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ONE-SIDED EDGE RESPONSES IN FOREST BIRDS FOLLOWING RESTORATION TREATMENTS

James Battin[1,3] and Thomas D. Sisk[2]

[1]*Department of Biological Sciences and Center for Environmental Sciences and Education, Northern Arizona University, Flagstaff, AZ 86011*
[2]*Center for Environmental Sciences and Education, Northern Arizona University, Flagstaff, AZ 86011*

Abstract. We studied the effects of the edge between two forest types on the probability of occurrence of seven species of birds and found that four responded to the edge on only one side. Over 4 years, we measured the responses of forest birds to the edge between ponderosa pine forest undergoing restoration and neighboring untreated stands. Of the seven species analyzed, one occurred most frequently near the edge. Of the remaining six, none responded to the edge in the treated forest, but four responded in the untreated forest. Relatively few studies have examined abundance changes on both sides of an edge between distinct habitats that support similar bird communities, and predictive models of edge effects used for mapping animal responses to habitat change often assume that animal abundance will change on both sides of this sort of edge, declining near the edge in the habitat in which the species is most abundant and increasing near the edge in the habitat in which the species is less abundant. One-sided edge effects, such as those we have documented, may lead to markedly different predictions of the effects of habitat change on bird abundance in heterogeneous landscapes.

Key words: edge effects, mixed model logistic regression, predictive model, ponderosa pine forest.

Respuestas de las Aves de Bosque a los Efectos de Borde de un Lado Luego de Tratamientos de Restauración

Resumen. Estudiamos los efectos de borde entre dos tipos de bosque en la probabilidad de ocurrencia de siete especies de aves y encontramos que cuatro respondieron al borde de un solo lado. Durante cuatro años medimos las respuestas de aves de bosque al borde entre un bosque de pino ponderosa bajo restauración y rodales colindantes sin tratar. De las siete especies analizadas, una presentó mayor frecuencia cerca del borde. De las seis restantes, ninguna respondió al borde en el bosque tratado, pero cuatro mostraron una respuesta al bosque sin tratar. Relativamente pocos estudios han examinado los cambios en la abundancia en ambos lados de un borde entre hábitats distintos que albergan comunidades de aves similares. Además, los modelos predictivos de efecto de borde utilizados para mapear las respuestas de animales al cambio de hábitat a menudo asumen que la abundancia animal cambiará en ambos lados de este tipo de borde, disminuyendo cerca del borde en el hábitat en el cual la especie es más abundante e incrementado cerca del borde en el hábitat en el cual la especie es menos abundante. Los efectos de borde de un solo lado, tales como los que documentamos, pueden llevar a predicciones marcadamente diferentes de los efectos de cambio de hábitat en la abundancia de aves en paisajes heterogéneos.

INTRODUCTION

Habitat edges have wide-ranging effects on animal abundance (Lidicker 1999, Sisk and Battin 2002), productivity (Paton 1994, Andrén 1995, Hartley and Hunter 1998, Lahti 2001), and behavior (Haddad 1999, Meyer and Sisk 2001, Ries and Debinski 2001), as well as on abiotic factors and habitat features that are important to animals (Matlack 1993, Sisk et al. 1997, Kristan et al. 2003). Edge effects on animal abundance are ubiquitous and may underlie other ecological phenomena such as area effects (Fletcher et al. 2007). Understanding how animals respond to habitat edges can be essential to conservation (Lidicker 1999) and to efforts to predict animal distributions in fragmented landscapes (Laurance and Yensen 1991, Sisk and Haddad 2002). The influence of edges on avian abundance has received considerable attention, but surprisingly few studies have looked at edge effects on both sides of any edge (Fonseca and Joner 2007). Even less work has been devoted to understanding edges between patches that support the same species but at different densities, despite the frequent occurrence of such edges in nature and in human-modified landscapes.

Manuscript received 22 February 2010; accepted 8 February 2011.
[3]E-mail: battinjames@gmail.com

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In the absence of data on such edges, attempts to model avian distributions in heterogeneous landscapes must either ignore edge effects or use some a priori model to predict the form of edge effects from data on animal abundance and/or habitat quality (Brand et al. 2006). Several attempts have been made to develop a mechanistic understanding of edge effects (McCollin 1998, Cadenasso et al. 2003, Ries et al. 2004), and the development of simple models of edge–abundance relationships (Kingston and Morris 2000, Ries and Sisk 2004) has provided a way of predicting animals' responses to habitat edges. These models can, in their simplest form, be used to predict edge responses (how abundance changes near a habitat edge) from habitat responses (how abundances in habitat interiors differ). The model of Ries and Sisk (2004) predicts edge responses on the basis of whether patterns of resource distribution between habitats are complementary (i.e., resources are divided between habitats, as when nest sites are found in one habitat and food in another) or supplementary (i.e., all necessary resources occur in each habitat, though possibly at different levels). When resources are divided between habitats or concentrated at the edge, animals are expected to reach their highest densities near the edge. When all resources occur in both habitats (possibly at higher concentrations in one habitat than in the other), the model predicts a "transitional" edge response, in which abundance changes gradually from the preferred habitat to the less preferred one (Fig. 1). For most species to which the model has been applied, a transitional response has been predicted (Ries et al. 2004).

The model of Kingston and Morris (2000), the only other a priori predictive model of which we are aware, is based on the assumption that home ranges are larger in the less preferred habitat and change gradually in size near the habitat edge, creating a smooth gradient in abundance across the edge. Although developed with small mammals in mind, this model applies equally well to territorial birds and yields a predicted edge response similar to the transitional response of Ries and Sisk (2004). The practical result of both models is to make possible predictions of edge responses based on the relative abundance of birds in adjoining habitat patches. These predictions provide a useful null model of edge effects. Traditionally, the only null model considered in edge-effect studies has been that of no edge response, but, as these studies demonstrate, in many cases an edge effect should be expected. Ries and Sisk's (2004) model has been shown to have a high degree of explanatory power for a wide range of taxa (Ries et al. 2004).

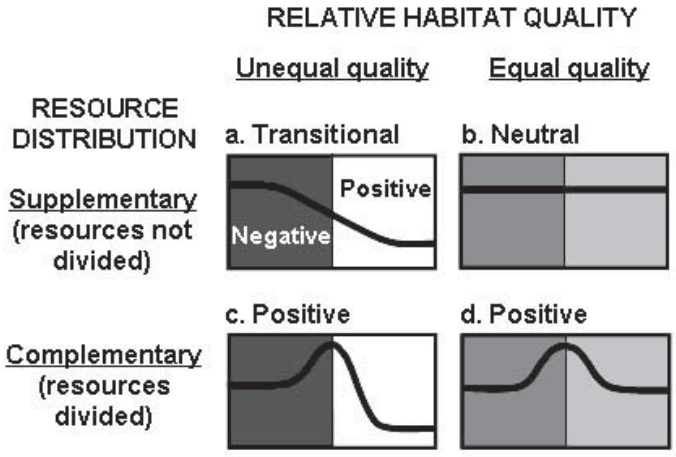

FIGURE 1. Model predictions of edge responses are transitional (a), neutral (b), or positive (c and d) based on relative habitat quality and resource distribution. Lower habitat quality is indicated by a white box, while habitats of higher or equal quality are shaded. The same resources are either available in both habitats (supplementary) or different resources are divided between habitats (complementary). Reprinted, with permission, from Ries and Sisk (2008).

Both models predict that, in the absence of other mechanisms (e.g., the influence of edge-related gradients in resources or competitors), animals should show a smooth gradient in abundance between habitats, except where they require access to resources that are separated by habitat. Animal abundance is expected to decline near the edge in the habitat in which it is higher and to increase near the edge in the habitat in which it is lower. The magnitude and depth of penetration of the edge effect may vary with the abruptness of the transition between habitats, but the idea that, in the absence of mechanisms that cause animals to reach peak abundance near the edge, animal abundance at edges should change gradually from higher in the interior of the preferred habitat to intermediate at the edge to lower in the adjacent habitat interior is a central and intuitively appealing—but largely untested—feature of our understanding of edge effects. In this study, we examine avian edge responses on both sides of an edge between two distinct habitat types that support a similar suite of bird species—although often at very different densities.

A novel form of large-scale habitat manipulation being undertaken in the southwestern United States provided us with a unique model system in which to study edge effects on birds. Concerns about declining forest health and the risk of high-intensity wildfires have led scientists and land managers to develop aggressive forest-management strategies to return the ponderosa pine forests covering large portions of the region to the more open condition that is believed to have predominated prior to European settlement (Allen et al. 2002, Friederici 2003a). This process, known as "forest restoration," is designed to reverse the combined effects of fire suppression, logging, and cattle grazing, which have, over the course of more than a century, transformed what was once a mixed forest/grassland system characterized by frequent, low-intensity ground fires into a closed-canopy forest subject to infrequent, high-intensity fires (Covington and Moore 1994, Covington et al. 1997). One effect of forest-restoration treatments is a rapid increase in the amount of treated–untreated forest edge in the landscape.

Restoration treatments provide a landscape-scale, replicated experimental system for studying a clearly defined edge demarcating two habitats that differ substantially in structure but that, for the most part, serve as habitat for the same bird species. The composition of the bird community changes very little between treated and untreated forest, although some species differ substantially in abundance between the two (Battin 2003). Because the edges considered in this study were created recently (0–3 years prior to the beginning of the study), there was insufficient time for the development of many secondary habitat changes often associated with edges (e.g., the formation of a transitional shrub layer). Furthermore, the uniformity of the treatment across the study area and the clearly defined nature of the edge eliminated many of the factors that have confounded other edge studies, including the uncertain location of the edge between two habitats and the presence of vegetation gradients across the edge (Murcia 1995).

In this study we ask two questions. (1) How, if at all, do birds respond to the edge between treated and untreated forest? (2) Are observed responses consistent with the predictions of a simple model based on the relative abundances of birds in each habitat (Ries et al. 2004, Ries and Sisk 2004)?

METHODS

STUDY AREA

The study was conducted at the Mt. Trumbull Resource Conservation Area in the Grand Canyon/Parashant National Monument, located just north of the Grand Canyon, approximately 200 km northwest of Flagstaff, Arizona. Soils in the area derive from volcanic parent material. Average rainfall at the site is approximately 40 cm per year, with most of that falling in the winter and during the July–September monsoon rains. Over the 4 years of this study, rainfall was below the long-term average, with 2002 seeing the lowest precipitation on record (McGlone at al. 2009). The vegetation at the site consists of ponderosa pine (*Pinus ponderosa*) and mixed ponderosa pine–Gambel oak (*Quercus gambeli*) forest. Other tree species occurring at low abundance include Utah juniper (*Juniperus osteosperma*), pinyon pine (*Pinus edulis*), New Mexico locust (*Robinia neomexicana*), and quaking aspen (*Populus tremuloides*).

The Mt. Trumbull area represents the first large-scale application of the "Flagstaff model" (Friederici 2003a) of forest restoration. Prior to restoration, trees' basal area averaged 33 $m^2\ ha^{-1}$ (Fulé et al. 2001). The restoration treatment at this site involved a combination of thinning and prescribed burning that, on average, reduced the trees' total basal area by 45% and pine-stem density by 80% (Fulé et al. 2001) and increased the cover of the herbaceous understory, both native and exotic species, substantially (McGlone et al. 2009). Approximately 1200 ha of forest, ranging from 2050 to 2200 m in elevation, are designated for restoration at Mt. Trumbull (Friederici 2003b). At the beginning of the study, in 1999, 1- to 3-year-old restoration treatments covered 80 ha of the study area, with 200 ha having been fully treated by the end of the study. The layout and implementation of the restoration treatment at this site was described in detail by Friederici (2003b).

BIRD SURVEYS

We developed a transect-based survey protocol that sampled a 100-m-wide band of habitat starting at the edge between treated and untreated forest and extending 200 m into the interior of the sampled patch. We truncated surveys at 200 m because some of the forest-restoration treatments were not large enough to allow the use of longer transects. We used mapped locations of individual birds as the basis of a fine-scale analysis of edge effects. Birds were surveyed each summer from 1999 through 2002 along 200-m transects running perpendicular to the treated–untreated edge. When possible, transects were paired, with one transect running into treated forest and another into untreated habitat from the same point at the edge. Because restoration treatments continued throughout the study, many edges at which we had placed bird-survey transects were destroyed in a subsequent year as adjacent forest stands were treated, creating new edges. Each year, therefore, some transects were lost and new ones were established, resulting in a different set of edge transects each year. In every year of the study, we placed transects at all available treated–untreated edges. The number of transects varied from 5 to 12 per habitat per year (Table 1). Over the course of the study, we placed transects in seven different treatment units and the untreated forest stands adjacent to them.

We surveyed each transect between 28 May and 10 July each year between 0.5 hours before sunrise and 4.5 hours after sunrise. Because of logistical and personnel constraints, we made only three surveys per transect in 1999 and 2002 but made four in 2000 and 2001. Time of day, direction in which transects were walked, and observer were rotated in order to minimize bias.

Each transect was surveyed for 30 min. We divided transects into four 50-m segments, each of which was surveyed for 7.5 min. Only birds within the 50-m segment currently being surveyed were recorded. Observers noted any individual bird thought to be detected on more than one segment during a given survey, and we chose one of these multiple observations at random for analysis. The division of the transect into 50-m

TABLE 1. Number of transects surveyed in treated and untreated forest in each year.

Year	Treated	Untreated
1999	8	8
2000	7	5
2001	10	5
2002	12	8

segments, coupled with the random selection of a single observation for any individual sighted in more than one segment, removed two spatial biases usually associated with transect surveys: (1) because observers walking along the transect are never more than 100 m from the center but can be up to 200 m from an end, the center of the transect is surveyed more thoroughly than either end, and (2) if observers record only the first location at which they detect a bird, observations tend to be biased toward the end of the transect at which the observer begins. For all birds within 50 m of the transect segment being surveyed, observers recorded species, detection method, and distance from the transect. The location of each bird along the transect was mapped and entered into a GIS. No formal assessment of the precision or accuracy of distance estimates was made. Observers were trained in distance estimation at the beginning of each field season through the use of repeated trials in which they estimated the distance to birds and objects in the forest, whose actual distances were verified with a tape measure. To further aid with distance estimation throughout the survey period, flagging of different colors was hung at distances of 30, 40, and 50 m from the transect at 100-m intervals along each transect.

STATISTICAL ANALYSES

Edge responses are likely to be consistent from year to year only when abundance patterns in the two habitats are also consistent from year to year (Ries et al. 2004). If birds respond differently in different years to the habitats on either side of the edge, it is likely that their response to the edge will also change. The first step of our analysis, therefore, was to test for a year-by-habitat interaction in abundance patterns. For species that showed no interaction, we were able to conduct a mixed-model analysis that combined data from all four years and had relatively high power to detect edge responses. Because of low sample sizes per year we did no further analyses for birds exhibiting year-by-habitat interactions.

We used the program DISTANCE to determine whether estimates of detectability based on distance sampling (Buckland et al. 1993) differed by habitat for each species. We compared the values of Akaike's information criterion (AIC) from two models of bird detectability: (1) a model including habitat type and (2) a global detectability function (i.e., no habitat term). The inclusion of the habitat term produced a superior model (lower AIC score) for only one species: Grace's Warbler (*Dendroica graciae*). For all other species, AIC chose the detectability model without a habitat term. This finding was not surprising, as all species we considered could be detected easily to distances well beyond 50 m in both treated and untreated forest. Because detectability did not, in general, appear to differ by habitat and because all edge effects were analyzed within a single habitat, we used locations of individual mapped birds, with no correction for detectability, as the basis for our analyses. This approach allowed us to use presence–absence data for a relatively fine-scaled analysis of edge effects. Between-habitat differences in Grace's Warbler abundance, however, may have been underestimated by this method because detectability appeared to be higher in the treated areas, where Grace's Warblers were found to occur at lower densities.

To assess between-habitat differences in abundance and the interaction between year and habitat in determining abundance patterns, we compared the interior portion of each transect (100–200 m from the edge) in the two habitats. We conducted a two-way analysis of variance on square-root-transformed relative abundances (SAS PROC GLM) with year and habitat (treated vs. untreated) as factors. We excluded from further analysis any species for which a significant ($P < 0.10$) year-by-habitat interaction was detected. We chose an α of 0.10 for this test to ensure that we were conservative about pooling data across years. For each species, we conducted a retrospective power analysis (Sokal and Rohlf 1995, Thomas 1997) to determine the magnitude of the between-habitat difference in abundance that could have been detected 80% of the time with $\alpha = 0.05$. This allowed an assessment of the likelihood that a meaningful between-habitat difference in abundance might have gone undetected because of low power.

Because bird abundances were low, there was often only one observation of a given species in a given edge-distance class for a single transect × year combination, and there were many segments for which there were no observations for a species. For this reason, we used presence–absence data in a logistic regression model to test for edge effects. We modeled edge effects in treated and untreated habitats separately because, if we included both habitats in a logistic regression model, different probabilities of occurrence in each habitat could result in a model with an apparent edge effect that was actually the result of the regression model extrapolating between the probabilities of occurrence in the two habitats.

We used random-effects mixed-model repeated-measures logistic regression to determine whether the probability of bird occurrence changed with respect to distance from the edge (SAS PROC MIXED with the GLIMMIX macro). Because the depth of penetration of edge effects varies widely among habitats and species, we employed a relatively fine scale of analysis (Brand and George 2001, Fletcher and Koford 2003). For analysis, we divided each 200-m transect into eight bins 25 m deep, effectively dividing each of the 50-m survey segments in two. For each 25-m bin we determined from mapped bird locations whether a given species was detected in that segment during any of the surveys in a given year. We then modeled the probability of bird occurrence as a function of distance from the edge for each habitat separately, with distance from the edge to the midpoint of each distance bin as the predictor variable and the species' presence as the response. We used an autoregressive covariance structure (SAS AR[1]) to account for spatial autocorrelation among transect

segments. We specified year and transect as random effects and distance category as a repeated measure. To compute degrees of freedom, we used the containment method (the default in PROC MIXED). Because the computation of degrees of freedom in mixed-model analyses is not entirely resolved, we conducted the same analysis using an extreme underestimate of degrees of freedom in which degrees of freedom were set equal to the number of transects used in the analysis. This analysis resulted in slightly higher *P*-values but did not change our conclusions in any way, indicating that the results of the analysis are robust to different methods of calculating degrees of freedom.

RESULTS

EDGE EFFECTS

Of the nine species detected most often in our study, two showed significant year-by-habitat interactions in abundance in our two-way ANOVA analysis (Table 2). Of the remaining seven species, two—the Western Bluebird (*Sialia mexicana*) and Yellow-rumped Warbler (*Dendroica coronata*)—exhibited no edge response in either habitat (Fig. 2a, b). The only species that responded to an edge in the treated habitat was the Dark-eyed Junco (*Junco hyemalis*), for which probability of occurrence peaked at the edge in both habitats (Fig. 2c). The remaining four species all exhibited edge responses in the untreated habitat but not in the treated habitat (Fig. 3). Probabilities of occurrence of the White-breasted Nuthatch (*Sitta carolinensis*), Chipping Sparrow (*Spizella passerina*), and Western Tanager (*Piranga ludoviciana*) increased near the edge (Fig. 3a, c, d), while that of Grace's Warbler decreased (Fig. 3b).

BIRD ABUNDANCE

Of the seven species not showing significant year-by-habitat interactions, three—the Western Bluebird, Chipping Sparrow, and Dark-eyed Junco—were significantly more abundant in treated than in untreated forest. For the remaining four species, we found no significant differences between habitats in abundance. Power analysis revealed that, with $\alpha = 0.05$, we would have been able to detect only a between-habitat difference in abundance of between 76% and 100% (depending on species) 80% of the time for these four species (Table 2). This result suggests that biologically meaningful differences in abundance between habitats may have gone undetected. Indeed, three of the four species for which we found no statistically significant between-habitat difference in abundance exhibited differences in mean abundance between habitats that might be judged biologically meaningful. Mean abundance was 34% and 41% higher in the treated forest than in the untreated forest for the White-breasted Nuthatch and Western Tanager, respectively. Mean abundance of the Grace's Warbler was 59% higher in the untreated forest than in the treated forest, and the difference for this species may have been underestimated because of differences between habitats in detectability (see Methods).

DISCUSSION

EDGE-RESPONSE PATTERNS

The preponderance of one-sided edge responses we observed is unusual among avian edge studies, something that may be explained in part by the relative rarity of studies considering both sides of a habitat edge (Sisk and Battin 2002, Fonseca and Joner 2007). Of the seven species for which full mixed-model analyses were possible, none displayed the type of two-sided transitional response predicted by a priori models (Kingston and Morris 2000, Ries and Sisk 2004). Four species—the White-breasted Nuthatch, Grace's Warbler, Chipping Sparrow and Western Tanager—displayed a one-sided edge response,

TABLE 2. Relative abundances (mean number of birds detected per survey ± 1 SE) of 9 bird species in two habitats: forest that had undergone a restoration treatment ("treated") and untreated forest ("untreated"). In two species, significant year*treatment interactions (labeled "I" in the *P*-value column) were found.

Species	Treated	Untreated	*P* [a]	Detectable difference (%)[b]
Mountain Chickadee (*Poecile gambeli*)	0.20 (±0.04)	0.34 (±0.08)	I	—
White-breasted Nuthatch (*Sitta carolinensis*)	0.53 (±0.09)	0.39 (±0.09)	0.47	76
Western Bluebird (*Sialia mexicana*)	0.80 (±0.12)	0.30 (±0.08)	0.001	68
Plumbeous Vireo (*Vireo plumbeus*)	0.22 (±0.04)	0.13 (±0.04)	I	—
Yellow-rumped Warbler (*Dendroica coronata*)	0.23 (±0.05)	0.27 (±0.05)	0.64	91
Grace's Warbler (*Dendroica graciae*)	0.18 (±0.04)	0.28 (±0.06)	0.31	95
Chipping Sparrow (*Spizella passerina*)	0.33 (±0.07)	0.06 (±0.03)	0.001	91
Dark-eyed Junco (*Junco hyemalis*)	0.28 (±0.06)	0.13 (±0.04)	0.01	93
Western Tanager (*Piranga ludoviciana*)	0.28 (±0.06)	0.20 (±0.05)	0.52	100

[a] *P*-value for between-habitat differences from ANOVA, I = significant interaction effect (year-by-year results reported in Table 3).
[b] From retrospective power analysis, the minimum between-treatment difference detectable 80% of the time at $\alpha = 0.05$, expressed as a percentage of the mean abundance in the habitat in which the species is more abundant.

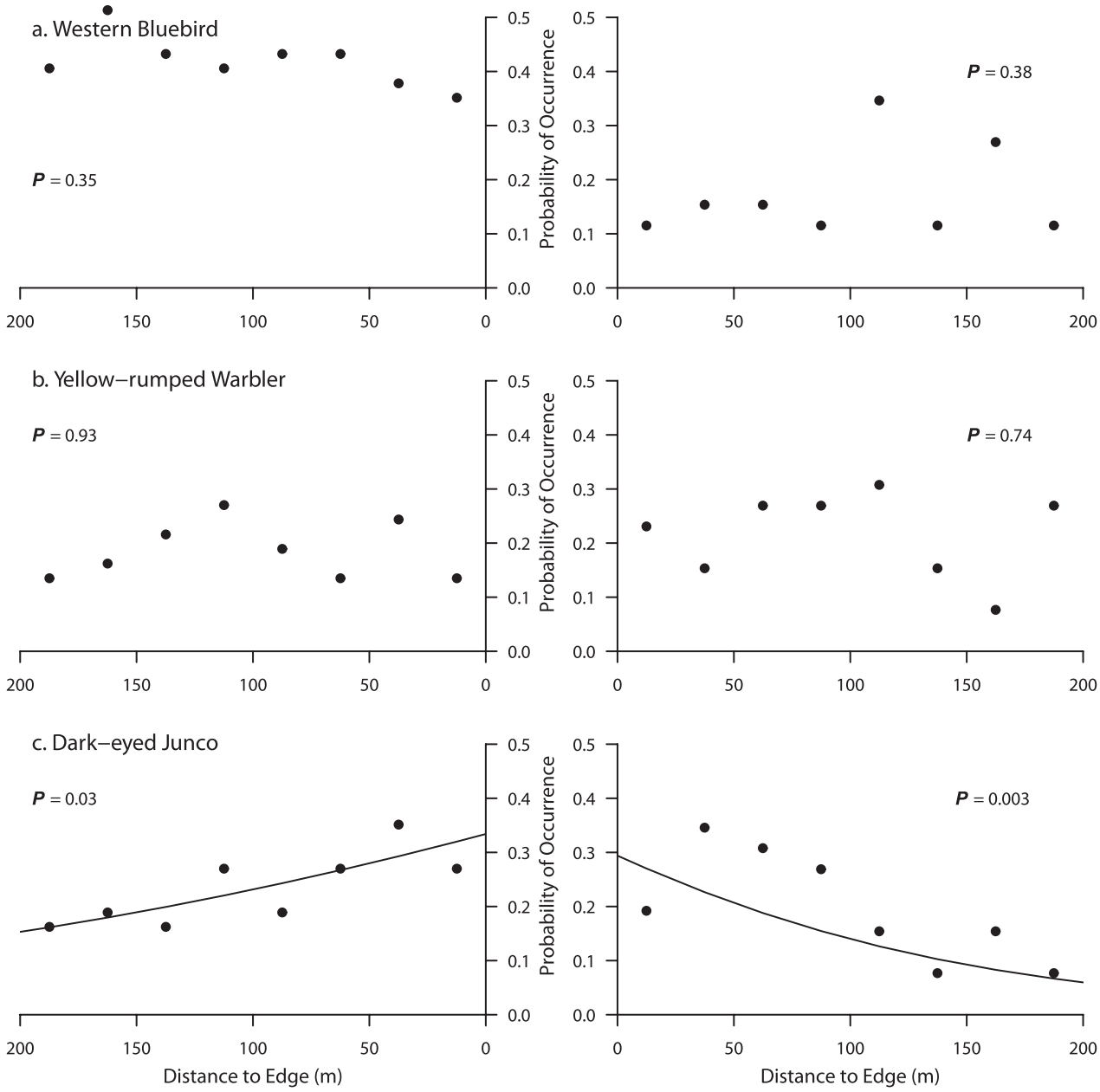

FIGURE 2. The relationship between the probability of bird occurrence and distance from the edge between treated and untreated forest stands for species exhibiting no edge response or an edge-exploiting response. Graphs on the left half of the figure represent treated habitat, those on the right untreated. Points represent mean probabilities of occurrence over 4 years for each edge-distance class. Lines represent significant relationships, from mixed-model repeated-measures logistic regression, between distance from edge and probability of occurrence for a species. *P*-values from logistic regression are shown for each analysis.

changing in abundance near the edge in the untreated forest but not in the treated forest. In all four cases, the probability of occurrence increased near the edge for species that were more abundant in the adjacent patches of treated forest and decreased for the species that was less abundant in the treated forest, as predicted by the transitional edge-response model. No species showed the opposite pattern. The Yellow-rumped Warbler, the species whose abundances in the two habitats were most similar, exhibited no edge response and may not have treated the edge between treated and untreated forest as an edge between two meaningfully different habitat types. The only species to respond to the edge in the treated forest was the Dark-eyed Junco, which displayed an edge-exploiting response, increasing at the edge in both habitats. The Western Bluebird, although

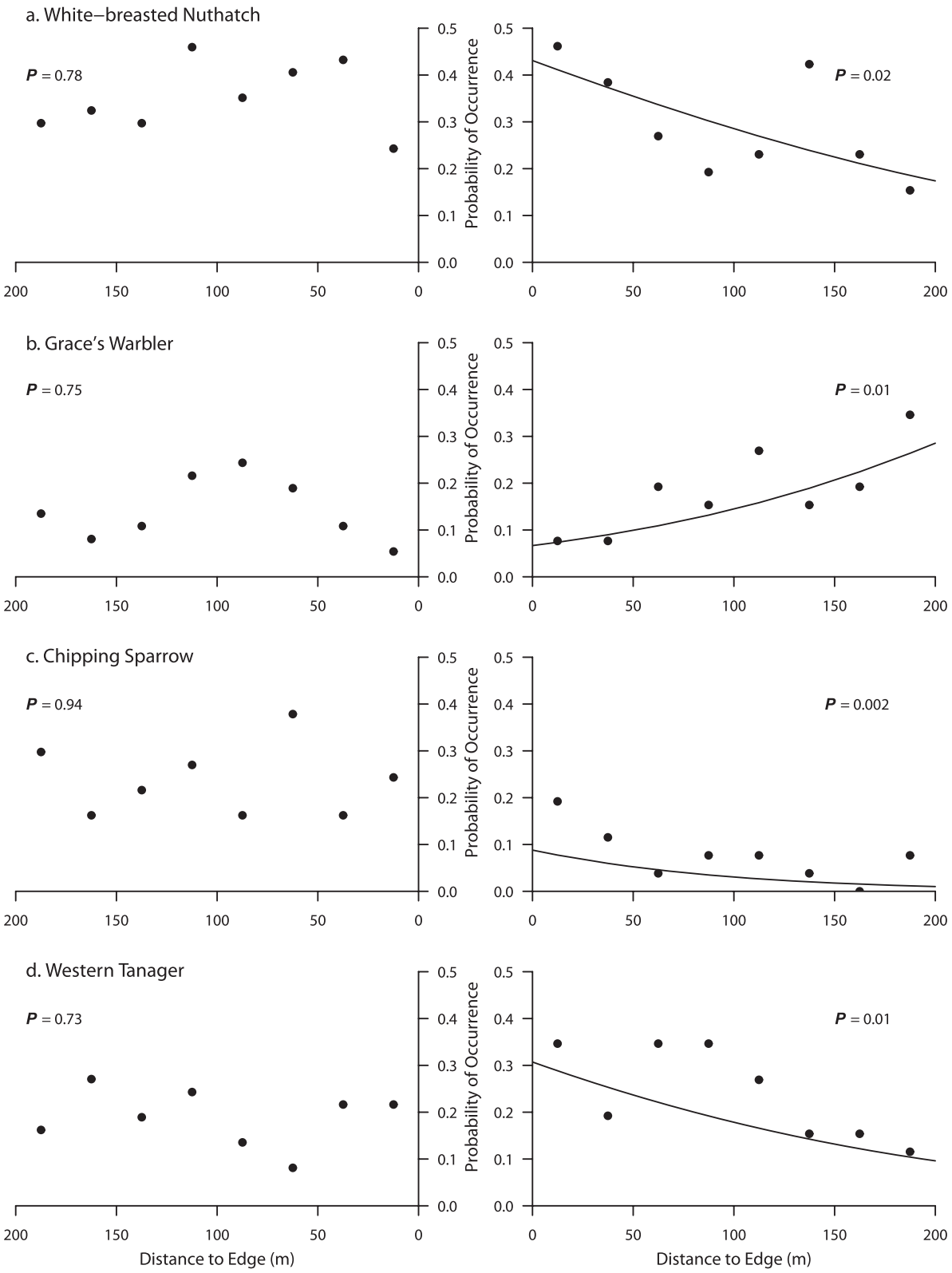

FIGURE 3. The relationship between the probability of bird occurrence and distance from the edge between treated and untreated forest stands for species exhibiting a one-sided edge response. Graphs on the left half of the figure represent treated habitat, those on the right untreated. Points represent mean probabilities of occurrence over 4 years for each edge-distance class. Lines represent significant relationships, from mixed-model repeated-measures logistic regression, between distance from edge and probability of occurrence for a species. *P*-values from logistic regression are shown for each analysis.

significantly more abundant in treated than in untreated forest (i.e., displaying a strong habitat response), exhibited no edge response in either habitat.

Between-treatment abundance patterns of two species—the Mountain Chickadee and Plumbeous Vireo—varied substantially from year to year. Similar patterns of temporal or spatial variability in avian habitat associations may explain some of the apparent inconsistencies among studies of avian edge responses (Sisk and Battin 2002). If between-habitat abundance patterns vary in space or time, one would not expect edge responses to be consistent across years or locations (Ries et al. 2004).

Of the four general classes of mechanism thought to cause gradients in animal abundance across habitat edges (Ries et al. 2004), two might cause a one-sided transitional response: (1) resource mapping, in which animal distributions map onto gradients in one or more resources (McCollin 1998, Ries et al. 2004) and (2) species interactions, in which the contact zone between two habitats creates opportunities for novel types of interaction (McCollin 1998, Fagan et al. 1999). One-sided edge responses could thus result from asymmetrical distributions of resources or other species.

Working at the same site in 1998 and 1999, Meyer et al. (2001) documented a one-sided pattern of microclimatic change across the treated–untreated forest edge. They found that morning and evening air temperature increased and relative humidity decreased from the interior to the edge in untreated forest but did not change with respect to the edge in treated areas. Microclimate in the untreated forest became more similar to that in the treated forest the nearer to the edge it was measured. Differences were especially pronounced in the morning, the period of highest bird activity and the period during which surveys were conducted. The correspondence between edge effects on microclimate and on birds raises the possibility that some species in this system respond either to the microclimatic gradient itself or to resources (e.g., food or cover) associated with it. Because the edges we studied were relatively young, the sort of gradient in understory vegetation characteristic of many more established edges (Cadenasso and Pickett 2001) was not apparent. Indeed, in the ponderosa pine forest ecosystem, given its relatively low productivity, such gradients are likely to develop slowly if at all. Other resources (e.g., arthropod prey), however, have been shown to map onto the microclimatic gradient (Meyer and Sisk 2001) even in the absence of a vegetation gradient.

The Dark-eyed Junco's edge response was unique among the seven species studied, in that it peaked at the edge. Such a response suggests division of resources between habitats or resource concentration at the edge (Ries et al. 2004). Of the species studied, the junco is the only ground nester. It is also a ground forager. It is possible that the treated areas, perhaps because of the burning of the understory, contained fewer suitable nest sites but a greater amount of forage than the untreated forest, causing juncos to seek out territories that encompassed some treated and some untreated forest. The junco has also been found to be associated with edges in other habitats (Sisk et al. 1997). The Western Bluebird's lack of an edge response in either habitat despite being over 2.5 times more abundant in treated forest suggests that it may be intrinsically "edge-insensitive" (Wiens et al. 1985, Lidicker 1999, Ries et al. 2004).

Most species in this system exhibited edge responses that were inconsistent with the predictions of the simple predictive model of Ries and Sisk (2004). When abundances in two habitats differ, the model predicts that animals will either reach peak abundance at the edge or decline in abundance symmetrically across the edge from the habitat in which abundance is higher to that in which it is lower. Two species—the Yellow-rumped Warbler, whose abundance in the two habitats did not differ and exhibited no edge response, and the Dark-eyed Junco, which peaked at the edge—conformed to model predictions. Of the other five, one showed no response where one would have been predicted. The other four displayed one-sided responses that were inconsistent with model predictions in treated patches but consistent with predictions in the untreated habitat. This could also be interpreted as the model making the correct prediction but the edge response being shifted entirely into one habitat. Either interpretation has important implications for predicting the effect of landscape change on birds (Brand et al. 2006), because it cannot be assumed that responses on one side of the edge will balance those on the other. Ries and Sisk (2010) examined the effect of different assumptions about the depth and form of edge effects on projected bird abundances in a fragmented landscape and found that changing the edge response from two-sided to one-sided altered projected bird abundances by 30–50%, a much greater effect than that of changing the modeled depth of edge-effect penetration.

IMPLICATIONS FOR THE DESIGN OF RESTORATION TREATMENTS

Treatment to restore ponderosa pine forest causes radical changes in forest-dwelling animals' habitat, among them creating a novel type of habitat edge. These edges are likely to become long-lasting features of the post-restoration landscape because of administrative boundaries (e.g., boundaries between public lands managed by different agencies with differing views on the desirability of restoration), difficulties in applying treatments to some areas (e.g., steep, remote, or wilderness areas), and the intentional maintenance of untreated areas as habitat for some sensitive species (Battin and Sisk 2003). Hundreds of thousands, if not millions, of hectares of forest may be treated over the coming decades (Allen et al. 2002), creating major habitat changes for a range of species and driving a shifting mosaic of forest and edge types across extensive areas (Battin and Sisk 2003).

The results of this study indicate that the edge between treated and untreated forest can have a substantial influence on avian abundance in the post-restoration landscape. Five of seven species studied responded to the edge in the untreated forest, while only one responded to the edge in the treated forest. The disproportionate number of species responding to edges in the untreated forest suggests that, when the effect of forest restoration is considered, it is especially important to consider edge effects on birds inhabiting remnant unrestored patches. Conversely, edge effects appear to be relatively unimportant, at least in the short term, in stands that have undergone a restoration treatment.

Although the forest-restoration treatment seems to increase the abundances of the majority of bird species, some species appear to favor untreated forest (Beier and Maschinski 2003). Restoration plans often call for the maintenance of untreated patches and/or corridors for the preservation of species such as the Mexican Spotted Owl (*Strix occidentalis lucida*) and cougar (*Felis concolor*) that are dependent on dense forest (e.g., Friederici 2003a). In general, however, planners attempt to keep the sizes of untreated patches to a minimum, allowing the restoration of as much forest area as possible. In order to ensure that sufficient interior habitat is protected, it will be important to take edge effects into account when the location, size, and configuration of such patches are planned. Of the species we studied, only the Grace's Warbler tended to be more abundant in the untreated forest, and its substantial decline near the edge may be representative of other species that favor untreated forest. This result suggests that it will be prudent to consider the possibility of species declining near edges when the shape and extent of remnant unrestored patches are planned and thus to preserve larger areas of untreated forest than might otherwise be retained.

The relatively large number of one-sided edge effects we documented is unusual in the edge literature, but this may well be the result of few edge studies having measured effects on two sides of edges separating distinct patches that both provide suitable habitat for the same species (Sisk and Battin 2002, Fonseca and Joner 2007). Although such edges are becoming increasingly common in managed and restored ecosystems, they have received considerably less attention than those between habitat and non-habitat. It is clear from this study that this type of edge can have meaningful effects on animal distributions.

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LITERATURE CITED

Allen, C. D., M. Savage, D. A. Falk, K. F. Suckling, T. W. Swetnam, T. Schulke, P. B. Stacey, P. Morgan, M. Hoffman, and J. T. Klingel. 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. Ecological Applications 12:1418–1433.

Andrén, H. 1995. Effects of landscape composition on predation rates at habitat edges, p. 222–225. *In* L. Hansson, L. Fahrig, and G. Merriam [eds.], Mosaic landscapes and ecological processes. Chapman & Hall, London.

Battin, J. 2003. Habitats and the animals that love them: avian habitat selection in a post-restoration landscape. Ph.D. dissertation, Northern Arizona University, Flagstaff, AZ.

Battin, J., and T. D. Sisk. 2003. Assessing landscape-level influences of forest restoration on animal populations, p. 175–190. *In* P. Friederici [ed.], Ecological restoration of southwestern ponderosa pine forests. Island Press, Covelo, CA.

Beier, P., and J. Maschinski. 2003. Threatened, endangered, and sensitive species, p. 306–333. *In* P. Friederici [ed.], Ecological restoration of southwestern ponderosa pine forests. Island Press, Covelo, CA.

Brand, L. A., and T. L. George. 2001. Response of passerine birds to forest edge in coast redwood forest fragments. Auk 118:678–686.

Brand, L. A., B. R. Noon, and T. D. Sisk. 2006. Predicting abundance of desert riparian birds: validation and calibration of the effective area model. Ecological Applications 16:1090–1102.

Buckland, S. T., D. R. Anderson, K. P. Burnham, and J. L. Laake. 1993. Distance sampling: estimating abundance of biological populations. Chapman & Hall, London.

Cadenasso, M. L., and S. T. Pickett. 2001. Effect of edge structure on the flux of species into forest interiors. Conservation Biology 15:91–97.

Cadenasso, M. L., S. T. A. Pickett, K. C. Weathers, and C. G. Jones. 2003. A framework for a theory of ecological boundaries. BioScience 53:750–758.

Covington, W. W., P. Z. Fulé, M. M. Moore, S. C. Hart, T. E. Kolb, J. N. Mast, S. S. Sackett and M. R. Wagner. 1997. Restoring ecosystem health in ponderosa pine forests of the Southwest. Journal of Forestry 95:23–29.

Covington, W. W., and M. M. Moore. 1994. Southwestern ponderosa forest structure. Journal of Forestry 92:39–47.

Fagan, W. F., R. S. Cantrell, and C. Cosner. 1999. How habitat edges change species interactions. American Naturalist 153:165–182.

Fletcher, R. J. Jr. and R. R. Koford. 2003. Spatial responses of Bobolinks (*Dolichonyx oryzivorus*) near different types of edges in northern Iowa. Auk 120:799–810.

Fletcher, R. J. Jr., L. Ries, J. Battin, and A. Chalfoun. 2007. The role of habitat area and edge in fragmented landscapes:

definitively distinct or inevitably intertwined? Canadian Journal of Zoology 85:1017–1030.

FONSECA, C. R., AND F. JONER. 2007. Two-sided edge effect studies and the restoration of endangered ecosystems. Restoration Ecology 15:613–619.

FRIEDERICI, P. 2003a. The "Flagstaff model," p. 7–25. *In* P. Friederici [ED.], Ecological restoration of southwestern ponderosa pine forests. Island Press, Covelo, CA.

FRIEDERICI, P. 2003b. Healing the region of pines: forest restoration in Arizona's Uinkaret Mountains, p. 197–214. *In* P. Friederici [ED.], Ecological restoration of southwestern ponderosa pine forests. Island Press, Covelo, CA.

FULÉ, P. Z., A. E. M. WALTZ, W. W. COVINGTON, AND T. A. HEINLEIN. 2001. Measuring forest restoration effectiveness in reducing hazardous fuels. Journal of Forestry 99:24–29.

HADDAD, N. M. 1999. Corridor use predicted from behaviors at habitat boundaries. American Naturalist 153:215–227.

HARTLEY, M. J., AND M. L. HUNTER JR. 1998. A meta-analysis of forest cover, edge effects, and artificial nest predation rates. Conservation Biology 12:465–469.

KINGSTON, S. R., AND D. W. MORRIS. 2000. Voles looking for an edge: habitat selection across forest ecotones. Canadian Journal of Zoology 78:2174–2183.

KRISTAN, W. B., A. J. LYNAM, M. V. PRICE, AND J. T. ROTENBERRY. 2003. Alternative causes of edge–abundance relationships in birds and small mammals of California coastal sage scrub. Ecography 26:29–44.

LAHTI, D. C. 2001. The "edge effect on nest predation" hypothesis after twenty years. Biological Conservation 99:365–374.

LAURANCE, W. F., AND E. YENSEN. 1991. Predicting the impacts of edge effects in fragmented habitats. Biological Conservation 55:77–97.

LIDICKER, W. Z. 1999. Responses of mammals to habitat edges: an overview. Landscape Ecology 14:333–343.

MATLACK, G. R. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. Biological Conservation 66:185–194.

MCCOLLIN, D. 1998. Forest edges and habitat selection in birds: a functional approach. Ecography 21:247–260.

MCGLONE, C. M., J. D. SPRINGER, AND W. W. COVINGTON. 2009. Cheatgrass encroachment on a ponderosa pine forest ecological restoration project in northern Arizona. Ecological Restoration 27:37–46.

MEYER, C., AND T. D. SISK. 2001. Butterfly response to microclimatic changes following ponderosa pine restoration. Restoration Ecology 9:453–461.

MEYER, C. L., T. D. SISK, AND W. W. COVINGTON. 2001. Microclimatic changes induced by ecological restoration of ponderosa pine forests in Northern Arizona. Restoration Ecology 9:443–452.

MURCIA, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends in Ecology and Evolution 10:58–62.

PATON, P. W. C. 1994. The effect of edge on avian nest success: how strong is the evidence? Conservation Biology 8:17–26.

RIES, L., AND D. M. DEBINSKI. 2001. Butterfly responses to habitat edges in the highly fragmented prairies of central Iowa. Journal of Animal Ecology 70:840–852.

RIES, L., R. J. FLETCHER JR., J. BATTIN, AND T. D. SISK. 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. Annual Review of Ecology, Evolution and Systematics 35:491–522.

RIES, L., AND T. D. SISK. 2004. A predictive model of edge effects. Ecology 85:2917–2926.

RIES, L., AND T. D. SISK. 2008. Butterfly edge effects are predicted by a simple model in a complex landscape. Oecologia 156:75–86.

RIES, L., AND T. D. SISK. 2010. Realizing the potential of the effective area model: refining the software and incorporating recent advances to maximize usefulness on military installations (SI-1597). Report to the U.S. Department of Defense, Strategic Environmental Research and Development Program by Northern Arizona University, Flagstaff, AZ.

SISK, T. D., AND J. BATTIN. 2002. Habitat edges and avian ecology: geographic patterns and insights for western landscapes. Studies in Avian Biology 25:30–48.

SISK, T. D., AND N. M. HADDAD. 2002. Incorporating the effects of habitat edges into landscape models: effective area models for cross-boundary management, pp. 208–240. *In* J. Liu and Taylor, W. [ED.], Integrating landscape ecology into natural resource management. Oxford University Press, Oxford, UK.

SISK, T. D., N. M. HADDAD, AND P. R. EHRLICH. 1997. Bird assemblages in patchy woodlands: modeling the effects of edge and matrix habitats. Ecological Applications 7:1170–1180.

SOKAL, R. R., AND F. J. ROHLF. 1995. Biometry: the principles and practice of statistics in biological research, 3rd edition. W. H. Freeman, New York.

THOMAS, L. 1997. Retrospective power analysis. Conservation Biology 11:276–280.

WIENS, J. A., C. S. CRAWFORD, AND J. R. GOSZ. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. Oikos 45:421–427.