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# Edge and Area Effects on the Occurrence of Migrant Forest Songbirds

TIMOTHY H. PARKER,<sup>\*†\*\*</sup> BROOKE M. STANSBERRY,<sup>\*‡</sup> C. DUSTIN BECKER,<sup>§</sup>  
AND PHILIP S. GIPSON<sup>\*</sup>

<sup>\*</sup>Kansas Cooperative Fish and Wildlife Research Unit, U.S. Geological Survey, Division of Biology, Kansas State University, Manhattan, KS 66506, U.S.A.

<sup>†</sup>Edward Grey Institute of Field Ornithology, Department of Zoology, University of Oxford, South Parks Road, Oxford, OX1 3PS, United Kingdom

<sup>‡</sup>Department of Geography, Kansas State University, Manhattan, KS 66506, U.S.A.

<sup>§</sup>Department of Horticulture, Forestry, and Recreation Resources, Throckmorton Plant Sciences Center, Kansas State University, Manhattan, KS 66506, U.S.A.

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**Abstract:** *Concerns about forest fragmentation and its conservation implications have motivated numerous studies that investigate the influence of forest patch area and forest edge on songbird distribution patterns. The generalized effects of forest patch size and forest edge on animal distributions is still debatable because forest patch size and forest edge are often confounded and because of an incomplete synthesis of available data. To fill a portion of this gap, we incorporated all available published data (33 papers) in meta-analyses of forest edge and area effects on site occupancy patterns for 26 Neotropical migrant forest-nesting songbirds in eastern North America. All reported area effects are confounded or potentially confounded by edge effects, and we refer to these as “confounded” studies. The converse, however, is not true and most reported edge effects are independent of patch area. When considering only nonconfounded studies of edge effects, only 1 of 17 species showed significant edge avoidance and 3 had significant affinity for edges. In confounded studies, 12 of 22 species showed significant avoidance of small patches and edges, and 1 had an affinity for small patches and edges. Furthermore, average effect sizes averaged across studies or species tended to be higher for confounded studies than for edge studies. We discuss three possible reasons for differences in results between these two groups of studies. First, studies of edge effects tended to be carried out in landscapes with greater forest cover than studies of confounded effects; among confounded effects studies, as forest cover increased, we observed a nonsignificant trend towards decreasing strength of small patch or edge avoidance effects. Thus, the weaker effects in edge studies may be due to the fact that these studies were conducted in forest-dominated landscapes. Second, we may have detected strong effects only in confounded studies because area effects are much stronger than edge effects on bird occurrence, and area effects drive the results in confounded studies. Third, edge and area effects may interact in such a way that edge effects become more important as forest patch size decreases; thus, both edge and area effects are responsible for results in confounded studies. These three explanations cannot be adequately separated with existing data. Regardless, it is clear that fragmentation of forests into small patches is detrimental to many migrant songbird species.*

**Key Words:** landscape, meta-analysis, Neotropical migrant

Efectos de Borde y de Área Sobre la Ocurrencia de Aves Canoras Migratorias

**Resumen:** *La preocupación sobre la fragmentación de bosques y sus implicaciones en conservación ha motivado numerosos estudios que investigan la influencia del área de parches de bosque sobre los patrones de*

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<sup>\*\*</sup>Current address: Division of Biology, Kansas State University, Manhattan, Kansas, 66506, U.S.A., email [tparker@ksu.edu](mailto:tparker@ksu.edu)  
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*distribución de aves canoras. Los efectos generalizados del tamaño del parche y del borde de bosque sobre la distribución de animales aun son debatibles porque el tamaño y borde a menudo son confundidos y porque la síntesis de los datos disponibles es incompleta. Para llenar parte de este hueco, incorporamos todos los datos disponibles publicados (33 artículos) sobre meta análisis de los efectos de borde y área sobre los patrones de ocupación de sitios de 26 especies de aves canoras migratorias Neotropicales que anidan en bosques del este de Norte América. Todos los efectos de área están enmascarados o potencialmente enmascarados por los efectos de borde, y nos referimos a estos como estudios "enmascarados." Sin embargo, lo contrario no es verdad y la mayoría de los efectos de borde reportados son independientes del área del parche. Al solo considerar estudios de efectos de borde no enmascarados, solo 1 de 17 especies mostró evasión significativa del borde y 3 tenían afinidad significativa por los bordes. En estudios enmascarados, 12 de 22 especies mostraron evasión significativa de parches pequeños y bordes, y 1 tenía afinidad por parches pequeños y bordes. Más aun, el promedio del tamaño de parche promediado para los estudios o especies tendía a ser mayor en los estudios enmascarados que en los estudios de borde. Hablamos tres posibles razones para la diferencias en resultados entre estos dos grupos. Primero, hubo una tendencia a efectuar los estudios de efectos de borde en paisajes con mayor cobertura forestal que los paisajes de estudios de efectos enmascarados; entre los estudios de efectos enmascarados, a medida que incrementó la cobertura forestal observamos una tendencia no significativa hacia la disminución en los efectos de parche pequeño o evasión de borde. Por lo tanto, los efectos más débiles en estudios de borde pueden deberse al hecho de que estos estudios se llevaron a cabo en paisajes dominados por bosques. Segundo, pudimos haber detectado efectos fuertes solo en estudios enmascarados porque los efectos de área son mucho más fuertes que los efectos de borde sobre la ocurrencia de las aves, y los efectos de área guían los resultados en estudios enmascarados. Tercero, los efectos de borde y de área pueden interactuar de tal manera que los efectos de borde son más importantes a medida que decrece el tamaño del parche de bosque; por lo tanto, tanto los efectos de borde como de área son responsables de los resultados en estudios enmascarados. Estas tres explicaciones no se pueden separar correctamente con los datos existentes. No obstante, es claro que la fragmentación de bosques es perjudicial para muchas especies de aves canoras migratorias.*

**Palabras Clave:** meta análisis, migratorio neotropical, paisaje

## Introduction

Certain bird species appear to be sensitive to habitat patch area (Robbins et al. 1989). Some species appear to avoid smaller patches (Robbins et al. 1989), and others suffer higher predation or brood parasitism in landscapes where patches tend to be small (Robinson et al. 1995). Smaller forests tend to have more edge per unit area, so it may be that risks associated with small forests actually result from proximity to edge (Mancke & Gavin 2000). In many regions forests have become limited to small patches with high edge:area ratios, and it is commonly hypothesized that declines in some forest-nesting songbirds are caused by the fragmented nature of remaining forest cover (Robinson et al. 1995).

Researchers have sought to explain the occurrence of forest songbirds by examining local edge and patch area effects (e.g., Blake & Karr 1987; Hawrot & Niemi 1996) and by assessing landscape mosaics (Hansson et al. 1995). There is evidence that effects of patch area and proximity to edge can interact with larger landscape patterns. For instance, nest predation risks increase with proximity to edge, but these patterns are stronger in agricultural or nonforested landscapes than in forest-dominated landscape matrices (Hartley & Hunter 1998; Chalfoun et al. 2002). There is also evidence that forest animals are more likely to be absent from smaller forest patches as the de-

gree of forest cover on a landscape drops (Andrén 1994) or patches become more isolated (Robbins et al. 1989). Thus, when seeking to explain variation in edge or patch area effects, it can be fruitful to consider variation in landscapes among studies.

Both edge and area effects are frequently cited as topics relevant to conservation, but it is not clear which is most relevant to occurrence of forest birds. If avoidance of small patches is simply a manifestation of edge avoidance (Mancke & Gavin 2000), then edge density is clearly the issue of greatest conservation importance. However, if a distinct process leads to small patch avoidance, then conservation efforts may need to account for both edge and area effects in proportion to their relative importance when setting priorities.

Many studies compare patterns of occurrence (presence or density) of bird species with distribution of habitat on the landscape. Assuming a range of available habitat options within potential dispersal distance, occurrence patterns measure the tendency of birds to settle in response to variables such as patch area. Although presence or high density of a species cannot be used to infer habitat suitability (Van Horne 1983; Brawn & Robinson 1996), locations that few or no individuals choose to occupy may be unsuitable (assuming adequate numbers of individuals within dispersal distance). Although in some cases absence from a habitat patch may persist because

of lack of social cues from conspecifics (Ward & Schlossberg 2004), this may be a symptom of other habitat factors (especially patch area, see Discussion) and does not necessarily diminish the usefulness of occurrence data as a partial measure of habitat suitability. Thus, when assessing conservation risk or designing conservation efforts, it is important to know whether individuals are absent or at low densities in habitats with certain characteristics.

Meta-analysis is an established method for compiling published data and drawing general conclusions from a suite of sometimes conflicting results. In meta-analysis statistical results from multiple studies are compiled, weighted according to sample size, and analyzed in a single statistical test of a hypothesis (Rosenthal 1984). Besides providing an unbiased summary, meta-analyses can identify differences among studies leading to differences in results and thus allow more general conclusions than single studies from single locations (e.g., Hartley & Hunter 1998; Chalfoun et al. 2002; Brotons et al. 2003). Meta-analyses do not replace large-scale studies with standard methods (e.g., Donovan et al. 1997; Rosenberg et al. 1999); instead, they do provide a systematic method for summarizing published research findings, and this can lead to important insights.

To date, no extensive reviews or meta-analyses combine the variable results from the literature on edge and patch-area effects on patterns of occurrence of forest bird species in North America. Our objectives in pursuing such a meta-analysis were to (1) locate published data from eastern North America describing edge and patch size effects on the occurrence of forest-nesting, Neotropical migrant songbirds; (2) assess the relative similarity between results of edge-effect studies and studies attempting to assess the effect of area (all confounded by edge and referred to hereafter as “confounded” studies); (3) determine which species’ site occupancy patterns appear influenced by distance to forest edge alone or by a confounded effect of forest patch area and distance to edge; (4) determine whether landscape characteristics of forest and agricultural cover surrounding study areas can explain the strength of effects in edge and confounded studies and differences between these effects; and (5) evaluate the role of study design, including choice of dependent variable, distances to edge examined, and sizes of patches examined, in determining the strength of observed effects in edge or confounded studies.

## Methods

### Locating and Sorting Data

We searched the literature for data regarding occurrence patterns of all forest-nesting Neotropical migrant songbirds related to either forest patch area or distance to forest edge in the eastern half of North America. In a

search of Biological Abstracts (1969–2002), we located at least one usable study for each of 29 species. All studies ( $n = 33$ ) are listed in the Appendix and further details are available from the authors upon request. For each study and species, we recorded the reported relationships between one of our dependent variables of interest (presence, density, or probability of occurrence) and one of our independent variables of interest (forest patch area, core forest area [area of a forest patch that is farther than some minimum distance from an edge], distance to edge, or forest edge versus forest interior). If statistics relating our independent and dependent variables of interest were not presented, we estimated correlation coefficients (for use in our meta-analyses) from other information in the paper, such as figures. We explain each such decision in appendices available from the authors upon request. Most effects we included in our meta-analyses were estimated in the original papers through univariate models. Because results from multivariate models are often less comparable among studies when different multivariate models are presented, we always selected results from univariate models if possible and accepted results from multivariate models only if the effect of interest (edge or area) appeared to be have been the first variable entered in a step-wise procedure or was the strongest effect in the model. The only results not included in the meta-analysis because of this rule were area effects reported from multivariate models for four species in Lynch and Whigham (1984). Univariate results were available or could be calculated in 30 of 33 studies. The remaining three studies (Lynch & Whigham 1984; Grant & Berkey 1999; Mancke & Gavin 2000) presented only multivariate models.

In at least 14 studies in which forest patch area was used as a predictor of species occurrence, sampling effort was greater in larger patches. Thus, sampling effort alone increased the probability of detecting a given forest species in a larger patch, even if that species did not avoid smaller forest patches. In most of these cases, the authors corrected for their sampling bias. In Forman et al. (1976), data and sampling effort are presented in such a way as to allow us to convert some abundance data to density and thus control for sampling bias. In four studies the authors present results that are not corrected for sampling bias and do not include sufficient data to allow correction of this bias. These studies were entirely (Hayden & Faaborg 1985; Villard et al. 1995; Fauth et al. 2000) or partially (Temple 1986) excluded from our meta-analyses.

Studies reporting results of the effect of distance to edge on bird occurrence were in most cases not confounded by patch area. This is because distance-to-edge studies typically assessed bird presence or density at different distances from edge within the same or similar large tracts of forest. Only 2 of 11 edge studies appear to have had their edge effect measures confounded by patch area (Mancke & Gavin 2000; Dunford et al. 2002), and one of these statistically controlled for area when assessing edge

effects (Dunford et al. 2002). Studies of the effects of forest patch area, however, all appear confounded by distance to edge. This is because patch area studies surveyed birds in the middle of patches or throughout the patch. In no cases were surveys of patch area standardized for the distance to the closest edge. Therefore, any results included in our meta-analysis could be due to edge effects. For meta-analyses, we divided studies into two groups: (1) studies that assess edge effects not confounded by area (including one study that statistically controlled for an area confound [Dunford et al. 2002]) and (2) studies that report area effects, all confounded by edge (the "confounded" studies). Also in the confounded studies group, we included one edge effect study (Mancke & Gavin 2000) confounded by area effects.

### Estimates of Landscape Cover

Because the proportion of forest or agricultural cover in a landscape may influence processes associated with edge or patch size (Andr n 1994; Robinson et al. 1995; Hartley & Hunter 1998; Chalfoun et al. 2002), we used satellite images to estimate forest and agricultural land cover surrounding all the study sites. For study sites within the United States, we used the National Land Cover Data (NLCD), a 30-m resolution coverage based on Landsat Thematic Mapper imagery from the early 1990s. This coverage is not available for sites in Canada, so for Canadian sites we used the Land Cover of North America, a portion of the Global Vegetation Monitoring (GVM) Landcover. This is a 1-km resolution coverage based on SPOT 4 satellite imagery from 2000.

Studies differed dramatically in scale, so we could not choose a standard area in which to assess landscape cover. For studies that gave precise delimitation of study area (latitude and longitude coordinates, counties, ranger districts), we assessed cover within relatively simple polygons or circles encompassing the described area.

Some papers identified a point near which the study was conducted. In these cases, we assessed forest and agricultural land cover within a 10-km radius of that point. Assessing land cover within a 10-km radius provides nearly identical estimates of forest and agricultural cover (repeatability >95%) to a 20-km radius. Thus, our estimates are not sensitive to moderate changes in the scale of assessment. We chose these scales in the hopes that the study areas would be encompassed without including large areas beyond the study sites of possibly lower biological relevance.

Several studies were conducted in multiple disjunct landscapes with radically differing forest cover (Robbins et al. 1989; Hobson & Bayne 2000; Austen et al. 2001). For these, we did not attempt to generate an estimate of landscape cover because we did not expect a single image to accurately represent patterns derived from different landscapes. We also did not generate an estimate for

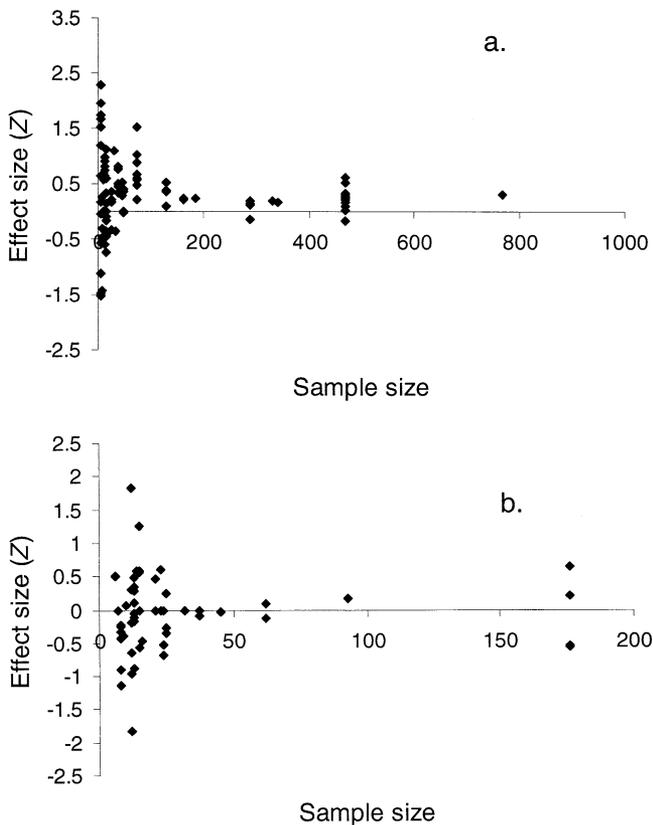
one study (Sallabanks et al. 2000) conducted on a long, narrow stretch of forested riparian corridor in an agricultural matrix. The proportion of forest cover generated from this landscape would have simply been proportional (inversely) to our assessment radius beyond the forested riparian corridor and as such would have been arbitrary. We describe the area examined for each study in appendices available from the authors upon request.

### Bias in Meta-Analysis

A classic problem in meta-analysis is the bias in available studies (Rosenthal 1984). Studies with nonsignificant results are often less likely to be published (Dickersin & Min 1993; Jennions & M ller 2002). It is possible, however, to make an educated guess as to the extent of this problem for a given set of studies. One of the simplest and most accepted ways to do this is to plot, for all the studies, effect sizes (e.g.,  $Z$  scores, a type of correlation coefficient) on the y-axis and sample sizes on the x-axis of a single graph (Light & Pillemer 1984; Palmer 1999). This typically produces a relatively high amount of scatter to the left, with a convergence of points to the right. The shape of this so-called funnel plot is due to high variance in effect sizes in studies with smaller sample sizes, and decreasing variance in effect sizes and a convergence on the true population value as sample sizes increase. If a set of studies on a topic is relatively unbiased with respect to publication of nonsignificant results, then the funnel should be symmetrical and should converge (to the right) on the mean effect size. If nonsignificant results have often gone unpublished, however, the sample mean will fall above the convergence of the funnel, and the funnel will be sparse or truncated in the lower left (where negative results from low-sample size studies would have been found). Funnel plots of our data did not show any noticeable trend in publication bias (Fig. 1).

### Meta-Analysis Details

Typically, correlation coefficients ( $r$ ) transformed to  $Z$  scores are the measure of strength and direction of pattern used in meta-analyses. Data analyses differed, however, among the various studies we located for our meta-analyses. Where a correlation coefficient was not available and could not be calculated based on the data provided, we converted the reported test statistics or one-tailed  $p$  values to correlation coefficient values ( $r$ ) that approximated the strength of the reported relationship with MetaWin (version 2.2, Rosenberg et al. 1997). Thus, although  $r$  values are the basis of our meta-analyses, many of these values were not derived through linear regression; rather, they were secondarily derived from other statistical tests by the methods we describe below. Our use of correlation coefficients does not rely on any secondary assumptions about the shape of the relationships between



**Figure 1.** The relationship between effect size ( $Z$  derived from  $r$ ) and sample size for each (a) study of confounded effects of area and edge and (b) study of edge effects on the distribution of Neotropical migrant, forest-nesting songbirds in eastern North America. Each point represents an effect size for a single species in a single study. Positive effects represent higher rates of occurrence in larger patches or farther from edges. Because the plots are relatively symmetrical, there is no indication of a strong bias in data publication (see text).

variables, although, our analyses were completely dependent on the original published analyses and the assumptions therein. For example if a published result was based on the application of linear tests to nonlinear trends, the strength of relationships reported from such tests is artificially lowered and this affected our meta-analysis estimates. Correlation coefficients were derived from Student's  $t$  as follows:  $r = [t^2/(t^2 + df)]^{1/2}$ . We derived correlation coefficients from one-tailed  $p$  values by initially converting the  $p$  to the standard normal deviate (Sokal & Rohlf 1995) ( $Z$ , not to be confused with Fisher's  $Z$  transformation described below) from which  $r$  was estimated:  $r = Z/(n^{1/2})$ . We then used MetaWin to convert correlation coefficients to  $Z$  scores (Fisher's  $Z$  transformation; the  $Z$  referred to throughout the rest of this paper):  $Z = 1/2 \ln [(1 + r)/(1 - r)]$ . Next we generated variances ( $v_z$ ) for the  $Z$  scores based on a given study's sample size

according to the following calculation:  $v_z = 1/(n - 3)$ . The sample sizes used in these analyses were either the number of forest patches in a study (putative patch area studies) or the number of locations where edge-interior comparisons were made (putative edge studies).

With the individual  $Z$  scores and corresponding variances, MetaWin calculates an overall effect size ( $Z$ , strength and direction of a relationship between two variables) for each species. We used the random effects option in MetaWin (Rosenberg et al. 1997) because random-effects (rather than fixed-effects) meta-analysis models are appropriate when there is an a priori expectation of differences among results caused by true differences in sampled populations (Raudenbush 1994; Rosenberg et al. 2000). To generate 95% confidence intervals around each effect size, we used MetaWin's bootstrap randomization procedure with 9999 iterations.

In the first meta-analysis, we compared the average effect sizes ( $Z$ ) between edge and confounded studies. To avoid pseudoreplication, we used a mean effect size (across all species) per study rather than individual effect sizes for each species. When calculating the means, we did not include species not on our target list (Table 1), such as nonmigrants or nonsongbirds. We also approached this problem another way. First, we selected only those species examined in both confounded and edge studies. Then for edge and confounded studies separately, we determined the mean (across studies) effect size and variance for each species. We then conducted a meta-analysis based on these per-species means to compare results between edge and confounded studies.

Next, we calculated average effect sizes for each species. We identified species with an overall effect size significantly greater than zero (95% bootstrap confidence interval [CI] did not include zero). These are the species that we concluded avoid edges or small forest patches. Two such species lists were generated, one for edge studies only and another for confounded studies only. For each list, once the sensitive species were identified, the data for all other species were discarded before further analyses. In other words, we used species showing significant edge avoidance in subsequent edge effects analyses and species showing significant responses in confounded studies in subsequent analyses of data from confounded studies. We did this because the subsequent tests were designed to determine what factors might influence the strength of edge or small-patch avoidance, and such analyses are relevant only for species that actually respond to these variables. Our lists are probably not complete. For instance, poorly studied species or species studied only under circumstances where their edge or small-patch avoidance behaviors were minimized might not have had confidence intervals sufficient to put them on our lists. Our lists, however, were the best estimate given the information available, and presumably most of the species on the lists have an actual tendency to avoid edges or small

**Table 1.** Relationships between bird occurrence and forest edge and forest patch area derived from random effects meta-analysis for studies in which area and edge effects are confounded and for nonconfounded edge studies.<sup>a</sup>

Species	Confounded studies			Edge studies		
	n	effect size	CI	n	effect size	CI
Acadian Flycatcher ( <i>Empidonax virescens</i> )	4	0.25	-0.61-1.00	3	0.88 <sup>b</sup>	0.29-1.83
American Redstart ( <i>Setophaga ruticilla</i> )	1			3	-0.29	-0.52-0.00
Black-throated Blue Warbler ( <i>Dendroica caerulescens</i> )	1			2	-0.34	-0.67-0.00
Black-throated Green Warbler ( <i>Dendroica virens</i> )	2	0.29 <sup>b</sup>	0.20-0.40	4	0.37	0.00-1.04
Black and White Warbler ( <i>Mniotilta varia</i> )	3	0.01	-0.29-0.33	3	-0.21	-0.42-0.25
Blue-gray Gnatcatcher ( <i>Poliophtila caerulea</i> )	4	0.25	-0.01-0.77	1		
Blue-headed Vireo ( <i>Vireo solitarius</i> )				1		
Canada Warbler ( <i>Wilsonia Canadensis</i> )	1			1		
Cerulean Warbler ( <i>Dendroica cerulea</i> )	2	0.41 <sup>b</sup>	0.32-0.53			
Chestnut-sided Warbler ( <i>Dendroica pensylvanica</i> )				1		
Easter Wood-Pewee ( <i>Contopus virens</i> )	7	0.06	-0.34-0.39			
Great-crested Flycatcher ( <i>Myiarchus crinitus</i> )	9	0.17	-0.20-0.61	3	-0.50 <sup>b</sup>	-0.90--0.20
Hooded Warbler ( <i>Wilsonia citrina</i> )				2	1.10	0.00-1.83
Indigo Bunting ( <i>Passerina cyanea</i> )	8	-0.24 <sup>b</sup>	-0.49--0.02	2	-1.18	-2.65-0.06
Kentucky Warbler ( <i>Oporornis formosus</i> )	3	0.14	-0.34-0.26	1		
Louisiana Waterthrush ( <i>Seiurus motacilla</i> )	1					
Northern Parula ( <i>Parula americana</i> )	3	0.40 <sup>b</sup>	0.24-1.53	2	-0.43	-0.96-0.00
Northern Waterthrush ( <i>Seiurus noveboracensis</i> )	2	0.25 <sup>b</sup>	0.15-0.35			
Ovenbird ( <i>Seiurus aurocapillus</i> )	13	0.52 <sup>b</sup>	0.26-0.72	5	0.22	-0.11-0.50
Red-eyed Vireo ( <i>Vireo olivaceus</i> )	11	0.37 <sup>b</sup>	0.03-0.78	8	0.19	-0.06-0.62
Rose-breasted Grosbeak ( <i>Pheucticus ludovicianus</i> )	5	0.34 <sup>b</sup>	0.19-0.49	2	0.05	0.00-0.12
Scarlet Tanager ( <i>Piranga olivacea</i> )	7	0.36 <sup>b</sup>	0.21-0.52	4	-0.15	-0.40-0.00
Summer Tanager ( <i>Piranga rubra</i> )	3	0.26	-0.10-1.94	3	-1.05 <sup>b</sup>	-1.83--0.24
Veery ( <i>Catharus fuscescens</i> )	3	0.24 <sup>b</sup>	0.14-0.45	2	0.22	0.00-0.49
White-eyed Vireo ( <i>Vireo griseus</i> )	2	0.53 <sup>b</sup>	0.39-1.18	1		
Wood Thrush ( <i>Hylocichla mustelina</i> )	7	0.22	-0.09-0.46	3	-0.19	-0.56-0.00
Worm-eating Warbler ( <i>Helminthos vermivorus</i> )	2	0.33 <sup>b</sup>	0.28-0.40	1		
Yellow-billed Cuckoo ( <i>Coccyzus americanus</i> )	6	0.38 <sup>b</sup>	0.11-0.89	3	-0.27 <sup>b</sup>	-0.64--0.05
Yellow-throated Vireo ( <i>Vireo flavifrons</i> )	3	0.32	-0.42-1.66	1		

<sup>a</sup>Key: n, number of studies from which the mean effect size was derived (at least two studies needed in a given category to conduct an analysis for a species); effect size, Z score, a type of correlation coefficient, positive effect sizes (Z scores) indicate avoidance of small patches or edges and negative effect sizes indicate affinity for small patches or edges; CI, bootstrap-generated 95% CI corresponding to the effect size estimate.

<sup>b</sup>An effect size significantly ( $p < 0.05$ ) different from zero.

patches. A few species showed a preference for edges or smaller patches. We also retained the data from these species for further analysis.

In subsequent meta-analyses based on these edge- and patch-size-sensitive species, we investigated the possible influence of several factors on these avoidance (or affinity) patterns. For both analysis groups, edge and confounded, we asked whether the percent forest or agricultural land on the landscape surrounding a study area influenced the strength of edge and small-patch sensitivity. We also asked whether the dependent variable selected by the researcher influenced the strength of the edge and small patch avoidance or affinity patterns detected. We investigated the effects of other study design factors as well. In analyses of edge studies we assessed the strength of edge avoidance or affinity observed as a function of both the shortest distance and the longest distance to edge surveyed. Similarly, for confounded studies, we compared the strength of effects with the minimum and maximum forest patch size examined in the study. In all these analyses, we assessed significance with  $p$  values

and 95% confidence interval generated by a randomization process in MetaWin. For some analyses with small sample sizes, MetaWin could not calculate random effects models, so we could not draw conclusions in these cases.

### Other Data Analyses

We asked whether edge and confounded studies differed in the amount of forest cover surrounding their study sites. We compared the two study types based on landscape forest cover with Student's  $t$  test. Because our data were percentages, we chose an arc-sine-square-root transformation to improve normality before analysis (Sokal & Rohlf 1995). We also compared amount of agricultural land cover in edge and confounded studies with the same method.

## Results

When per-study mean effect sizes for both edge and confounded studies were analyzed together, confounded

**Table 2.** Relationships, determined from random effects meta-analyses, between the proportion of forest and agriculture land cover in the surrounding landscape and either effects from studies where edge and patch area are confounded or from studies of nonconfounded edge effects.<sup>a</sup>

Species <sup>a</sup>	Confounded studies <sup>b</sup>					Edge studies <sup>b</sup>				
	n	forest		agriculture		n	forest		agriculture	
		slope	p	slope	p		slope	p	slope	p
Acadian Flycatcher						3	— <sup>c</sup>			— <sup>c</sup>
Indigo Bunting	5	-1.24	0.34	0.62	0.31					
Ovenbird	10	-0.80	0.08	0.45	0.92					
Red-eyed Vireo	8	-1.81	0.06	0.67	0.64					
Rose-breasted Grosbeak	3	— <sup>c</sup>		— <sup>c</sup>						
Scarlet Tanager	4	-0.30	0.12	— <sup>c</sup>						
Summer Tanager						3	2.29	0.34	-4.12	0.99
Yellow-billed Cuckoo	3	4.97	0.67	0.17	0.17	3	— <sup>c</sup>		— <sup>c</sup>	

<sup>a</sup> Only species with a demonstrated sensitivity to area confounded by edge or to edge alone are included in these analyses.

<sup>b</sup> Key: n, number of studies from which the mean effect size was derived (three or more studies with land-cover data required to estimate the influence of land cover on effect sizes for a particular species, species with inadequate data not shown); slope, positive slope indicates effect sizes (Z scores) are larger with larger proportion of forest or agriculture cover; p values generated through a bootstrap randomization process.

<sup>c</sup> Random effects model could not be calculated.

studies had a significantly stronger overall effect size than did edge studies (confounded effect =  $0.27 \pm 0.15$  [CI]; edge effect =  $-0.03 \pm 0.12$  [CI];  $p = 0.05$ ). In other words, occurrence of migrant songbirds was more likely in larger patches, further from the edge, but in general, when edge was not confounded by area, no edge effect was detected. We found this same pattern when per-species mean effect sizes were used instead (confounded effect =  $0.29 \pm 0.08$  [CI]; edge effect =  $-0.09 \pm 0.20$  [CI];  $p = 0.002$ ).

Among the 22 species with at least two estimates of response from confounded studies, 1 showed significant preference for small patches or edges, but 12 showed significant avoidance of small patches or edges (Table 1). When we considered only these 13 species, we found no significant ( $p < 0.05$ ) relationship between effect size and landscape forest cover, agricultural cover (Table 2), or dependent variable (Table 3). The two species with largest

sample sizes (Ovenbird and Red-eyed Vireo—scientific names for all species are in Table 1), however, showed marginally significant ( $0.10 > p > 0.05$ ) trends to more strongly avoid small patches and edges in landscapes with less forest cover. Northern Parulas had stronger small-patch or edge avoidance in studies with smaller minimum patch area, and Yellow-billed Cuckoos showed stronger small-patch or edge avoidance when the maximum patch area considered was smaller (Table 4).

Among the 17 species with at least two estimates of response to forest edge, 3 had a significant preference for edge and 1 had a significant tendency to avoid edges (Table 1). Because of small sample sizes, we were able to assess the effects of covariates in only a few cases. In these cases, species responding either positively or negatively to edge showed effect sizes that were unrelated to landscape forest and agricultural cover (Table 2) or minimum and maximum distance from edge (Table 4).

**Table 3.** Tests for effects of choice of dependent variable on observed confounded effects of patch area and edge on bird occurrence.

Species <sup>a</sup>	dependent variable	Confounded studies			
		n <sup>b</sup>	effect size <sup>c</sup>	CI <sup>d</sup>	p <sup>e</sup>
Indigo Bunting	presence	2	0.00	0.00-0.00	0.48
	density	5	-0.43	-0.54-0.04	
Red-eyed Vireo	presence	2	0.75	0.75-0.75	0.34
	density	8	0.22	-0.16-0.70	
Yellow-billed Cuckoo	density	4	0.25	-0.07-0.63	0.47
	probability of detection	2	0.83	0.35-2.30	

<sup>a</sup> Only species with a demonstrated sensitivity to area confounded by edge are included in these analyses.

<sup>b</sup> Number of studies from which the mean effect size was derived. For two dependent variables to be compared, at least four studies, two for each dependent variable, were needed. Among edge studies, there were insufficient numbers of different types of dependent variables to allow comparisons.

<sup>c</sup> The Z score, a type of correlation coefficient. Positive effect sizes (Z scores) indicate avoidance of small patches or edges and negative effect sizes indicate affinity for small patches or edges.

<sup>d</sup> Bootstrap-generated 95% CI corresponding to the effect size estimate.

<sup>e</sup> Values generated through a bootstrap randomization process.

**Table 4.** Tests for influences of minimum and maximum patch area (confounded studies) and minimum and maximum distances to edge (edge studies) on observed area and edge effects on bird occurrence.<sup>a</sup>

Species <sup>a</sup>	Confounded studies <sup>b</sup>						Edge studies <sup>b</sup>					
	minimum patch area			maximum patch area			minimum distance to edge			maximum distance to edge		
	n	slope	p	n	slope	p	n	slope	p	n	slope	p
Indigo Bunting	7	-0.008	0.28	7	0.000	0.35						
Northern Parula	3	-0.045	0.0001	3	-0.000	0.17						
Ovenbird	11	-0.001	0.12	11	0.000	0.38						
Red-eyed Vireo	10	-0.068	0.57	10	-0.000	0.56						
Rose-breasted Grosbeak	4	— <sup>c</sup>		4	— <sup>c</sup>							
Scarlet Tanager	6	-0.040	0.28	6	0.00	0.76						
Summer Tanager							3	0.02	0.67	3	-0.01	0.17
Yellow-billed Cuckoo	6	-0.002	0.17	6	-0.0002	0.02						

<sup>a</sup>Only species with a demonstrated sensitivity to area confounded by edge or to edge alone are included in these analyses.

<sup>b</sup>Key: n, number of studies from which the mean effect size was derived (three or more studies with distance or area data required to estimate influence of these variables on effect sizes for a particular species); slope, positive slope indicates that effect sizes (Z scores) are larger with larger patch size or distance to edge; p values generated through a bootstrap randomization process.

<sup>c</sup>Random effects model could not be calculated.

Edge studies were conducted in landscapes with significantly more forest cover than were confounded studies (based on untransformed data: confounded = 35% ± 7 [SE],  $n = 17$ , edge = 70% ± 7 [SE],  $n = 10$ , based on data transformed by arc-sine square root: two-tailed Student's  $t = -3.14$ ,  $df = 25$ ,  $p = 0.004$ ). Differences between edge and confounded studies in the amount of agricultural cover in the surrounding landscape were not significant (based on untransformed data: confounded = 30% ± 7 [SE],  $n = 17$ , edge = 12% ± 8 [SE],  $n = 10$ , based on data transformed by arc-sine square root: two-tailed Student's  $t = 1.98$ ,  $df = 25$ ,  $p = 0.06$ ).

## Discussion

Individual species' trends for response to edges or small patches were not always expected based on other reviews of the literature. For instance, the Acadian Flycatcher, reportedly an area-sensitive species (Whitehead & Taylor 2002), showed more consistent edge avoidance and did not show a significant trend in the confounded studies where patch-size effects would have been detected. In contrast, the Rose-breasted Grosbeak and Northern Waterthrush are two species not generally considered area sensitive (Eaton 1995; Wyatt & Francis 2002), although our analyses suggest they may be. The preference of Summer Tanagers for edges (Robinson 1996) and of a number of other species (Black-throated Green Warbler, Cerulean Warbler, Ovenbird, Red-eyed Vireo, Scarlet Tanager, Worm-eating Warbler, Yellow-billed Cuckoo) for larger patches had been reported in previous reviews (Poole & Gill 1992–2002), and our analyses strengthen these conclusions. Interestingly, preference for disturbed

habitats in the Veery (Moskoff 1995) did not preclude avoidance of smaller patches or edges. The Yellow-billed Cuckoo, also a species with reported affinity for regenerating areas (Hughes 1999), showed a preference for edges in the edge-only analyses but avoidance of small patches or edges in the confounded analyses.

Because studies of patch-area effects have all been confounded by distance to edge, it has been argued that alleged area effects on bird density are actually edge effects (Mancke & Gavin 2000). However, because almost no one has examined the effect of forest patch area independent of the effect of distance from forest edge, the question of whether effects of area exist that are distinct from effects of edge remains unanswered. Designing an area-effect study that completely controls for edge effect may be impossible because even if the distance to the closest edge is controlled, edge distances in other directions are bound to vary with varying patch area. No standardization has been attempted, however, of even the distance to the closest edge. Thus, it is important to consider our finding that confounded studies, which include edge and area effects, and studies reporting edge effects alone differ in the strengths and direction of the effects reported. Confounded studies tend to report strong positive effects (avoidance of small patches or edges), whereas edge studies often show weak and negative (affinity for, rather than avoidance of, edges) effects. Several hypotheses may explain this difference, and we focus on three here.

First, it could be that different trends for edge and area studies are caused by bias in study location. In landscapes where edge effects were examined, forest cover averaged 100% higher than in landscapes where confounded studies were conducted, and it may be that the amount of landscape forest cover influences whether songbirds avoid edges and small patches. Although trends for

decreasing effect size with increasing forest cover within confounded or edge studies were not significant at  $p < 0.05$  (Table 2), this result is not conclusive. The two species with the largest samples had marginally significant trends toward weaker small-patch or edge avoidance in landscapes with more forest. In light of these suggestive results and previously reported tendencies for stronger patch-size effects in less-forested landscapes or with more-isolated patches (Robbins et al. 1989; Andrén 1994), this alternative appears likely to be at least a partial explanation of the stronger effects in confounded studies than edge studies. We did not detect a significant difference in amount of agricultural cover between edge and confounded studies, although confounded studies showed a nonsignificant trend to have more agricultural land. Amount of agricultural cover in a landscape, however, was unrelated to the response to edges or patch area in any species. Thus the data are more consistent with a role for landscape forest cover rather than agricultural land cover in influencing forest bird presence and density.

Second, a nonexclusive alternative is that migrant forest birds tend to avoid small forest patches more readily than edges. If edge and patch-size effects are simply additive, the absence of strong tendencies toward edge avoidance in the unconfounded edge studies would suggest that the strong effects of confounded studies can be attributed to area effects. Further efforts to experimentally and statistically isolate patch-area effects from distance-to-edge effects will be needed before we can determine whether small-patch avoidance is more prevalent than edge avoidance. If there are distinct edge and area effects, what mechanisms might be at work? Apparent edge avoidance could relate to increased predation or brood parasitism risks in these locations (Hartley & Hunter 1998; Lahti 2001; Chalfoun et al. 2002), either because predators depress bird populations or because birds recognize the risk and avoid edges. Area effects are often assumed to involve factors such as island biogeography and metapopulation theory (MacArthur & Wilson 1967; Hanski 1999). If individual patches are too small to sustain a population, however, and dispersing and migrating birds can easily move among patches then island biogeography and metapopulation theory will not apply to the system (Andrén 1994). These situations are probably often true for Neotropical migrant songbirds. Thus in many systems of fragmented forests in eastern North America, area effects may require other explanations. One possible mechanism is territory aggregation. If individuals of songbird species prefer to aggregate their territories (Muller et al. 1997), young birds may choose an already partially occupied forest patch in which to settle (Ward & Schlossberg 2004). Because a larger patch should, by chance alone, be more likely to contain an occupied territory when yearling birds are settling in spring, first-time breeders looking for conspecifics should be attracted to

these already occupied, larger patches. This could lead to greater occupancy of larger patches.

Third, it may be that edge and area effects are not additive but interact to produce the observed pattern. If edge avoidance were more likely in small forest patches, this would create the pattern we found: little to no edge avoidance in studies of edge effects alone, which are generally conducted in large tracts of contiguous forests, but strong effects in confounded studies conducted in smaller forest fragments. Experimental designs to assess this possibility should be relatively straightforward, but at this point have yet to be implemented.

Regardless of which mechanisms are at work, the result remains that for many species, occurrence rates are lower in small forest fragments. Thus, although it is important to test alternative hypotheses to explain this phenomenon, this should not preclude management to limit further forest fragmentation.

We found limited evidence that other factors may influence observed patterns of edge and small patch avoidance. Choice of dependent variable (presence/absence versus density) did not significantly influence the strength of effects observed. We had data from only a few presence/absence studies, however, so we may have had insufficient sample sizes to detect this effect. We observed two species for which the sizes of patches included in a study appeared to influence effect size. Thus, some species may only appear to respond to patch area when an appropriate range of patch areas is examined.

Much of the variance in our data set is attributable to sampling error associated with small sample sizes (Fig. 1) and as such is probably not biologically meaningful. It is possible, however, that other factors, ecological or experimental, unexamined by our analyses could be at work in influencing the observed strength of forest edge and small forest patch avoidance in Neotropical migrant songbirds. A well-known problem with bird occurrence surveys is inconsistent detection probability (e.g., Sauer et al. 1994; Farnsworth et al. 2002). One of the most problematic examples occurs when mated males decrease their singing rate and thus become less likely to be detected by researchers. Therefore, sites with the highest reproductive success could appear, falsely, to have lower occupancy rates (Gibbs & Faaborg 1990). Studies may have varied in their success in identifying true occupancy rates, and this may be one source of unidentified variance in our data. Results of studies that examined multiple predictors of bird occurrence often show that edge or patch area measures combined with local habitat variables or landscape variables such as degree of patch isolation or the amount of forest cover surrounding individual patches describe the most variance (Robbins et al. 1989; Lynch & Whigham 1984; Howell et al. 2000; Lee et al. 2002). Because details of habitat and surrounding landscape on a patch-by-patch basis were not available to us and because we are generalizing across such a large area, we expect

there is biologically meaningful variance that we cannot account for.

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**Appendix 1. Studies from which we obtained relationships between the occurrence of Neotropical migrant songbirds in eastern North America and distance to edge or the confounded effects of patch area and distance to edge.**

Study	Study type
Ambuel & Temple 1983	confounded
Askins et al. 1987	confounded
Austen et al. 2001	confounded
Bancroft et al. 1995	confounded
Blake & Karr 1984, 1987	confounded
Bollinger et al. 1997 <sup>a</sup>	confounded
Burke & Nol 1998	confounded
Duguay et al. 2001	edge
Dunford et al. 2002	edge and confounded <sup>b</sup>
Flaspohler et al. 2001	edge
Forman et al. 1976	confounded
Friesen et al. 1995	confounded
Germaine et al. 1997	edge
Gibbs & Faaborg 1990	confounded
Grant & Berkey 1999	confounded
Hobson & Bayne 2000	confounded
Kilgo et al. 1997	confounded
King et al. 1997	edge
Kroodsma 1984, 1987	edge
Lee et al. 2002	confounded
Lynch & Whigham 1984	confounded
Mancke & Gavin 2000	confounded
Morneau et al. 1999	edge
Noss 1991	edge
Ortega & Capen 2002	edge
Porneluzi et al. 1993	confounded
Robbins et al. 1989	confounded
Sabine et al. 1996	confounded
Sallabanks et al. 2000	confounded
Strelke & Dickson 1980	edge
Temple 1986	confounded
Van Horn et al. 1995	confounded
Wenny et al. 1993 <sup>a</sup>	confounded

<sup>a</sup>Results from these studies could not be included in meta-analyses because sample size must exceed three to allow calculation of the variance corresponding to the Z score (see Methods).

<sup>b</sup>This study presents edge effects statistically controlling for area effects and area effects not controlling for edge effects.