continental scale.

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 brings 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. 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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APPENDIX

Reproductive data, minimum habitat requirements for a 50% probability of presence, and the number of landscapes used in the analysis for each of 41 forest-breeding bird species are available in ESA's Electronic Data Archive: *Ecological Archives* E084-069-A1.