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# Demographic Responses by Birds to Forest Fragmentation

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**Abstract:** *Despite intensive recent research on the effects of habitat loss and fragmentation on bird populations, our understanding of underlying demographic causes of population declines is limited. We reviewed avian demography in relation to habitat fragmentation. Then, through a meta-analysis, we compared specific demographic responses by forest birds to habitat fragmentation, providing a general perspective of factors that make some species and populations more vulnerable to fragmentation than others. We obtained data from the scientific literature on dispersal, survival, fecundity, and nesting success of birds. Birds were divided into subgroups on the basis of region, nest site, biogeographical history, and migration strategy. Species most sensitive to fragmentation were ground- or open-nesters nesting in shrubs or trees. Residents were equally sensitive to fragmentation in the Nearctic and Palearctic regions, but Nearctic migrants were more sensitive than Palearctic migrants. Old World species were less sensitive than New World species, which was predicted based on the history of forest fragmentation on these two continents. Pairing success was the variable most associated with fragmentation, suggesting an important role of dispersal. Fledgling number or condition, timing of nesting, and clutch size were not associated with sensitivity to fragmentation, suggesting that negative fragmentation effects on birds do not generally result from diminished food resources with increasing level of fragmentation. Future studies on demographic responses of birds to habitat fragmentation would be more effective if based on a combination of measures that can distinguish among the demographic mechanisms underlying population changes related to habitat fragmentation.*

**Key Words:** bird demography, edge effects patch size, habitat loss, meta-analysis, patch isolation

Respuestas Demográficas de Aves a la Fragmentación de Bosques

**Resumen:** *A pesar de la reciente investigación intensiva sobre los efectos de la pérdida y fragmentación del hábitat sobre poblaciones de aves, nuestro entendimiento de las causas demográficas subyacentes en las declinaciones poblacionales es limitado. Revisamos la demografía aviar en relación con la fragmentación del hábitat. Posteriormente, mediante un meta análisis comparamos las respuestas demográficas específicas de aves de bosque a la fragmentación del hábitat, lo que proporcionó una perspectiva general de los factores que hacen que algunas especies y poblaciones sean más vulnerables a la fragmentación que otras. Obtuvimos datos de la literatura científica sobre dispersión, fecundidad y éxito de anidación de aves. Las aves fueron divididas en subgrupos con base en la región, sitio de anidación, historia biogeográfica y estrategia de migración. Las especies más sensibles a la fragmentación anidaban sobre el suelo o áreas abiertas en matorrales o árboles. Las especies residentes fueron igualmente sensibles a la fragmentación en las regiones Neártica y Paleártica, pero los migrantes Neárticos fueron más sensibles que los migrantes Paleárticos. Especies del Viejo Mundo fueron menos sensibles que las del Nuevo Mundo, lo que se predijo con base en la historia de la fragmentación de bosques en esos dos continentes. El éxito de apareamiento fue la variable más asociada con la fragmentación, lo que sugiere un papel importante de la dispersión. El número o condición de los volantones, la temporalidad*

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*de la anidación y el tamaño de la nidada no estuvieron asociados con la sensibilidad a la fragmentación, lo que sugiere que los efectos negativos de la fragmentación sobre las aves generalmente no resultan de la disminución de recursos alimenticios con el incremento del nivel de fragmentación. Los estudios futuros sobre respuestas demográficas de aves a la fragmentación del hábitat serán más efectivos si se basan en una combinación de medidas que puedan distinguir los mecanismos demográficos subyacentes en los cambios poblacionales relacionados con la fragmentación del hábitat.*

**Palabras Clave:** aislamiento de parche, demografía de aves, efectos de borde, meta análisis, pérdida de hábitat, tamaño de parche

## Introduction

Habitat alteration by human activity may explain the recent decline of plant and animal species (e.g., Pimm et al. 1995). Landscape change involves two different, generally simultaneous processes. First, and likely the most important, is the loss of original habitat via proliferation of human-dominated habitats (e.g., Pimm et al. 1995; Schmiegelow & Mönkkönen 2002). Second, with habitat loss the remaining area often becomes fragmented (i.e., subdivided into isolated remnant patches.) Fragmentation can exacerbate the effects of pure habitat loss potentially producing population decline at landscape scales greater than expected solely on the basis of remaining area (Andrén 1994; Bender et al. 1998), which may result in population extinction even if suitable habitat still exists. It is important to distinguish between pure habitat loss and fragmentation effects because management to remedy their negative effects may differ (Fahrig 1997).

In forest birds, population density, distribution, and species richness are affected by habitat fragmentation (e.g., Villard et al. 1998; Donovan & Flather 2002), but experimental evidence is scant (McGarigal & Cushman 2002). Bender et al. (1998) and Connor et al. (2000) reviewed studies of numerical responses (changes in density and abundance) of birds to varying patch sizes. Others found that avian numerical responses to patch size effects depend on landscape context (i.e., the type of disturbed habitat where patches of original habitat are embedded; e.g., Ricketts [2001]; Brotons et al. [2002]).

Despite recent work (Porneluzi & Faaborg 1999, Stephens et al. 2003), our understanding remains limited regarding the demographic causes behind the effects of habitat loss and fragmentation on populations. Numerical responses, particularly those of songbirds, are relatively easy to detect compared with demographic responses, which may require intensive and long-term field studies of populations. Proper understanding of the mechanisms involved in demographic changes in bird populations as a consequence of habitat fragmentation is crucial because only then can steps be taken to remedy negative fragmentation effects.

We argue that avian numerical responses to habitat fragmentation stem from demographic changes. If, for exam-

ple, nesting success is negatively affected by fragmentation, this will lead to decreases in population size more than those expected by habitat loss alone, and eventually regional population extinction may occur even if suitable habitat is still available. Demographic changes, however, are necessary but not sufficient for true fragmentation-driven population declines. Low nesting success in fragmented habitats does not inevitably lead to population decline or extinction if it is compensated by higher nesting success elsewhere (e.g., source-sink dynamics; Pulliam 1988). It is also important to distinguish between landscape (population) level and local (individual) level processes even though generally their effects are parallel (Andrén 1994). Responses of individuals nesting in small patches can be considered proximate processes, whereas population responses are ultimate processes and more directly linked to population persistence.

Habitat loss alone implies no changes in population density and demographic parameters in remnant habitat. Thus, we focused on true fragmentation effects indicated by changes in bird populations associated with patch size, patch isolation, and edge effects. We distinguish three demographic components: (1) annual survival rate, (2) fecundity (i.e., the investment of a female or a pair of birds in offspring), and (3) nesting success (i.e., the rate or probability with which fecundity leads to independent offspring).

Mechanisms affecting these components of demography can be divided into three broad categories. First, predation on adult birds and their offspring (nest predation, including nest parasitism) can have a strong effect on population demography, particularly survival and nesting success. Several researchers have shown that landscape change can result in dramatic changes in predator species assemblages, overall density of predators, and predation pressure on birds and their nests (Andrén 1992, 1995; Bayne & Hobson 1997). Second, habitat fragmentation may affect the availability of critical resources such as food in many ways. According to the "resource concentration hypothesis" (Root 1973) there is a greater likelihood of critical resources being present in larger habitat patches, resulting in higher population growth rates. Finally, habitat fragmentation may disrupt the functional connectivity in the landscape. For example, some patches in the

**Table 1.** Effects of different mechanisms, related to fragmentation, on demographic variables of forest birds.<sup>a</sup>

<i>Variable</i>	<i>Direct effects</i>	<i>Indirect effects</i>
Survival		
annual survival	predation, food	predation
annual turnover	predation, dispersal	nest predation
site fidelity	dispersal	predation, nest predation, food
age structure	nest predation	predation
Fecundity		
pairing success	dispersal	food
sex ratio		predation, dispersal
clutch size <sup>b</sup>	food	
timing <sup>b</sup>	food	
Nesting success		
nest success rate <sup>b</sup>	predation, nest predation	
nest parasitism rate <sup>b</sup>	nest predation	
number of fledglings <sup>b</sup>	nest predation, food	predation
fledgling quality <sup>b</sup>	food	

<sup>a</sup>Predation covers only predation of adult birds.

<sup>b</sup>Measurements taken from nests.

landscape, if too isolated from other patches, may become unreachable by individuals, thereby lowering pairing success (e.g., Cooper & Walters 2002, Brooker & Brooker 2003). These changes in demography may eventually manifest themselves in abundance of individuals via realized changes in the ratio between births and deaths and between immigration and emigration. Numerical responses may also result from demographic effects anticipated by individual birds in cases where they adaptively respond to landscape changes, for example, by deserting small habitat patches where nesting success is likely to be low (Holmes et al. 1996; Bayne & Hobson 2002).

There are several alternative ways to measure each of these aspects of population demography (Table 1). Individual survival can be measured directly with mark-recapture techniques or indirectly through annual turnover of individuals. Fecundity can be measured directly by clutch size or the number of broods or indirectly by the timing of nesting because early clutches are generally larger than late clutches in single-brood species (Klomp 1970). For multiple-brood species, early nesting is more likely to result in multiple broods (Perrins 1970). Pairing success and population sex ratio are also important components of fecundity. Finally, rates of nest predation, parasitism, and the number of fledglings and their quality are measurements all associated with nesting success. These measurements can also be divided into those taken from adult birds (e.g., survival, pairing success, sex ratio) and those taken from nests (e.g., clutch size, rate of nesting success).

Likewise, predation availability of resources and functional connectivity have direct and indirect effects on demography and on measurements taken from populations. For example, predation directly affects annual survival but may indirectly affect sex ratio or age structure if it is either sex or age biased. Nest predation has direct effects on nest

success rate and on population age structure. Nest predation may indirectly affect site fidelity and therefore annual turnover in local populations because experimental evidence shows that birds tend to disperse away from sites after their own (Haas 1998) or even neighbors' (Doligez et al. 2002) unsuccessful nesting attempts. One potentially important message can be derived if one considers the potential direct and indirect links between the mechanisms and measurements. Generally only one mechanism can be singled out as a putative factor for demographic changes in measurements that can be taken from nests (Table 1). All other mechanisms, except dispersal, can be addressed by studying nests. Thus, it seems as if a clearer idea of important mechanisms affecting population demography can be achieved by inspecting nests.

The measurements can be ranked by order of difficulty. Compared with demographic responses, it is relatively easy to assess population densities; therefore numerical responses are well known (Bender et al. 1998; Connor et al. 2000). Unfortunately, by measuring density only, one cannot make any firm conclusions about the mechanisms causing the numerical responses (e.g., van Horne 1983). Pairing success, timing of nesting, and clutch size are also relatively easy to measure because they require only single or few observations from individuals. Nest success and fledgling quality require more detailed monitoring of the nests but are still more convenient measures of demography than those requiring capturing adult birds (sex ratio, age structure) or measurements of survival (annual survival, site fidelity), which require long-term monitoring of individually marked populations. These types of studies are not numerous in avian landscape ecology (e.g., Brooker & Brooker 2003).

Even though our first goal was to provide a quantitative, exploratory overview of fragmentation effects on population demography of birds, earlier studies on numerical

responses can be used to generate hypotheses for testing with the demographic literature available. Results of several earlier studies suggest that there is a marked difference between biogeographic regions in the overall susceptibility of birds to fragmentation. McLellan et al. (1986) conclude that a larger proportion of forest bird species in eastern Nearctic than in Britain is affected negatively by subdivision of their habitat. Differences between Palearctic and Nearctic patterns may result from the history of human-induced forest fragmentation. In the western Palearctic, several species were driven into extinction long ago and provided time for other species to evolve adaptations to the new range of habitats in fragmented landscapes. By contrast, many of the western Palearctic landscapes already existed thousands of years ago, whereas the eastern deciduous forests of the Nearctic region were largely intact as recently as 300 years ago. Bender et al. (1998) show that birds in the western hemisphere (Neotropic & Nearctic) have a stronger negative numerical response to fragmentation than those in the eastern hemisphere (Europe & Africa).

Mönkkönen and Welsh (1994) further developed the idea of relative differences between geographical regions in susceptibility to fragmentation by forest birds. They suggested that species that evolved in the New World (Nearctic & Neotropical) should be the most negatively affected by fragmentation because they were unexposed (and could not develop adaptations to) habitat fragmentation during the Pleistocene. By contrast, the western Palearctic species have gone through several fragmentation periods and bottlenecks in habitat availability during their Pleistocene and Holocene history and therefore should be resilient to fragmentation effects. Mönkkönen and Welsh (1994) also hypothesize that birds inhabiting boreal forests both in the Palearctic and Nearctic regions are more resilient to fragmentation than temperate forest birds because of the dynamic nature of boreal forest biome where disturbances at different spatial scales have provided a wide variety of habitat types and ecotones for forest specialists. Overall, Mönkkönen and Welsh (1994) suggested a greater role of history in explaining responses to fragmentation than autoecological factors such as migratory habits (Bender et al. 1998). Thus, it follows that besides numerical responses, demographical responses should also differ among regions.

Nest predation and nest parasitism have been considered prime mechanisms for negative fragmentation effects on birds, particularly in the eastern Nearctic. Results of many studies show increased predation rates with increasing habitat fragmentation and proximity to habitat edges, particularly in open-nesting birds (Chalfoun et al. 2002). Cavity nesters are usually considered relatively safe from nest predation (but see Martin 1993). We therefore expect that nest site is an important factor making some species more susceptible to forest fragmentation than others.

Bender et al. (1998) showed that population densities increase with patch size for habitat-interior birds but decrease for species associated with habitat edge. Thus, for interior species, the decline in population size resulting from habitat fragmentation should be greater than predicted from pure habitat loss only. Edge, interior, and generalist categories such as used in Bender et al. (1998) are problematic, however, because of geographic variation in species' habitat requirements (Villard 1998) and conceptual limitations (Imbeau et al. 2003). More robust categories of habitat affinity, such as mature forest specialists versus forests generalists, are associated with numerical responses to fragmentation (Hannon & Schmiegelow 2002) and could therefore be associated with demographic responses to fragmentation as well.

Following from these predictions, we made a quantitative comparison through a meta-analysis of specific demographic responses of forest birds to habitat fragmentation and provide a general perspective of factors rendering some species and populations more vulnerable to fragmentation than others. Furthermore, we measured the associations among nest site, migration status, region, and biogeographical history of the bird species, and its demographic response to fragmentation. We also examined whether the scale of study (edge, patch, or landscape) is related to the strength of response. Overall, our aim was to reveal the most sensitive areas and species for fragmentation.

## Methods

We searched peer-reviewed, published literature with the Biosis Previews database (<http://web5.silverplatter.com/webspirs/start.ws?customer=finelib>). We used a combination of keywords (Table 1) and included in our review all studies on forest fragmentation and demographic responses of living birds. We selected only data on species that breed in forest habitats, excluding information on species typical from agricultural or other nonforested habitats. No limits were imposed with respect to year of publication. Artificial nest experiments were excluded from this study because generalizing from those studies to the effects of fragmentation on survivorship of real bird nests has proven difficult (e.g., Faaborg 2004; Thompson & Burhans 2004). After searching articles, we went through the reference list of all selected papers to increase the number of relevant studies. All articles selected tested for associations between at least one demographic variable and fragmentation in at least one forest bird species. A full list of publications used in this study is available from <http://cc.oulu.fi/~mmonkkon/publication.html>.

Obviously our sample is not a random selection of bird species. Naturally, most studies of fragmentation effects are on species that are beforehand thought to be sensitive

to fragmentation. We do not see species selection as an issue here, however, because our aim is to compare differences in responses among the fragmentation-sensitive species, not to study the effects of fragmentation on birds in general.

We divided demographic variables into three groups: (1) fecundity (pairing success, clutch size, and timing), (2) breeding success (nest success, fledgling condition, nest predation, and nest parasitism), and (3) survival of adults. Also we included some dispersal studies, even though dispersal is a mechanism rather than a demographic variable.

We considered 37 articles and 155 species responses. All articles, however, did not provide the information necessary to calculate effect size, so we were unable to use all these data in meta-analysis. The number of species responses suitable for meta-analysis was 80 (in 26 different articles). Some studies did not provide test statistics, and in some others even the direction of fragmentation response was unclear. The lack of statistical details caused relatively low sample sizes regarding the testing for some hypotheses. It also seemed that test statistics were missing much more often when results were not significant, possibly causing publication bias. Thus, we used a more conventional vote counting method in addition to our meta-analysis. Vote counting has been criticized for bias because vote counting gives equal weight to studies of different sample size (one vote), and small sample sizes are less likely to provide significant results (Gurevitch & Hedges 1993). Meta-analysis and vote counting can be used jointly to determine the magnitude of an effect (meta-analysis) and test for generality of a pattern when only a few effect sizes are available for testing (vote counting). In vote counting, we lumped positive and nonsignificant fragmentation effects together and contrasted their frequency with the frequency of negative responses with chi-square statistics and log-linear modeling.

We defined  $N$  as number of species responses (species  $\times$  demographic variable). In other words, if pairing success, clutch size, and nest predation rate of species  $X$  were measured in a study, this would yield  $n = 3$ . All species responses were treated as independent samples.

## Estimation of Effect Sizes

Effect size in a meta-analysis is defined as the level of statistical relationship between two variables of interest (i.e., patch area and demographic parameter for a particular species, Hedges & Olkin [1985]). We used the Pearson product-moment correlation coefficient,  $r$ , as a measure of the fragmentation effect. The Pearson coefficient not only describes the strength and direction of the relationship between patch area and a demographic parameter but also can be used as a measure of the intensity of the

fragmentation effect. An effect size with a positive absolute value indicates that a species benefits from fragmentation (Bender et al. 1998) and negative effect sizes indicate that a species suffers from fragmentation effects. Correlation coefficients are widely used in a meta-analytic framework, and procedures for calculating and combining effect sizes based on  $r$  are well developed (Hedges 1994, Raudenbush 1994). In addition, many demographic studies report  $r$ , which makes it a convenient effect size. For studies that did not report  $r$  or that did not provide the data necessary to calculate  $r$ , we applied the procedure outlined in Cooper and Hedges (1994) to estimate  $r$  from other test statistics such as Student's  $t$  in conjunction with the treatment means to determine the sign of  $r$  (Connor et al. [2000] describes a similar approach). Effect sizes were normalized with the Fisher's transformation of  $r$ ,  $Z_r$  (Sokal & Rolf 1995).

## Meta-Analysis

To analyze the relationship between population demography and patch area within a landscape type using individual species estimates, we combined estimates of effect size obtained for individual species by using the procedures outlined in Cooper and Hedges (1994), Hedges (1994), and Raudenbush (1994) for random-effects models. We fitted random-effects models for all hypothesis tests because it is more appropriate to consider the effect size estimate for each species or fauna to be drawn from an underlying distribution of effect sizes rather than to consider each species as an estimate of a single, common effect size (see also Connor et al. 2000).

A random-effects meta-analysis is equivalent to a mixed-effects linear model, with fixed effects as covariates and the random effects being the deviation of the true effect size of a study from the value predicted by the model (Raudenbush 1994). Weighted averages of effect sizes within various categories were obtained by weighting effect sizes by their variances. For random-effects models this consisted of weighting  $Z_r$  values by the reciprocal of the sum of their conditional variance ( $1/[n - 3]$ , where  $n$  is the sample size of the effect size estimate) and the between-study variance (Raudenbush 1994). We used the iterative maximum likelihood procedure presented by Raudenbush (1994) to estimate random effects variance. Given that the effect-size estimates were weighted by their variances, model fitting involved weighted least-squares regression (Hedges 1994). All meta-analytic procedures were performed with Metawin software (version 2.1.3.4; Rosenberg et al. 2000).

We wanted to test whether the scale of the study was related to the strength of response. All studies were classified in three categories according to scale: (1) Edge studies usually considered individual birds at local scales

and tested whether bird demography was associated with the proximity of forest-open habitat edge. (2) Patch-scale studies also considered responses of individuals, testing the idea that survival, fecundity, or nesting success is related to patch size. (3) Landscape-level studies typically contrasted two or more landscapes fragmented to varying degrees and tested for population-level effects of fragmentation on demography.

We distinguished two biogeographic regions, Nearctic and Palearctic. For several reasons, we did not include studies from tropical regions. First, certain patterns and processes might differ significantly between tropical and Arctic regions. For example, timing of nesting is a relevant predictor of nest success in the Arctic regions but not in the tropics. Also, clutch size is fairly invariable in many tropical birds. Second, there are few studies from tropical settings that address demographic responses by birds to forest fragmentation. We removed these few potentially very contrasting studies from our data.

To determine whether species life-history traits were related to their demographic response, we checked the literature for predictor variables for each species. We defined nest site into three categories (cavity, open nest in tree or shrub, ground) based on Ehrlich et al. (1988). To test whether nest site is a significant predictor of demographic response, we included only effects related to nest success (Table 1). We determined migratory status based on Marshall and Richmond (1992) and Snow and Perrins (1998) and divided species into two broad categories, migrants and residents. To test hypotheses derived from species numerical responses we included in the migrants category only long-distance (tropical) migrants, which are thought to be time-limited in their breeding, unlike residents and partial or short-distance migrants (Mönkkönen 1992). When testing for differences between biogeographic regions in how migrants and residents respond to habitat fragmentation we used vote counting because too few effect sizes were available for Nearctic residents ( $n = 5$ ) and for Palearctic migrants ( $n = 4$ ).

We assigned species to faunal type (Old World, New World) according to Mayr (1946) to evaluate the historical scenario by Mönkkönen and Welsh (1994). Finally, for each species, habitat associations were defined to in-

clude two broad categories, mature forest specialists and forest generalists (following Raivio & Haila [1990] and Imbeau et al. [2003] for Palearctic species and Ehrlich et al. [1988] and Imbeau et al. [2003] for Nearctic species). Forest specialists are species closely associated with mature forests, whereas generalists, even though preferring mature forests, make use of a wide variety of successional stages of forests and even nonforested habitats.

We tested publication bias of meta-analysis data with graphical methods (funnel and normal quantile plots) and using rank correlation (Kendall's tau) (Rosenberg et al. 2000, Sokal & Rohlf 1995).

## Results

There was no strong publication bias in our data set, although some indication of it existed (Kendall's Tau =  $-0.128$ ,  $p = 0.090$ ) possibly because of careful planning of time-consuming experiments. Research interests differed regionally. There were a handful of studies done in Australia, and we found no studies associated with forest bird demographics and fragmentation effects done, for example, in the Afrotropics or Neotropics. Researchers in North America stressed breeding success more than those in Europe, where both breeding success and fecundity were given equal attention (Table 2). In general, nesting success was more often negatively affected by forest fragmentation than fecundity was (proportion of significant cases 44% vs. 24%). There were relatively few studies of fragmentation effects on survival or dispersal. These are usually much more labor intensive than measurements taken from nests, and perhaps researchers planned these studies more carefully and selected the most susceptible species. Consequently, nearly all dispersal and survival studies reported significant results. Most studies from the Nearctic region considered migrants and most studies from the Palearctic region considered residents (Table 2).

Of all studies, 41.9% (65 cases out of 155) of the species demographic responses to forest fragmentation were significantly negative, 55.5% (86) were not significant, and 2.6% (4) were positive. Of the studies used in the meta-analysis ( $n = 82$ ), figures were 39.0%, 58.5%, and 2.4%

**Table 2.** Number of species effects included in this study by region and demographic parameter measured and number of significant negative versus nonsignificant or positive species effects by region and migration behavior.

Region	Fecundity	Nesting success	Survival	Dispersal	Response (migrants/residents)	
					negative	nonsignificant or positive
Palearctic	27	31	2	3	2/12	12/37
Nearctic	14	68	6	4	39/5	41/7
Total	41	99	8	7		
Meta-analysis*	25	43	6	2		

\*Number of species effects suitable for meta-analysis.

respectively. Thus, studies included in the meta-analysis did not show on average more negative results than the rest. Overall mean effect size (E++) was  $-0.18$  and differed significantly from 0 (bootstrap CI  $-0.27$  to  $-0.07$ ). Thus, overall, forest birds responded negatively to fragmentation, although nonrandom species selection may affect this figure. Scale (edge, patch-size vs. landscape-level studies) did not have a significant effect on results ( $Q = 7.9$ ,  $p = 0.08$ ).

There was no overall difference between migrants and residents or between Nearctic and Palearctic regions. However, there may be a significant interaction between these two variable groups. As predicted, Nearctic migrants seemed to be more sensitive to fragmentation than Palearctic migrants, but between residents there was no such difference (Table 2). Sensitivity to fragmentation depended on migration strategy but was not the same for the two continents (log-linear analysis, 3-way interaction  $\chi^2 = 2.74$ ,  $p = 0.09$ ). Faunal type was associated with resilience to forest fragmentation as predicted ( $Q = 6.79$ ,  $p = 0.034$ ; mean effect size: Old World  $-0.11$ , New World  $-0.32$ ). Surprisingly, mature forest species were not more sensitive to fragmentation than others ( $Q = 5.36$ ,  $p = 0.178$ ).

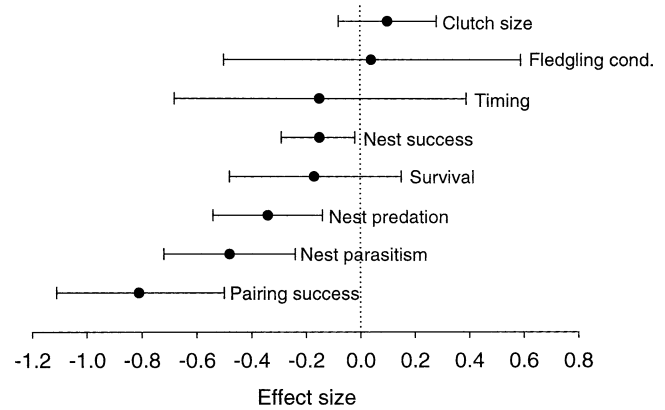
As groups, fecundity and breeding-success effect sizes did not differ (sample size for survival studies was too low to be included into comparison). When demographic variables were analyzed separately, there were significant differences in responses among variables. Associations among fragmentation and nest success, nest predation, nest parasitism, and pairing success were all significantly negative. There was no overall effect of fragmentation on fledgling condition, clutch size, timing of nesting, or adult survival (Fig. 1).

Nest-site groups differed significantly (only nesting success parameters included). Cavity nesters were least sensitive to fragmentation and bird species breeding in ground or in open nests in trees or scrubs were more (and equally) sensitive (Fig. 2).

## Discussion

### Division of Research Interest

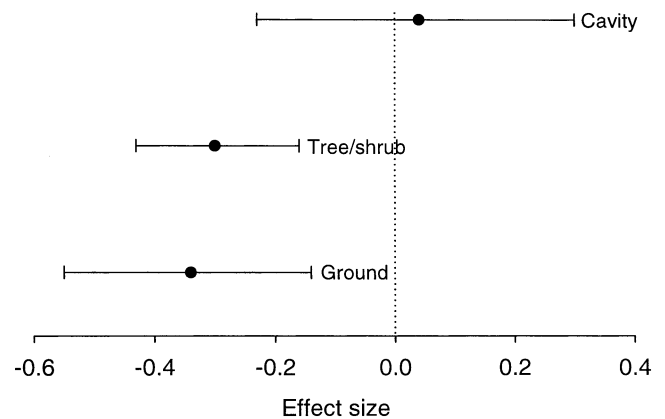
Nearly all studies on fragmentation effects on demography of forest birds have been carried out in boreal and temperate regions, even though the majority of the biodiversity of birds (and other wildlife) is in the tropics. We are aware of only three studies of this kind being conducted in tropical regions compared with 37 from boreal and temperate regions. Thus, we cannot make any comparisons between tropical and extratropical forest biomes, even though this would be of considerable conservation interest. There have been notable differences in research interests between Palearctic and Nearctic regions (Table



**Figure 1.** Response of different demographic variables to fragmentation (mean effect size  $\pm$  95% CI). Difference among variables is significant ( $Q = 53.0$ ,  $p = 0.001$ ). Pairing success and nest predation/parasitism are parameters most sensitive to fragmentation.

2). Decline in numbers of Neotropical migrants has received much attention in North America (Terborgh 1989; Donovan et al. 2002), whereas in Europe more attention is paid to resident species. And decline in numbers of resident forest birds has been more prevalent in Europe (e.g., Niemi et al. 1998; Imbeau et al. 2001).

Of demographic variables, the focus has been on measuring nesting success or fecundity, possibly because they are easier to obtain than other demographic variables. When available, long-term survival and dispersal associations with fragmentation nearly always have been significant. The latter associations, however, may result from a bias toward vulnerable species as subjects of expensive and time-consuming experiments. The emphasis on



**Figure 2.** Response of different nest-site groups to fragmentation (mean effect size  $\pm$  95% CI). Overall difference among groups is significant ( $Q = 7.72$ ,  $p = 0.049$ ). Effect size of cavity-nesting birds does not deviate from zero unlike other groups.

fecundity and nesting success probably reflects the assumption among researchers that these aspects are important. Particularly in North America, roles of nest predation, nest parasitism, and nesting success in general have received much attention (Stephens et al. 2003). Our results provide support for this assumption and earlier results that nest success is negatively affected by fragmentation (Fig. 1). Our results may have been affected by the nonindependence of different demographic variables, however, although differences among variables were so large (Fig. 1) that we believe this issue should not affect the conclusion. Further, our results also confirm that nest parasitism and predation are important mechanisms in eliciting these demographic responses.

Of demographic variables, pairing success was the one most associated with fragmentation. This indicates either an important role of dispersal or a female preference to mate with males in larger or less-isolated patches. All studies in which dispersal was addressed directly showed a significant negative effect of fragmentation (Table 1), further pointing out the importance of this parameter. This is notable because birds are generally regarded as good dispersers. If bird populations are so readily isolated from each other when forests become fragmented, the negative effects of isolation on other taxa are likely to be more pronounced.

Harrison and Bruna (1999) pointed out a mismatch between ecological theory and empirical studies of fragmentation in that theory emphasizes the role of dispersal, landscape connectivity, and spatial configuration of landscape elements for population persistence, whereas existing empirical evidence points out the importance of habitat degradation (e.g., because of physical and biological edge effects). Our results, by contrast, support an emphasis on dispersal. Still, only Cooper and Walters (2002) provided convincing evidence for greater constraint of avian dispersal in fragmented habitats.

Because fledgling number or condition, timing of nesting, and clutch size did not show any response to fragmentation (Fig. 1), one could conclude that negative fragmentation effects on bird populations do not generally come from diminished food resources with increasing level of fragmentation. All these demographic parameters are more likely to be affected by food resources than by other mechanisms (Table 1). Therefore, the resource concentration hypothesis, which states that there is a greater concentration of critical resources in larger habitat patches (Root 1973), is not supported by our results. In fact, studies have shown increased abundance of insect food for birds with increasing fragmentation compared with habitat interior (Helle & Muona 1985; Jokimäki et al. 1998), but evidence of the opposite exists also (Zanette et al. 2000; van Wilgenburg et al. 2001). A recent study in the Neotropics failed to find a relationship between amount of invertebrates in stomachs of insectivorous birds and the level of fragmentation (Sekercioglu et al. 2002).

When all results were combined, migrants and residents seemed equally sensitive to fragmentation. There was an interaction, however, between region and migration status as predicted by Mönkkönen and Welsh (1994). Residents were equally sensitive to fragmentation in the Nearctic and Palearctic regions, but Nearctic migrants were more sensitive than Palearctic ones. Most residents in these two regions are closely related, whereas tropical migrants tend to be more distantly related (Mönkkönen et al. 1992). Old World and New World faunal types also differed, which was predicted based on the history of forest fragmentation on these two continents.

As expected, breeding success of cavity-nesting birds suffered least from fragmentation, whereas birds breeding on the ground or in trees or shrubs responded negatively. This probably means that the role of nest predation in fragmentation effects is significant. Fragmentation is generally thought to affect birds through predation so that numbers and predatory activity of predators increase when the amount of edge habitat increases in a landscape (Chalfoun et al. 2002). In general, however, cavity nesters and particularly secondary cavity nesters have suffered from forestry practices because intensive forestry greatly reduces the availability of nesting cavities and more generally the number of snags per unit area (Imbeau et al. 2001). Most of the cavity-nesting species included in our analysis either are cavity excavators or nest in nest boxes. This might cause distortion of results. Martin (1995) has shown that only primary cavity nesters have significantly lower nest predation rates compared with open-cup nesters, secondary cavity nesters (nonexcavators) being equal in this sense to open-cup nesters.

## Implications for Conservation and Future Studies

We propose that studies on demographic responses of birds to habitat fragmentation would be more effective if they were based on measures that can be easily taken, but effort should be taken beforehand to select those measures that can be used to distinguish among mechanisms. A good combination of nonexperimental measurements would be to monitor pairing success, nest success rate, and fledgling quality simultaneously because pairing success is most likely affected by only dispersal and nest success, and fledgling quality can be used to distinguish between the effects of nest predation and resource acquisition. Fledgling quality reflects the effects of resources but is only slightly affected by predation (on adults or nests).

According to our results, species most sensitive to fragmentation, from the geographically limited perspective of this study, are Nearctic long-distance migrants that nest on the ground and specialize on mature forests. The Ovenbird (*Seiurus aurocapillus*) is a prime example, and it is



not surprising that it is also the most frequently used avian subject in fragmentation studies (e.g., Donovan et al. 1995; Porneluzi & Faaborg 1999; Flaspohler et al. 2001).

Based on our results, we suggest that future conservation efforts to remedy effects of forest fragmentation on birds focus on decreasing predation pressure and improving dispersal chances of birds. The latter, however, might be difficult to realize in practice. This result might also apply to other taxa as well, but further research is needed.

It is obvious that our global knowledge of fragmentation effects on forest birds cannot be complete before several studies have been made in tropical regions. Such studies would probably reveal patterns we do not even suspect. Within Arctic regions, more studies of Palearctic migrants responses to fragmentation are needed to confirm our results, which suggest that Nearctic migrants are more sensitive to fragmentation than Palearctic ones.

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