# HABITAT LOSS AND POPULATION DECLINE: A META-ANALYSIS OF THE PATCH SIZE EFFECT

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*Abstract.* We evaluated the conditions under which patch size effects are important determinants of local population density for animals living in patchy landscapes. This information was used to predict when patch size effects will be expected to occur following habitat loss and fragmentation. Using meta-analysis, we quantitatively reviewed the results of 25 published studies that tested for a relationship between patch size and population density. Patch size effects were strong for edge and interior species (negative and postive patch size effects, respectively), but negligible for generalist species that use both edge and interior habitat. We found significant differences in mean patch size effects between migratory and residential species, between herbivores and carnivores, and among taxonomic groups. We found no evidence that patch size effects were related to landscape characteristics such as the proportion of landscape covered by habitat, median patch size, or the scale at which a study was conducted. However, species in the Western Hemisphere tended to have larger absolute effect sizes, and eastern species tended to be more variable in their response.

For landscapes undergoing habitat loss and fragmentation, our results predict the following: (1) among generalist species that use both the edge and the interior of a habitat patch, the decline in population size associated with habitat destruction should be accounted for by pure habitat loss alone; (2) for interior species, the decline in population size associated with habitat fragmentation per se will be greater than that predicted from pure habitat loss alone; (3) for edge species, the decline in population size will be less than that predicted by pure habitat loss alone; (4) these relative effects will not be influenced by the extent of habitat loss, but they will be affected by the pattern of habitat when large or small patches are preferentially removed; and (5) as loss and fragmentation increase within a landscape, migratory species will generally suffer less of a decline in population size than resident species.

*Key words: conservation; fragmentation; habitat destruction; landscape change; meta-analysis; patch size effects; patchiness; population density; review article.*

## INTRODUCTION

Human activities, such as forest clear-cutting or the expansion of agricultural land, have exacerbated the natural fragmentation of landscapes. For many organisms, new habitat patches are interspersed in an unfamiliar or hostile environment, which leads to the heterogeneous distribution of populations at different scales (Weins 1989*a*, Gilpin and Hanski 1991). There has been considerable interest in modeling the spatial dynamics of populations in patchy or fragmented landscapes so that we may better understand how the spatial pattern of the landscape influences population processes (reviewed by Levin 1976, Hastings 1990, Kareiva 1990, Dunning et al. 1995). Recently, there has been a growing interest in applying these models in conservation strategies (Fahrig and Merriam 1994), particularly for determining the consequences of habitat fragmentation on resident populations (e.g., Mur-

phy and Noon 1992, Lamberson et al. 1994, Baz and Garcia-Boyero 1995, Turner et al. 1995).

Habitat fragmentation is a term that has been used in many different ways. Habitat fragmentation, by definition, is an event that creates a greater number of habitat patches that are smaller in size than the original contiguous tract(s) of habitat. Yet, the term commonly is used to describe human practices that destroy habitat. This usage is misleading because there are situations in which habitat can be removed without fragmenting the landscape whatsoever. To avoid confusion, we define our terms here. We use the term habitat destruction to refer to processes, particularly anthropogenic, that remove habitat cover. Habitat destruction can then be pictured as having two distinct components: habitat loss per se and habitat fragmentation (Fahrig 1997). The effect of losing habitat is obvious: when habitat is lost from the landscape, the animals that are subsequently displaced may also be lost, producing a population decline. The effects of fragmentation are less obvious, but they are very important; fragmentation effects can potentially compound the effects of pure

habitat loss, often producing an even greater population decline.

We examined the most notable effect of habitat destruction: the reduction in average patch size. In patchy or fragmented landscapes, patch size effects should be relatively simple to detect. Consider the following illustration. Habitat loss is expected to produce a proportional decline in the number of animals living in a particular landscape. For example, if a piece of forest habitat supports a large population of some animal and 50% of that forest is removed, then one might expect a decline in animal abundance of 50%. However, it often has been found that species abundance declines beyond that predicted by habitat loss alone. This difference stems from the effects of reduced mean patch size and decreased connectivity in the landscape (i.e., a reduction in the rate of successful dispersal, sensu Merriam 1984; see also Venier and Fahrig 1996). A common way to test for patch size effects is to compare the relative densities of organisms within different-sized patches. If patch size effects account for any additional decline in abundance, then we would expect density to be positively related to patch size. Therefore, the strength of the relationship between patch size and density can be used to index the strength of the patch size effect.

Our first goal in this study was to evaluate the conditions under which patch size effects are important determinants of local population size for animals living in patchy landscapes. To accomplish this, we quantitatively reviewed results of published studies that tested for the presence of patch size effects on population density. Using these results, we generalized about the conditions under which patch size effects influence population size. Because habitat fragmentation creates patchy landscapes, such generalizations are useful for generating predictions about situations in which patch size effects will emerge when a landscape undergoes loss and fragmentation. Thus, our second goal was to formulate testable predictions about how patch size effects are expected to affect the population size of animals following habitat loss and fragmentation.

## METHODS

We adopted a procedure that is relatively new to ecological research (Arnqvist and Wooster 1995), known as meta-analysis. Meta-analysis is a powerful, quantitative form of analysis used for summarizing and analyzing multiple independent studies. In this form of analysis, the statistical results (as opposed to the raw data) of numerous studies are analyzed to determine whether studies share a common statistical relationship, and whether any ''general'' relationships are influenced by one or more predictor variables. Although the benefits and criticisms of using meta-analysis in ecological research can be found elsewhere (Gurevitch et al. 1992, Gurevitch and Hedges 1993, Arnqvist and Wooster 1995), we wish to emphasize that meta-analysis is par-

ticularly suited to studies that examine large-scale phenomena. Large-scale studies are often impractical to conduct because of the time, effort, and money that must be devoted to a single project. For example, it is very difficult to experimentally test hypotheses about habitat fragmentation because the units of observation are landscapes. However, a large body of literature deals with research conducted on single landscapes. Meta-analysis is a more practical approach to studying large-scale questions, because it allows one to accumulate information from these independent studies and to view each as replicates or observations in subsequent statistical analysis. Using meta-analysis, one can test for relationships that occur between the characteristics of a study (e.g., landscape attributes) and their outcomes.

The intent of our literature review was to accumulate the findings of a number of studies that directly or indirectly tested for the effects of patch size on density. Any study that explicitly examined the relationship between habitat patch size and the local population density of a species was considered. In the literature, the most common method for assessing this relationship has been to sample the abundance of a species in different habitat patches within a landscape, and then to test for a correlation between patch area and population density. To be used in our meta-analysis, a study needed to have quantified this patch size–density relationship. Normally, we used the test statistic reported in the study, such as the Pearson product–moment correlation coefficient, $r$, that described the patch size–density relationship. This value not only describes the strength of the relationship between patch size and density, but also can be used as a measure of the intensity of the patch size effect on density. In meta-analysis terms, a statistic such as $r$ is called an ''effect size'' (Hedges and Olkin 1985), although other effect size metrics can be used (see Rosenthal 1994). In this study, effect sizes with very large absolute values indicate a strong association between patch size and population density (hereafter, called the ''patch size effect''), and very small effect sizes indicate that population density was unrelated to patch size.

We used the following criteria when selecting studies for our analysis. First, each study had to examine the relationship between habitat patch size and the population density for at least one species occurring in a patchy landscape. Most studies quantified this relationship by regressing observed within-patch abundance on patch area. This method is somewhat problematic, because different-sized patches require different sampling efforts if one wishes to provide equally reliable estimates of patch density. Accordingly, we excluded any study that did not consider this potential bias. Also, we did not use studies that combined several species into a single density estimate, although multiple effect sizes were obtained from a single study if there was a separate density estimate for each individual spe-

TABLE 1. Description of predictor variables used in the meta-analysis of studies examining the relationship between patch size and local population density.

| Variable | Describes | Name | Description |
|---|---|---|---|
| Percent cover | landscape | COVER | proportion of landscape covered by habitat |
| Geographic location | landscape | LOCATION | Eastern continents vs. Western continents |
| Median patch size | landscape | PSIZE | median size of all censused habitat patches |
| Scale of study | landscape | AREA | absolute size of study area |
| Range in patch sizes | landscape | RANGE | maximum $\log_{10}$(patch size) minus minimum $\log_{10}$(patch size) |
| Habitat association | species | HABITAT | edge, interior, generalist |
| Migratory status | species | MIGRATION | migrant, resident |
| Taxonomic group | species | TAXON | bird, mammal, insect |
| Trophic level | species | TROPHY | herbivore, carnivore |

cies. Second, the landscape type (e.g., forest habitat in an agricultural landscape) and the species name had to be given. Third, the test statistic for the patch size–density relationship was required, and either sample size or the $P$ value of the test had to be given. If these values were not provided, but raw data were provided in the paper, we calculated these values ourselves. When these data existed in the form of a graph, we extracted numerical values from the figure using a Summagrid III digitizer (Summagraphics, Austin, Texas, United States) and SPANS TYDIG digitizing software (INTERA TYDAC Technologies, Nepean, Ontario, Canada). The Pearson product–moment correlation coefficient was calculated. Transformations that linearized the data (e.g., log transformation) were not used. Fourth, each study had to provide enough information for us to describe the study area landscape. In all cases, we used the definition of a habitat patch that was presented by the authors, i.e., we took all measurements of patch size and associated population density at face value. For many studies, this was necessary because the authors did not provide detailed information about each patch that was censused in the landscape.

We wished to determine whether characteristics of the landscape or certain life history traits of the organism were related to the presence and strength of patch size effects. To do this, we estimated a number of predictor variables for each patch size–density relationship (Hedges and Olkin 1985, Rosenthal 1991), which are summarized in Table 1. Values for the landscape attributes were generally given by each study. However, for the variables COVER and AREA, it was sometimes necessary to estimate values from maps of the study area (Bach 1984, Lynch and Whigham 1984, Adler et al. 1986, Nilsson 1986, Herkert 1994, Martin et al. 1995, Telleria and Santos 1995), or to obtain these values through direct communication with the authors (Blake and Karr 1987, Hertzberg et al. 1994).

We assessed whether the amount of habitat in the landscape influenced the presence of patch size effects. It has been hypothesized that patch size effects should be most pronounced at low levels of habitat cover (Andrén 1994, Bascompte and Solé 1996, Fahrig, *in press*). These studies have also suggested that there may be a

threshold value of habitat destruction that determines when fragmentation effects will emerge. Because the presence of such a threshold would implicitly predict that the relationship between habitat cover and fragmentation effects would not be a simple, linear one, we used polynomial regression to test for a nonlinear trend in addition to a linear trend.

The variables PSIZE, RANGE, and AREA were included in the analysis to determine if the scale of a study influenced its outcome, and to statistically control for such effects in our analysis. The variable PSIZE was calculated as the average (median) patch size observed in a study. The variable RANGE was calculated as the difference in the log-areas of the largest and smallest patches. Note that we used difference in log-patch size (i.e., difference in log values rather than absolute values) for the variable RANGE. This method was used because we wanted to give equal weight to studies that spanned equal orders of magnitude of patch sizes, regardless of the absolute scale at which the studies were conducted. The variable AREA was calculated simply as the overall extent at which each study was conducted, which can also be thought of as the landscape size. Thus, RANGE and AREA give relative and absolute measures of scale, respectively.

An important objective of this paper was look for general characteristics that make an animal prone to patch size effects. To characterize each species, we examined a number of life history traits, which were obtained either directly from the paper reporting the study or from other sources (Burt and Grossenheider 1980, National Geographic Society 1987, Bruun et al. 1988, Freemark and Collins 1992, Sibley and Monroe 1990).

We defined habitat association (HABITAT) to include three categories of species: edge, interior, and generalist (see also Hayden et al. 1985, Askins and Philbrick 1987, Freemark and Collins 1992). Edge species were defined as those associated primarily with the perimeter of a habitat patch and not the core. Interior species were those associated with the center of patches and that avoided the edge habitat. Generalist species were defined as those that utilized both edge and interior habitat. Such designations are very important in this study, because habitat patch size is re-

lated to the proportional amounts of edge and interior habitat. If the boundary for edge and interior habitat is defined at a fixed distance inward from the perimeter of the patch, then large patches will contain a greater proportion of interior habitat and a lower proportion of edge habitat than small patches (Wiens 1989*a*). Thus, we predicted that, for interior species, animal densities should be higher in large patches than in small patches, and vice versa for edge species. We wanted to assess such differences, and if present, to control for this effect while examining the influence of other variables.

The variable MIGRATION was used to distinguish migrant bird species from residents. Recently, there has been considerable interest in the effects of habitat fragmentation on bird populations, especially migratory songbirds (Askins et al. 1990, Askins 1995). Some have suggested that differences may exist in population trends between migrant and resident bird species, and that migrants may be more prone to fragmentation effects (e.g., O'Connor 1992, Maurer and Heywood 1993, Flather and Sauer 1996). We defined migrants as species that were represented within the study area on a seasonal basis; resident species were represented within the study landscape all year round (Askins and Philbrick 1987). Classification of migrants and residents was done on a study-by-study basis, rather than a species-by-species basis. We used the classification reported by the authors of each study, when available. Otherwise, we classified species as residents or migrants based on published range descriptions and/or maps (National Geographic Society 1987, Bruun et al. 1988, Sibley and Monroe 1990).

We also were interested in knowing whether there are differences in broad geographic locales, namely between the Eastern Hemisphere (Europe and Africa) and the Western Hemisphere (North and South America). This is particularly important for migrant birds, because their composition may be very different between hemispheres. For example, large-scale anthropogenic disturbance occurred earlier and to a wider extent in the Eastern continents, where, as a result, there appear to be fewer area-sensitive species and greater numbers of generalists (see Askins et al. 1990, Mönkkönen 1994, Newton 1995). The variable LOCATION was included to determine if such differences are related to the incidence of patch size effects, and to control for their effect.

We also categorized each effect size by the species' taxonomic group (TAXON) at the class level: birds, mammals, or insects. We wanted to assess patch size effects independently to control for potential differences in vagility and demographic characteristics between taxonomic groups. We also considered which trophic level the species occupied (TROPHY) to determine whether herbivores and carnivores shared similar responses to changes in patch size. Organisms were classified simply as either herbivores or carnivores. The carnivore category was comprised of all second-order or higher consumers, including insectivores, piscivores, and omnivores.

## Statistical methods

Each suitable study provided at least one effect size for the meta-analysis. Each effect size represented a value that quantified the statistical relationship between patch size and population density for a particular species. There are several possible measures of effect size (Rosenthal 1991), but we used the Pearson product–moment correlation coefficient, $r$. We did not differentiate between $r$ values from simple correlation tests or partial $r$ values that appeared in multiple correlation tests. It was possible to obtain multiple effect sizes from a single study when the patch size–density relationship was tested for more than one species. In many cases, $r$ was not reported directly within a study, but could be obtained either (1) from reported raw data or (2) by transforming into $r$ other test statistics (e.g., $F$, $t$) that tested for a relationship between patch size and density (see Rosenthal 1991). Occasionally, the actual value of the test statistic was not reported, but could be calculated when both the $P$ value and degrees of freedom were provided. Prior to analysis, all effect sizes were transformed using the Fisher's $Z$ transformation suggested by Rosenthal (1991).

We used a meta-analytic procedure that is analogous to parametric multiple regression analysis (Hedges and Olkin 1985, Hedges 1994*a*). In our analysis, the transformed effect sizes were used as the dependent variable in the regression equations, and various combinations of predictor variables were used as independent variables. This technique followed a fixed-effects, weighted least squares approach, in which each effect size was weighted by the inverse of its associated sampling variance (see Hedges and Olkin 1985, Hedges 1994*a*). For correlation coefficients, the sampling variance is a function of sample size and is directly related to the statistical power of the test. Thus, each effect size, $r$, was weighted by an index of its reliability. Studies with a high probability of Type II error, therefore, contributed less weight to the analysis than did those with greater statistical power.

One question in the literature is whether fixed-effects meta-analytic procedures are appropriate when the intent of the meta-analysis is to form broad generalizations (e.g., Hedges 1994*b*, Shadish and Haddock 1994). Although the conventional approach is to use fixed-effects models, Gurevitch and Hedges (1993) strongly encourage the use of mixed-effects models, which are more likely to satisfy statistical assumptions. However, to the best of our knowledge, no one has developed procedures for conducting multivariate, mixed-effects meta-analysis using correlation coefficients as the metric of effect size. As a compromise, we also conducted our meta-analysis using a combination of the more conservative random-effects procedure (following the

weighted-variance method in Shadish and Haddock 1994) and residual analysis (to remove the effect of habitat association).

Two types of significance tests were performed because two types of predictor variables were used. The first type were variables describing the landscape of a particular study (see Table 1). Often, we were able to obtain multiple effect sizes from a single study; however, these multiple effect sizes were not true replicates, because they were representative of a single landscape. To ensure that each study made an equal contribution to the fit of the regression and that we did not overestimate our statistical confidence, we applied a correction factor to each study with multiple effect sizes whenever we assessed the significance of a landscape variable (see Appendix A). The second type of predictors were categorical variables describing life history traits of the animal for which each effect size was generated. Multiple effect sizes were never reported for a single species within a study, so no correction factor was applied. These variables were simply coded to dummy variables so that they could be used in the regression models. Interactions between the two types of variables were assessed by using uncorrected significance tests.

We used two methods to assess statistical comparisons among groups. Pairwise comparisons were assessed using 95% confidence intervals, and multiple comparisons were performed using the Bonferroni adjustment described by Hedges (1994a).

## RESULTS

Although we found >200 studies that examined patch size effects on animals in patchy landscapes, only 25 studies were suitable for our analysis. Most of the excluded studies could not be incorporated because either they did not examine the effect of patch size on population density (patch size and species richness relationships were more commonly tested), or they did not report sufficient statistical information to derive an effect size. The 25 studies examined patch size–density relationships for 134 different species of birds, mammals, and insects, and we were able to derive 153 effect sizes for the meta-analysis (Appendices B and C). Note that some species were represented more than once: 16 species of birds were represented twice, one mammal species was represented twice, and one bird species was represented three times (see Appendix C). Because each set of replicated species was censused by different authors at different sites in different years, we assumed that their effect sizes were reasonably independent of one another, and we did not subject them to any special analysis.

The first stage in the meta-analysis was to test for the presence of a common effect size among the data. The grand weighted-mean effect size ($\pm 1$ SE) was $Z_r$ = 0.0982 $\pm$ 0.0416. Although very small, this mean value was significantly different from zero, using 95%

confidence intervals. The overall heterogeneity of effect sizes was very large ($Q_{TOTAL}$ = 1590 [where $Q$ approximates an asymptotic chi-squared distribution], $n$ = 153, $P < 0.001$), indicating that the individual effect sizes in our data did not share a common value. In other words, there were very highly significant differences among the reported relationships between patch size and density.

The next stage in the meta-analysis was to determine which predictor variables, alone or in combination, best accounted for the high degree of variation among effect sizes. The variable accounting for the greatest amount of variation was HABITAT ($Q$ = 486.4, df = 2, $P < 0.001$). When the individual effect sizes were categorized by habitat association, distinct differences were evident between groups (Fig. 1). On average, effect sizes for interior species tended to be strong and positive, whereas effect sizes for edge species were also strong, but negative. This indicates that there is a strong relationship between patch size and density for these two groups, although the direction of the relationship differs. The weighted-mean effect size for generalist species was positive, but very small, and did not differ significantly from zero (based on 95% CI; see Fig. 1), indicating no relationship between patch size and density for this group. To ensure that the effect of habitat association did not mask the effects of other underlying relationships, we performed all subsequent analyses by including HABITAT in each statistical model to control for its effects.

We found little evidence that COVER was related to the effect size reported by a study, although the association between COVER and effect size was negative and nearly significant after controlling for the effects of HABITAT ($Q$ = 3.69, df = 1, $P$ = 0.06; Fig. 2). However, the significance of this variable always decreased when other predictor variables (e.g., LOCATION, MIGRATION, TROPHY) were included in the statistical model, suggesting that the near-significant relationship for COVER and HABITAT was spurious. The addition of second- and third-order polynomial terms did not significantly improve the fit of the model, indicating lack of evidence for a nonlinear relationship between effect size and COVER.

None of the remaining landscape variables, PSIZE, AREA, or RANGE, accounted for significant amounts of variation between effect sizes. We tested nearly all of the possible combinations of predictor variables and first-order interactions, yet found no cases in which any of the remaining landscape-level variables were significant predictors of effect size.

The effects of MIGRATION and LOCATION were examined simultaneously in a three-way model that also included the variable HABITAT. To determine if the effects of MIGRATION would be contingent upon LOCATION, we tested for the presence of an interaction between these two variables. Weighted-mean effect sizes differed significantly between Eastern and
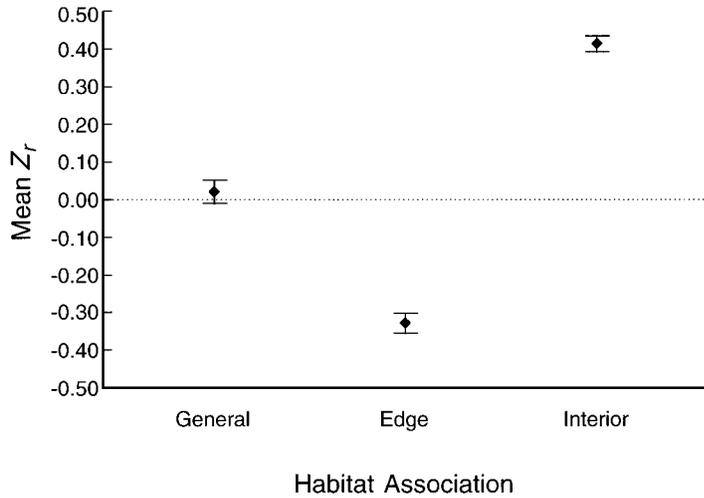
FIG. 1. Mean patch size effects ($Z_r$) categorized by the habitat association of the species. Edge species are those associated with the periphery of a habitat patch; interior species are "edge avoiders" that tend to be associated with the center of patches; generalists are species associated with both edge and interior habitat. Error bars indicate 95% CI.

Western Hemisphere species ($Q = 12.79$, df $= 1$, $P < 0.001$). The absolute values of effect sizes tended to be greater for Western species, as predicted, although the difference was only significant for interior species. Eastern species also appeared to be more variable in their response to patch size effects than Western species (Fig. 3). Contrary to prediction, the interaction term between MIGRATION and LOCATION was not significant ($Q = 2.59$, df $= 1$, $P = 0.110$), although there was a strong interaction between HABITAT and LOCATION ($Q = 13.05$, df $= 2$, $P = 0.001$). After controlling for the effects of HABITAT and LOCATION, there was a significant difference in weighted-mean effect sizes between migrant and resident species ($Q = 27.28$, df $= 1$, $P < 0.001$). On average, migrant species tended to have lower effect sizes than resident species for both the edge and interior groups, although

no differences occurred for generalists (Fig. 4). The interaction term for MIGRATION and HABITAT was not significant ($Q = 2.94$, df $= 2$, $P = 0.230$). Because birds accounted for all of the migrant species in this analysis, we removed the mammals and insects from the data set and recomputed the analysis. The observed trends were nearly identical to those shown in Fig. 4, although the significance of MIGRATION increased slightly ($Q = 32.9$, df $= 1$, $P < 0.001$).

After controlling for the effects of HABITAT, there were differences between mean effect sizes among the three taxonomic groups and the two trophic levels (TAXON: $Q = 11.10$, df $= 2$, $P = 0.004$; and TROPHY: $Q = 13.77$, df $= 1$, $P < 0.001$). On average, mammals tended to have higher effect sizes than birds, although these differences were not significant at the $\alpha = 0.05$ level (Fig. 5). There were no significant differences
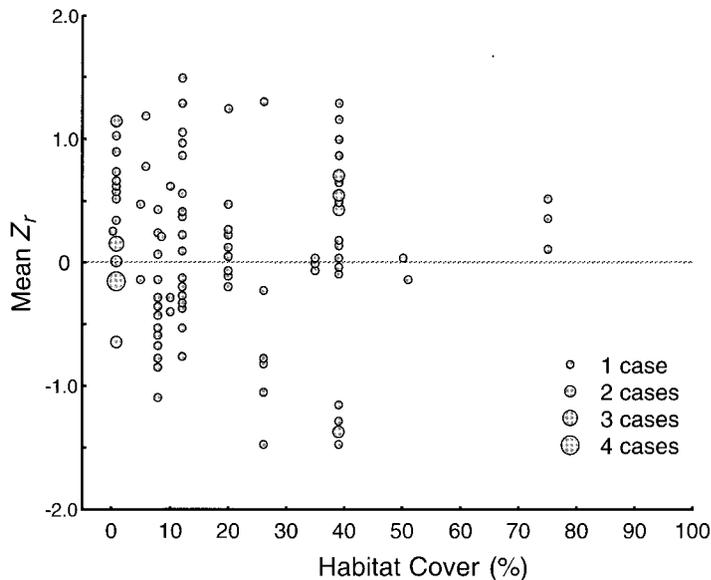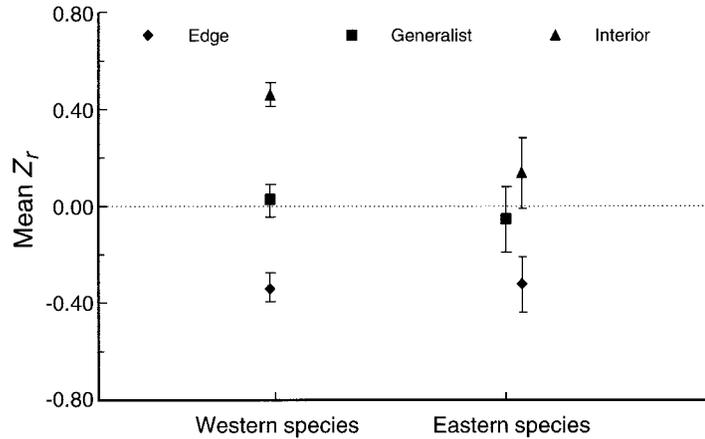


FIG. 2. Scatter plot of individual effect sizes against the percentage of landscape covered by habitat. Larger circles indicate points for which there is more than one effect size.

FIG. 3. Mean patch size effects ($Z_r$) for Western (North and South American) and Eastern (European and African) species. Error bars indicate 95% CI.

between herbivores and carnivores for either the interior or generalist species. However, herbivore edge species tended to have greater negative effect sizes than did carnivore edge species (Fig. 6).

Although the patterns reported by the random-effects models were very similar to those generated in the fixed-effects procedure, the conclusions were not identical. Using the more conservative random-effects procedure, the variables TAXON and TROPHY were not significant, and the variable MIGRANT was only marginally significant ($P < 0.10$). We include this information so that the reader is aware that the generality of our results for these three factors may not be as strong as our fixed-effects analysis appears to indicate.

### DISCUSSION

Habitat association explained most of the variation in effect sizes. Patch size effects were commonly observed for edge and interior species, but were not common for habitat generalists (Fig. 1). We anticipated this result, because animal densities were calculated in a biased fashion by many investigators. This bias occurred when the density of a species within a patch was calculated using total patch area, rather than the

area of the inhabited portion of the patch. When the animal densities are calculated using total patch size, values for edge and interior species are always underestimated. This underestimate is most pronounced in large patches for edge species, and in small patches for interior species, which we call the "geometric" effect. Because the degree of underestimation depends on patch size, there will always be an apparent relationship between density and patch size for edge and interior species. This effect was remarkably evident in our study and has been reported numerous times in the literature (e.g., Whitcomb et al. 1981, Lynch and Whigham 1984, Freemark and Merriam 1986, Blake and Karr 1987, Merriam and Wegner 1992, Johns 1993, McGarigal and McComb 1995).

Although we observed a large patch size effect for edge and interior species, we cannot say how much of this effect is attributable to the geometric effect alone. It could be hypothesized that edge and interior species are more prone to patch size effects for reasons other than the geometric effect; i.e., that other factors were also contributing to the effect sizes we observed. One could test this hypothesis by using an unbiased density measure, calculated using the area of the patch that is



FIG. 4. Mean patch size effects ($Z_r$) for migrant and resident species. Error bars indicate 95% CI.
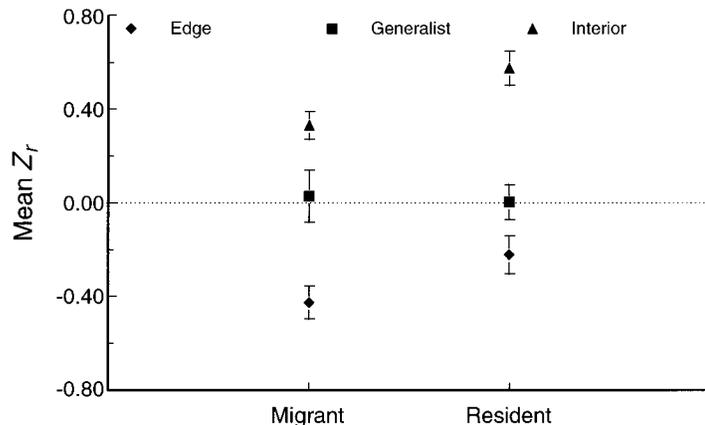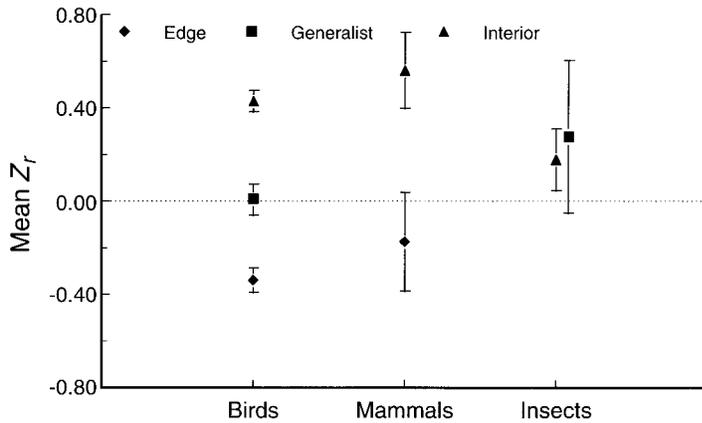
FIG. 5. Mean patch size effects ($Z_r$) for birds, mammals, and insects. Error bars indicate 95% CI.

actually inhabited by any given species rather than the entire patch area. Thus, a measure of the strength of the relationship between usable patch area and density would not be subject to the geometric effect, and a significant patch size effect would be attributable to something inherent in edge and/or interior species themselves. The difficulty in applying such an approach is that it is usually not possible or practical to determine the actual proportion of each patch that is used by a particular species. Although boundary distances have been reported for a few species (e.g., Kroodsma 1984), the actual boundaries that separate edge and interior habitat are difficult to define because they are "fuzzy," meaning that there is no distinct threshold beyond which the distribution of an animal abruptly begins or ends. The vast majority of studies that we reviewed for this paper made no attempts to distinguish between usable habitat and total habitat in a patch. It is also not appropriate to make simplifying assumptions about patch shape and the position of the boundary between edge and interior habitat within the patch to estimate the proportion of a patch that is usable. Such boundary distances are most certainly site specific because they are determined by local conditions (e.g., microclimate,

vegetation composition, presence of ecological enemies). Therefore, boundary distance estimates may be relevant only to the population under study and may not be reliably extrapolated to other populations within a species. For these reasons, we did not attempt to measure patch area at the resolution of usable patch area.

Perhaps our most interesting result was that generalist species regularly showed a mean patch size effect that was very close to zero, regardless of which landscape or life history variables were included in the statistical models (Figs. 3–6). This result suggests that for species not subject to geometric effects, patch size effects tend to be small or negligible. The paramount question then becomes, would edge and interior species show similarly negligible patch size effects had density been measured only for the habitable portion of the patch? Our results indicate that other variables, such as migration strategy or animal taxa, are related to the occurrence of patch size effects, which suggests that the relationship is more complex. This question has received remarkably little attention in the literature, and certainly warrants further investigation.

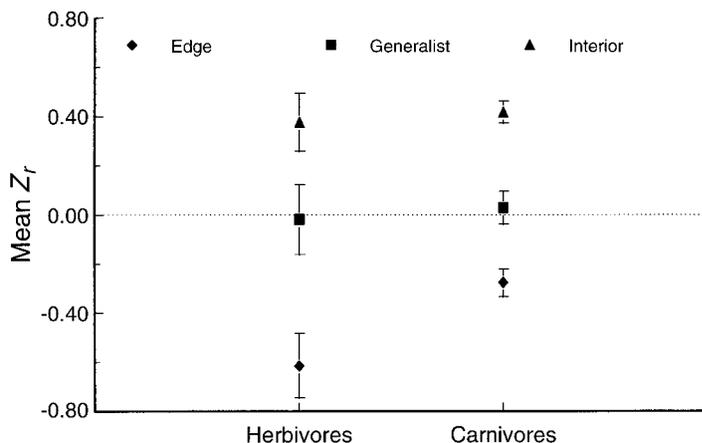Although we could not partition out the source(s) of



FIG. 6. Mean patch size effects ($Z_r$) for herbivorous and carnivorous species. Error bars indicate 95% CI.

the strong patch size effects that were observed for edge and interior species, this result is still interesting. It confirms that the patch size effect is a general and predictable effect that occurs for a broad set of edge and interior species living in patchy landscapes. Regardless of the mechanism(s), this result predicts that habitat loss and fragmentation will greatly affect the abundance of edge and interior species. In situations in which habitat loss and fragmentation create a greater number of smaller patches from pieces of previously contiguous habitat, interior species should always suffer a decline in population, attributable to these patch size effects, that occurs in addition to the decline attributable to habitat loss. This is because the actual density of the species within patches will be predicted to decline as patches get smaller and smaller. The opposite effect should be seen in edge species, for which population densities may actually increase as patches become smaller and proportional amounts of edge habitat increase. The pattern will continue as patches decline in size, until each patch no longer contains any interior habitat and is all edge habitat. This increase in density will offset the decline in population size associated with habitat loss that occurs when habitat is destroyed.

We also stress that these predictions are contingent upon the pattern of habitat destruction. They are based on the assumption that habitat destruction will subdivide existing habitat patches to form new patches that are (necessarily) smaller than those previously in the landscape (i.e., the process of fragmentation). Habitat destruction that only removes habitat and has little effect on the fragmentation of patches in the landscape will not produce the predicted effects. In fact, certain patterns of loss could produce the opposite effect. For example, one can envision a pattern of habitat destruction that removes all the small patches from a landscape, but nothing else. In this case, the layout of habitat patches within the landscape has not changed much, but the effect on edge and interior species will be opposite to our predictions. The removal of small patches will have more of an impact on edge species than on interior species, because small patches contain proportionally more edge habitat. Consequently, observed declines in regional abundance potentially will be greater for edge species than for interior species in such a case. Therefore, for edge and interior species, the decline in population size associated with habitat destruction will depend both on habitat fragmentation per se and on the pattern of habitat loss if large or small patches are preferentially removed.

We hypothesized that a number of different factors relating to landscape characteristics or species life history traits might explain when patch size effects are important determinants of population density. To remove the predictable geometric effect, we statistically controlled for the average effect of habitat association before assessing the significance of other predictor variables. We found no relationship between effect size and COVER, so it appears that the proportion of habitat in the landscape does not determine the emergence of patch size effects. This result apparently contradicts the conclusions of another literature review (Andrén 1994) that demonstrated a tendency for patch size and isolation effects to emerge as percent cover decreased. Andrén predicted that, as the extent of habitat fragmentation within a landscape increased, patch size and isolation effects would emerge and contribute to the decline of species richness and abundance that occurs due to pure habitat loss alone. Andrén also suggested the presence of a threshold value of percent cover below which these patch size and isolation effects would begin to emerge, but we found no evidence of such a relationship in the studies we reviewed.

We offer two possible explanations for the apparent disagreement between Andrén's (1994) results and ours. First, Andrén used a vote-counting method to summarize the findings of each study he reviewed, which is prone to error. His response variable was simply a ''yes'' or ''no'' vote that described whether the study rejected the random-sample hypothesis. This type of response is very coarse in comparison to the continuous response variable we used in the meta-analysis approach. Also, this method does not account for direction of the effect. In meta-analysis, positive and negative effects tend to cancel each other out, whereas in a vote-counting approach, two opposing effects would appear to support one another. Thus, the two methods can yield different results even when similar data are used.

A second explanation for the discrepancy is that Andrén's (1994) review used studies that examined the effect of both patch size and patch isolation, whereas ours was concerned only with patch size effects. We did not assess isolation in our analysis because the data were simply not available. The isolation of individual patches was almost never given, even when patch size was reported. Andrén (1994) did assess isolation, but he did not differentiate between studies that reported significant patch size–density relationships and those that reported patch isolation–density relationships. Therefore, it is possible that many of the significant results Andrén encountered may have been due to isolation effects and not to patch size effects. An important, unanswered question is which effect is more important: patch size or isolation? Given that it is difficult to gather enough field data to assess this issue, spatially explicit population modeling is likely to be the most successful approach to answering this question.

The purpose of including the variables PSIZE, AREA, and RANGE was to determine whether the study design would influence the outcome of the test for a patch size–density relationship. We found no evidence that either the absolute scale of the study or the range in patch sizes was related to the study outcome. Further, these variables were never significant predic-

tors of effect size in any of the multivariate regression models, suggesting that the differences between studies that could be attributable to design were negligible. These results suggest that either (1) studies generally were conducted at spatial scales that were meaningful to the organism, or that (2) studies generally were never conducted at meaningful scales. Although we cannot conclude which is the case, we assume that it is the former.

Migratory status was the most significant life history predictor of the patch size effect. Many migrant species are thought to be more area sensitive, whereas resident species are said to be more "tolerant" of fragmentation effects because of differences in life history traits. For example, residents are reported to exhibit differences in nest-building behaviors that make them less susceptible to predators (Weins 1989*b*, Hansen and Urban 1992, Bohning-Gaese et al. 1993). However, our results contradict the literature, and suggest that the relationship is more complex. We found that patch size effects were contingent upon both migratory status and habitat association. Our results show that, on average, migrant species had significantly lower effect sizes than did residents (generalists exempt; Fig. 4). Therefore, as habitat loss and fragmentation occur and habitat patches are reduced in area, patch size effects should produce a greater decline for resident interior species than for migrant interior species. Because the patch size effects are negative for edge species, migrant edge species will be predicted to show a greater increase in density, due to patch size effects, than will resident edge species. In both cases, the population decline associated with patch size effects is predicted to be greater for resident than for migrant species, which is contrary to current conviction. It is likely that the current view has arisen from confusions in the use of the term habitat fragmentation. The term has often been used to imply both habitat loss and fragmentation, even though these are two different effects. Such a definition is dangerous because one can always expect an effect of habitat loss, even when there is no effect of habitat fragmentation. If one cannot separate these two effects, one will conclude that there is a "fragmentation" effect, even when habitat loss is the only factor affecting population decline (Fahrig 1997).

We also note that the differences we report between migrants and residents may have nothing to do with migratory habits at all, but rather they could be explained by phylogenetic differences between the two groups of species. For example, if all of the birds in the migratory class belonged to one taxon and the residents to another, then our results could also be explained in terms of phylogeny. However, this was not the case in our study, because we have a reasonably broad diversity of taxa from many different geographic locales (Appendix C). Although it would have been possible to examine phylogeny, we felt that a phylogenetic explanation for the pattern we observed was unlikely, given the breadth and interspersion of bird species in our data.

One may have expected that patch size effects would differ between birds, mammals, and insects, because of differences in their ability to disperse between patches and across hostile territory. Presumably, flying animals should be better equipped to move around the landscape and to exploit the maximum amount of available habitat. However, our results indicate that dispersal ability may not be an important factor. In the only other study that has tested this prediction, Andrén (1994) demonstrated similar results that, surprisingly, there was no significant difference between birds and mammals in their responses to habitat fragmentation.

Our results suggest that fragmentation may actually have a tendency to increase densities of herbivore edge species more so than for carnivores (Fig. 6). We can only speculate on the reason, but it is possible that herbivore densities may be more closely linked to food production in edge habitat. It has been shown that the diversity and productivity of edge plant species is greater in small than in large patches (Levenson 1981). Relatively greater levels of primary productivity may result in greater amounts of food for edge herbivores, particularly small, frugivorous mammals (Santos and Telleria 1994). Food levels for carnivores will not necessarily follow this same pattern.

### Summary

The goal of this study was to summarize the patch size–density relationship for a variety of animals occurring in different landscape types to predict when patch size effects should be important determinants of population size. Using meta-analysis, we were able to produce generalizations that define the conditions under which patch size effects are expected to occur, and that allow us to predict the direction and magnitude of those effects. For landscapes undergoing habitat loss and fragmentation, it is important to know when patch size effects will emerge, because they will either contribute to or offset the decline of organisms that is attributable to habitat loss. The following is a summary of predictions that are based on results of our review:

1. *For generalist species that are not associated with only the edge or only the interior habitat, the decline in population size associated with habitat destruction should be accounted for by pure habitat loss alone.*—In other words, patch size effects are not expected to be an important factor in determining the population size of generalist species in fragmented landscapes.

2. *For interior species, the decline in population size associated with habitat fragmentation per se will be greater than that predicted from pure habitat loss alone.*—This will always occur, because the ratio of interior habitat to total patch size declines as patches become smaller following habitat fragmentation and loss.

3. *For edge species, the decline in population size will be less than that predicted by pure habitat loss alone.*—In fact, relative abundances of edge species may actually increase in the landscape following fragmentation, especially if fragmentation serves to increase the total amount of edge habitat for these species.

4. *These relative effects will not be influenced by the extent of habitat loss, but they will be affected by the pattern of habitat loss for edge and interior species if only small or large patches are preferentially removed.*—In other words, patch size effects are not expected to be dependent upon the amount of habitat cover that is present in the landscape. However, if the pattern of loss removes predominantly only small patches, pure habitat loss will have a greater effect on edge species than on interior species. Likewise, if only large patches are removed, habitat loss will have a greater effect on interior species.

5. *As fragmentation increases within a landscape, migratory species will generally suffer less of a decline in population size than resident species.*—Resident interior species show the largest patch size effects, indicating that this group should suffer the greatest amount of decline associated with habitat fragmentation. Conversely, migrant edge species show the most negative patch size effects, which will offset the population decline associated with habitat loss.

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# APPENDIX A

Procedures for determining the loss function of the weighted least squares regression equations for landscape-level variables.

All effect sizes within an individual study shared common values for each of the landscape-level variables. Because of this, a single study with multiple effect sizes could produce a cluster of data points that would potentially bias the fit of the regression equations in the meta-analysis. This would be particularly evident if there were some aspect of the study that resulted in consistently high or low effect sizes. In such a case, the effect of the within-study bias would be a function of the number of effect sizes contributed by that study, such that a greater number of effect sizes would translate into a greater bias.

When landscape-level variables were tested, we ensured that each study contributed an equal weight to the fit of the regression equations, regardless of the number effect sizes contributed. To achieve this, we modified the loss function of the regression equation so that each effect size was also weighted by the inverse of the number of effect sizes contributed by its respective study.

The unmodified loss function used for calculating the regression coefficients in the meta-analysis was

$$\sum (Y_{ij} - Y_{\text{predicted}})w_{ij} \tag{A.1}$$

where $w_{ij}$ is the reciprocal of the sampling variance for the $j$th effect size of the $i$th study.

A second weighting factor was applied to Eq. A.1 so that each effect size was weighted by the reciprocal of the number of effect sizes that each study reported. The modified loss function then became

$$\sum (Y_{ij} - Y_{\text{predicted}})w_{ij}n_i^{-1} \tag{A.2}$$

where $n_i$ is the number of effect sizes contributed by the $i$th study. Therefore, the relative contribution of each study to the fit of the regression equation was equal, after weighting by sampling variance. This method is preferable because it approximates a significance test that uses only a single sampling unit per study, but accounts for variable responses (i.e., many effect sizes) that may occur within a study.

**APPENDIX B**
Summary of studies and data used in the meta-analysis.

| Source | Journal | Taxon | Number of effect sizes | Habitat type |
|---|---|---|---|---|
| Adler et al. (1986) | *Journal of Mammalogy* | mammals | 1 | salt-marsh |
| Ambuel and Temple (1983) | *Ecology* | birds | 1 | forest |
| Apeldoorn et al. (1992) | *Oikos* | mammals | 1 | forest |
| Bach (1984) | *Ecology* | insects | 2 | forest |
| Bach (1988) | *Ecology* | insects | 3 | artificially constructed landscape; host plant: buttercup squash |
| Blake and Karr (1987) | *Ecology* | birds | 15 | forest |
| van Dongen et al. (1994) | *Acta Oecologia* | insects | 1 | forest |
| Fitzgibbon (1993) | *Journal of Applied Ecology* | mammals | 1 | forest |
| Hanski et al. (1995) | *Oikos* | insects | 1 | grassland |
| Henderson et al. (1985) | *Biological Conservation* | mammals | 1 | forest |
| Herkert (1994) | *Ecological Applications* | birds | 12 | grassland |
| Hertzberg et al. (1994) | *Ecography* | insects | 4 | grassland (*Carex* tussocks) |
| Keith et al. (1993) | *Canadian Journal of Zoology* | mammals | 1 | forest |
| Launere and Murphy (1994) | *Biological Conservation* | insects | 1 | grassland |
| Loman (1991) | *Landscape Ecology* | mammals | 3 | non-agricultural habitat patches in agricultural landscape |
| Lynch and Whigham (1984) | *Biological Conservation* | birds | 22 | forest |
| Martin and Lepart (1989) | *Journal of Biogeography* | birds | 23 | forest |
| Martin et al. (1995) | *Oikos* | birds | 24 | forest |
| Nilsson (1977) | *Oikos* | birds | 8 | forest |
| Nilsson (1986) | *Biological Conservation* | birds | 14 | wetlands |
| Robbins et al. (1989) | *Wildlife Monographs* | birds | 4 | forest |
| Rolstad and Wegge (1987) | *Oecologia* | birds | 1 | forest |
| Smith (1974) | *Ecology* | mammals | 1 | forest |
| Telleria and Santos (1995) | *Biological Conservation* | birds | 7 | forest |
| Thiollay and Meyburg (1988) | *Biological Conservation* | birds | 1 | forest |

**APPENDIX C**
Species used in the meta-analysis.

| Species | Locality | Habitat | Status | No. pat-ches | Effect size ($r$) | Study |
|---|---|---|---|---|---|---|
| A) Birds | | | | | | |
| *Aegithalos caudatus* | Spain | generalist | resident | 31 | 0.03 | Telleria and Santos (1995) |
| *Agelaius phoeniceus* | Illinois, USA | edge | migrant | 14 | 0.59 | Blake and Karr (1987) |
| *Agelaius phoeniceus* | Illinois, USA | edge | migrant | 24 | −0.57 | Herkert (1994) |
| *Ammodramus henslowii* | Illinois, USA | interior | migrant | 24 | 0.81 | Herkert (1994) |
| *Anas crecca* | Sweden | edge | migrant | 27 | −0.59 | Nilsson (1986) |
| *Anas platyrhynchos* | Sweden | edge | resident | 30 | −0.69 | Nilsson (1986) |
| *Anthus trivialis* | Finland | edge | migrant | 11 | 0.36 | Martin and Lepart (1989) |
| *Archilochus colubris* | Maryland, USA | edge | migrant | 10 | 0.24 | Lynch and Whigham (1984) |
| *Ardea cinerea* | Sweden | edge | migrant | 8 | −0.13 | Nilsson (1986) |
| *Bartramia longicauda* | Illinois, USA | edge | migrant | 24 | 0.14 | Herkert (1994) |
| *Branta canadensis* | Sweden | generalist | migrant | 22 | −0.53 | Nilsson (1986) |
| *Bucephala clangula* | Sweden | edge | resident | 20 | −0.49 | Nilsson (1986) |
| *Cardinalis cardinalis* | Illinois, USA | generalist | resident | 14 | 0.50 | Blake and Karr (1987) |
| *Carduelis pinus* | British Columbia, Canada | interior | resident | 65 | 0.82 | Martin et al. (1995) |
| *Carduelis spinus* | Finland | interior | migrant | 12 | 0.51 | Martin and Lepart (1989) |
| *Catharus guttatus* | British Columbia, Canada | interior | migrant | 65 | 0.41 | Martin et al. (1995) |
| *Certhia americana* | British Columbia, Canada | interior | resident | 65 | 0.57 | Martin et al. (1995) |
| *Cistothorus platensis* | Illinois, USA | interior | migrant | 24 | 0.14 | Herkert (1994) |
| *Coccyzus americanus* | Illinois, USA | interior | migrant | 14 | 0.63 | Blake and Karr (1987) |
| *Coccyzus americanus* | Maryland, USA | interior | migrant | 72 | 0.25 | Lynch and Whigham (1984) |
| *Colaptes auratus* | British Columbia, Canada | edge | migrant | 65 | −0.04 | Martin et al. (1995) |
| *Colaptes auratus* | Maryland, USA | edge | resident | 106 | 0.07 | Lynch and Whigham (1984) |
| *Columba palumbus* | Finland | edge | migrant | 6 | 0.78 | Martin and Lepart (1989) |
| *Contopus virens* | Maryland, USA | interior | migrant | 71 | 0.08 | Lynch and Whigham (1984) |
| *Corvus caurinus* | British Columbia, Canada | edge | resident | 65 | −0.88 | Martin et al. (1995) |
| *Corvus corax* | British Columbia, Canada | edge | resident | 65 | 0.18 | Martin et al. (1995) |
| *Corvus corone* | Finland | edge | migrant | 13 | −0.24 | Martin and Lepart (1989) |
| *Cuculus canorus* | Finland | generalist | migrant | 5 | 0.90 | Martin and Lepart (1989) |
| *Cyanocitta cristata* | Maryland, USA | generalist | resident | 156 | −0.05 | Lynch and Whigham (1984) |
| *Dendragapus obscurus* | British Columbia, Canada | interior | resident | 65 | 0.40 | Martin et al. (1995) |
| *Dendroica caerulescens* | Maryland and W. Virginia, USA | interior | migrant | 13 | 0.48 | Robbins et al. (1989) |
| *Dendroica townsendi* | British Columbia, Canada | interior | migrant | 65 | 0.04 | Martin et al. (1995) |
| *Dolichonyx oryzivorus* | Illinois, USA | interior | migrant | 24 | 0.81 | Herkert (1994) |
| *Dryocopus martius* | Finland | interior | resident | 5 | −0.64 | Martin and Lepart (1989) |
| *Dryocopus pileatus* | Maryland, USA | interior | resident | 6 | 0.85 | Lynch and Whigham (1984) |
| *Dumetella carolinensis* | Maryland, USA | edge | migrant | 24 | 0.44 | Lynch and Whigham (1984) |
| *Emberiza schoeniclus* | Sweden | edge | migrant | 6 | −0.90 | Nilsson (1977) |
| *Empidonax difficilis* | British Columbia, Canada | interior | migrant | 65 | 0.70 | Martin et al. (1995) |
| *Empidonax virescens* | Maryland, USA | interior | migrant | 101 | 0.07 | Lynch and Whigham (1984) |
| *Empidonax virescens* | Illinois, USA | interior | migrant | 14 | 0.73 | Blake and Karr (1987) |
| *Erithacus rubecula* | Finland | generalist | migrant | 12 | 0.86 | Martin and Lepart (1989) |
| *Fringilla coelebs* | Sweden | edge | migrant | 6 | −0.78 | Nilsson (1977) |
| *Gavia arctica* | Sweden | edge | migrant | 10 | −0.65 | Nilsson (1986) |
| *Geothlypis trichas* | Illinois, USA | generalist | migrant | 24 | −0.14 | Herkert (1994) |
| *Helmintheros vermivorus* | Maryland, USA | interior | migrant | 15 | −0.19 | Lynch and Whigham (1984) |
| *Hylocichla mustelina* | Illinois, USA | interior | migrant | 14 | 0.55 | Blake and Karr (1987) |
| *Ixoreus naevius* | British Columbia, Canada | interior | migrant | 65 | 0.86 | Martin et al. (1995) |
| *Junco hyemalis* | British Columbia, Canada | interior | resident | 65 | 0.61 | Martin et al. (1995) |
| *Larus argentatus* | Sweden | generalist | migrant | 9 | 0.40 | Nilsson (1986) |
| *Larus canus* | Sweden | edge | resident | 34 | −0.35 | Nilsson (1986) |
| *Larus marinus* | Sweden | generalist | migrant | 8 | −0.28 | Nilsson (1986) |
| *Loxia curvirostra* | British Columbia, Canada | interior | resident | 65 | 0.71 | Martin et al. (1995) |
| *Melanerpes carolinus* | Illinois, USA | generalist | resident | 14 | 0.64 | Blake and Karr (1987) |
| *Melospiza georgiana* | Illinois, USA | edge | migrant | 24 | −0.14 | Herkert (1994) |
| *Melospiza melodia* | Illinois, USA | edge | migrant | 24 | −0.57 | Herkert (1994) |
| *Melospiza melodia* | British Columbia, Canada | edge | migrant | 65 | −0.88 | Martin et al. (1995) |
| *Mergus merganser* | Sweden | edge | resident | 16 | −0.24 | Nilsson (1986) |
| *Mergus serrator* | Sweden | edge | resident | 6 | 0.07 | Nilsson (1986) |
| *Mniotilta varia* | Maryland, USA | interior | migrant | 12 | 0.22 | Lynch and Whigham (1984) |
| *Molothrus ater* | Illinois, USA | edge | migrant | 14 | 0.58 | Blake and Karr (1987) |
| *Motacilla alba* | Sweden | generalist | migrant | 6 | −0.66 | Nilsson (1977) |
| *Muscicapa hypoleuca* | Finland | edge | migrant | 7 | 0.11 | Martin and Lepart (1989) |
| *Muscicapa striata* | Finland | generalist | migrant | 8 | −0.27 | Martin and Lepart (1989) |
| *Myiarchus crinitus* | Maryland, USA | edge | migrant | 102 | −0.07 | Lynch and Whigham (1984) |
| *Pandion haliaetus* | Sweden | generalist | migrant | 12 | −0.40 | Nilsson (1986) |
| *Parus atricapillus* | Illinois, USA | generalist | resident | 14 | 0.62 | Blake and Karr (1987) |
| *Parus bicolor* | Illinois, USA | generalist | resident | 14 | 0.48 | Blake and Karr (1987) |

**APPENDIX C.** Continued.

| Species | Locality | Habitat | Status | No. pat-ches | Effect size (r) | Study |
|---|---|---|---|---|---|---|
| *Parus bicolor* | Maryland, USA | generalist | resident | 181 | −0.05 | Lynch and Whigham (1984) |
| *Parus caeruleus* | Finland | generalist | resident | 8 | −0.35 | Martin and Lepart (1989) |
| *Parus caeruleus* | Spain | generalist | resident | 31 | −0.07 | Telleria and Santos (1995) |
| *Parus carolinensis* | Maryland, USA | generalist | resident | 159 | −0.05 | Lynch and Whigham (1984) |
| *Parus cristatus* | Spain | generalist | resident | 31 | 0.07 | Telleria and Santos (1995) |
| *Parus major* | Finland | generalist | resident | 12 | −0.49 | Martin and Lepart (1989) |
| *Parus major* | Spain | generalist | resident | 31 | 0.00 | Telleria and Santos (1995) |
| *Parus montanus* | Finland | generalist | resident | 8 | −0.19 | Martin and Lepart (1989) |
| *Parus rufescens* | British Columbia, Canada | interior | resident | 65 | 0.50 | Martin et al. (1995) |
| *Parus* spp. | Sweden | generalist | resident | 6 | 0.86 | Nilsson (1977) |
| *Passerella iliaca* | British Columbia, Canada | edge | migrant | 65 | −0.90 | Martin et al. (1995) |
| *Phasianus colchicus* | Illinois, USA | generalist | resident | 24 | −0.14 | Herkert (1994) |
| *Pheucticus ludovicianus* | Maryland and W. Virginia, USA | interior | migrant | 56 | 0.10 | Robbins et al. (1989) |
| *Pheucticus ludovicianus* | Wisconsin, USA | interior | migrant | 26 | 0.44 | Ambuel and Temple (1983) |
| *Phylloscopus sibilatrix* | Finland | interior | migrant | 8 | 0.70 | Martin and Lepart (1989) |
| *Phylloscopus trochilus* | Finland | edge | migrant | 13 | 0.09 | Martin and Lepart (1989) |
| *Phylloscopus trochilus* | Sweden | edge | migrant | 6 | −0.68 | Nilsson (1977) |
| *Picoides pubescens* | Illinois, USA | generalist | resident | 14 | 0.52 | Blake and Karr (1987) |
| *Picoides villosus* | Illinois, USA | interior | resident | 14 | 0.77 | Blake and Karr (1987) |
| *Picoides villosus* | British Columbia, Canada | interior | resident | 65 | 0.76 | Martin et al. (1995) |
| *Picoides villosus* | Maryland, USA | interior | resident | 44 | −0.10 | Lynch and Whigham (1984) |
| *Pipilo erythrophthalmus* | Maryland, USA | edge | resident | 116 | −0.06 | Lynch and Whigham (1984) |
| *Piranga olivacea* | Maryland, USA | interior | migrant | 155 | −0.05 | Lynch and Whigham (1984) |
| *Piranga olivacea* | Illinois, USA | interior | migrant | 14 | 0.72 | Blake and Karr (1987) |
| *Podiceps cristatus* | Sweden | edge | migrant | 16 | −0.80 | Nilsson (1986) |
| *Polioptila caerulea* | Maryland, USA | edge | migrant | 26 | 0.14 | Lynch and Whigham (1984) |
| *Prunella modularis* | Finland | edge | migrant | 10 | 0.75 | Martin and Lepart (1989) |
| *Regulus ignicapillus* | Spain | interior | migrant | 31 | −0.07 | Telleria and Santos (1995) |
| *Regulus regulus* | Spain | interior | migrant | 31 | −0.07 | Telleria and Santos (1995) |
| *Regulus regulus* | Finland | interior | migrant | 13 | 0.39 | Martin and Lepart (1989) |
| *Regulus satrapa* | British Columbia, Canada | interior | resident | 65 | 0.50 | Martin et al. (1995) |
| *Seiurus noveboracensis* | Maryland and W. Virginia, USA | interior | migrant | 33 | 0.34 | Robbins et al. (1989) |
| *Selasphorus rufus* | British Columbia, Canada | edge | migrant | 65 | −0.86 | Martin et al. (1995) |
| *Sitta canadensis* | British Columbia, Canada | interior | resident | 65 | 0.45 | Martin et al. (1995) |
| *Sitta carolinensis* | Maryland, USA | interior | resident | 14 | −0.20 | Lynch and Whigham (1984) |
| *Sitta carolinensis* | Illinois, USA | interior | resident | 14 | 0.64 | Blake and Karr (1987) |
| *Sitta europaea* | Spain | interior | resident | 31 | 0.02 | Telleria and Santos (1995) |
| *Sphyrapicus ruber* | British Columbia, Canada | interior | resident | 65 | 0.14 | Martin et al. (1995) |
| *Spilornis cheela* | Java | interior | resident | 5 | 0.75 | Thiollay and Meyburg (1988) |
| *Spiza americana* | Illinois, USA | interior | migrant | 24 | 0.14 | Herkert (1994) |
| *Spizella pusilla* | Illinois, USA | edge | migrant | 24 | −0.14 | Herkert (1994) |
| *Sterna hirundo* | Sweden | generalist | migrant | 14 | −0.27 | Nilsson (1986) |
| *Sturnella magna* | Illinois, USA | interior | migrant | 24 | 0.57 | Herkert (1994) |
| *Sturnus vulgaris* | Illinois, USA | edge | resident | 14 | −0.55 | Blake and Karr (1987) |
| *Sylvia borin* | Finland | edge | migrant | 10 | 0.42 | Martin and Lepart (1989) |
| *Sylvia borin* | Sweden | edge | migrant | 6 | −0.21 | Nilsson (1977) |
| *Sylvia curruca* | Finland | interior | migrant | 13 | 0.22 | Martin and Lepart (1989) |
| *Tetrao urogallus* | Norway | interior | resident | 11 | 0.04 | Rolstad and Wegge (1987) |
| *Thryothorus ludovicianus* | Maryland, USA | edge | resident | 75 | 0.08 | Lynch and Whigham (1984) |
| *Tringa hypoleucos* | Sweden | edge | migrant | 6 | −0.66 | Nilsson (1977) |
| *Troglodytes troglodytes* | British Columbia, Canada | edge | resident | 65 | −0.09 | Martin et al. (1995) |
| *Troglodytes troglodytes* | Finland | interior | migrant | 7 | −0.11 | Martin and Lepart (1989) |
| *Turdus iliacus* | Finland | edge | migrant | 11 | −0.13 | Martin and Lepart (1989) |
| *Turdus merula* | Finland | generalist | migrant | 13 | −0.17 | Martin and Lepart (1989) |
| *Turdus merula* | Sweden | generalist | migrant | 6 | −0.22 | Nilsson (1977) |
| *Turdus migratorius* | British Columbia, Canada | edge | migrant | 65 | 0.61 | Martin et al. (1995) |
| *Turdus philomelos* | Finland | edge | migrant | 8 | −0.31 | Martin and Lepart (1989) |
| *Turdus pilaris* | Finland | edge | migrant | 6 | 0.23 | Martin and Lepart (1989) |
| *Vermivora celata* | British Columbia, Canada | edge | migrant | 65 | −0.82 | Martin et al. (1995) |
| *Vireo flavifrons* | Maryland, USA | interior | migrant | 11 | 0.23 | Lynch and Whigham (1984) |
| *Vireo griseus* | Maryland, USA | generalist | migrant | 34 | 0.12 | Lynch and Whigham (1984) |
| *Vireo olivaceus* | Maryland, USA | generalist | migrant | 172 | 0.05 | Lynch and Whigham (1984) |
| *Vireo olivaceus* | Illinois, USA | generalist | migrant | 14 | 0.63 | Blake and Karr (1987) |
| *Wilsonia canadensis* | Maryland and W. Virginia, USA | interior | migrant | 22 | 0.36 | Robbins et al. (1989) |
| *Wilsonia pusilla* | British Columbia, Canada | interior | migrant | 65 | 0.40 | Martin et al. (1995) |

**APPENDIX C.** Continued.

| Species | Locality | Habitat | Status | No. patches | Effect size $(r)$ | Study |
|---|---|---|---|---|---|---|
| B) Insects | | | | | | |
| *Acalymma innubom* | U.S. Virgin Islands | interior | resident | 18 | 0.66 | Bach (1984) |
| *Acalymma innubon* | U.S. Virgin Islands | interior | resident | 32 | 0.17 | Bach (1984) |
| *Acalymma vittatum* | Michigan, USA | interior | resident | 21 | −0.04 | Bach (1988) |
| *Diabrotica undecimpunctata* | Michigan, USA | generalist | resident | 21 | 0.26 | Bach (1988) |
| *Diabrotica virgitera* | Michigan, USA | generalist | resident | 21 | 0.28 | Bach (1988) |
| *Euphydryas bayensis* | California | interior | resident | 27 | 0.21 | Launere and Murphy (1994) |
| *Folsomia quadrioculata* | Sweden | interior | resident | 30 | 0.82 | Hertzberg et al. (1994) |
| *Folsomia sexoculata* | Sweden | interior | resident | 30 | −0.71 | Hertzberg et al. (1994) |
| *Hypogastrura longispina* | Sweden | interior | resident | 30 | −0.79 | Hertzberg et al. (1994) |
| *Nelitaea cinxia* | Finland | interior | resident | 30 | 0.25 | Hanski et al. (1995) |
| *Onychiurus groenlandicum* | Sweden | interior | resident | 30 | 0.83 | Hertzberg et al. (1994) |
| *Operophtera brumata* | Belgium | generalist | resident | 7 | 0.79 | van Dongen et al. (1994) |
| C) Mammals | | | | | | |
| *Clethrionomys glareolus* | Sweden | edge | resident | 11 | −0.38 | Loman (1991) |
| *Clethrionomys glareolus* | Netherlands | interior | resident | 46 | 0.23 | van Apeldoorn et al. (1992) |
| *Lupus americana* | Wisconsin, USA | edge | resident | 7 | −0.13 | Keith et al. (1993) |
| *Microtus agrestis* | Sweden | edge | resident | 11 | −0.28 | Loman (1991) |
| *Ochotona princeps* | California | interior | resident | 78 | 0.65 | Smith (1974) |
| *Peromyscus leucopus* | Massachusetts, USA | interior | resident | 21 | 0.33 | Adler et al. (1986) |
| *Sciurus carolinensis* | England | edge | resident | 68 | −0.13 | Fitzgibbon (1993) |
| *Sorex araneus* | Sweden | interior | resident | 11 | 0.55 | Loman (1991) |
| *Tamias striatus* | Ontario, Canada | interior | resident | 5 | 0.83 | Henderson et al. (1985) |