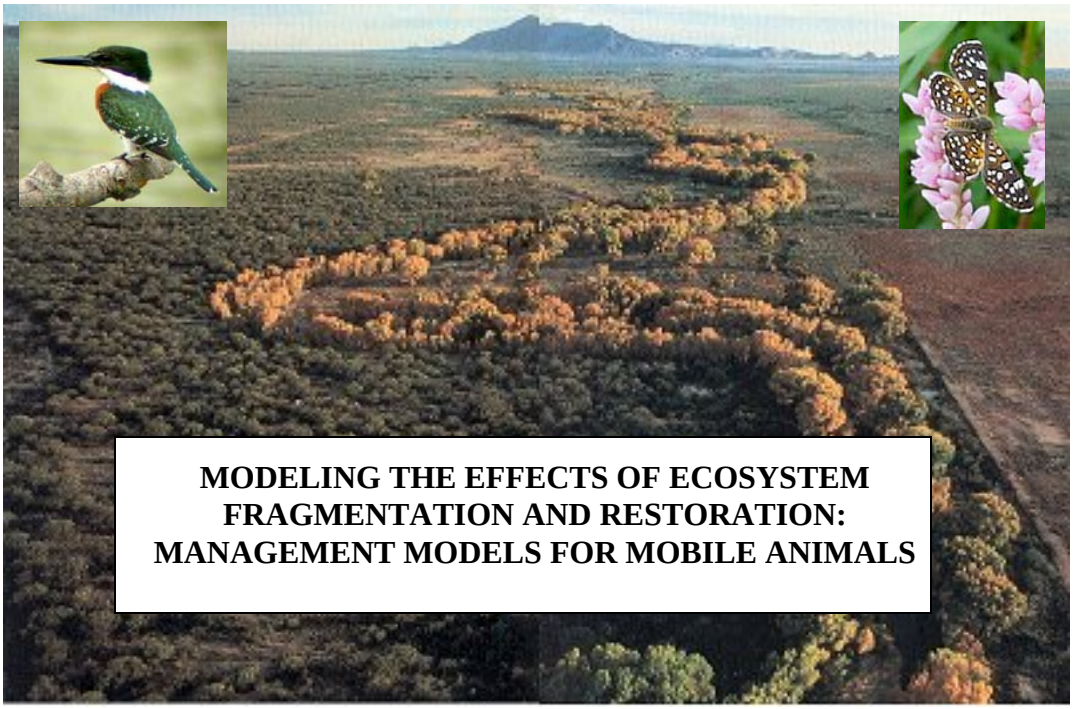
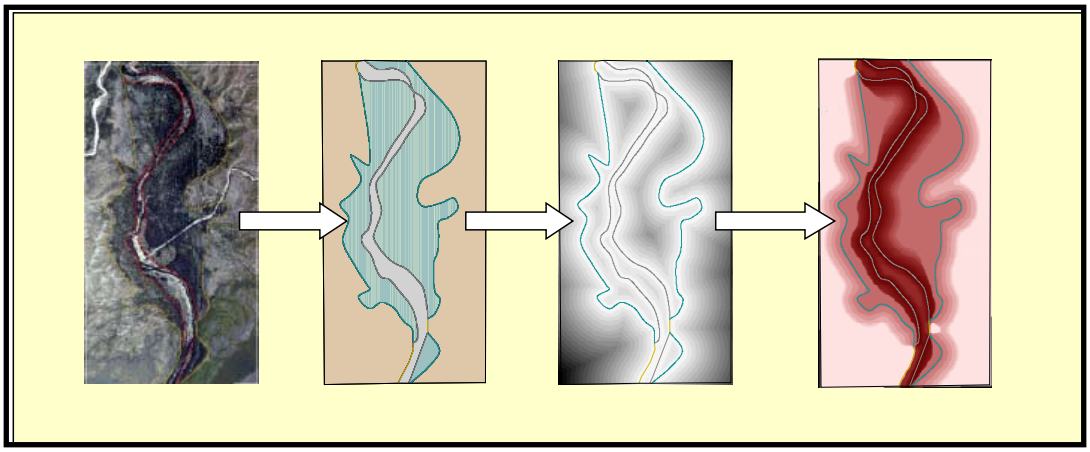
FINAL REPORT

Appendix Volume 2 (Appendices III-VII)

SERDP PROJECT CS-1100





1 DECEMBER 2003

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APPENDIX III: Presentations (1998-2003, chronologically)

1) The Influence of Habitat Edges on Avian Ecology: Geographic Patterns and Insights for Western Landscapes. T.D. Sisk and W.J. Battin. Oral presentation to the *Cooper Ornithological Society*, Portland, OR, March 1999.

2) Demographic models of bird populations in Western North America. B.R. Noon, Studies in Avian Biology. Oral presentation to the *Cooper Ornithological Society*, Portland, OR, March 1999.

3) Assessing Species Viability at Landscape Scales. B.R. Noon, T.D. Sisk and H.M. Hampton. Plenary address to the conference *Predicting Species Occurrences: Issues of Scale and Accuracy*, Snowbird, UT, October 1999.

4) A Spatial Model of Animal Density Incorporating Edge Effects. H.M. Hampton, T.D. Sisk and B.R. Noon. Poster presentation to *the 5th Biennial Conference of Research on the Colorado Plateau*, Flagstaff, AZ, October. 1999.

5) The response of *Colia eurytheme* (Lepidoptera: Pieris) and *Neophasia menapia* (Lepidoptera: Pieris) to the structural edge created by ponderosa pine restoration in northern Arizona. C.L. Meyer and T.D. Sisk. Oral presentation to the *5th Biennial Conference of Research on the Colorado Plateau*, Flagstaff, AZ, October. 1999.

6) Responses of passerine birds to ponderosa pine forest restoration. J.Battin and T.D. Sisk. Oral presentation to the *5th Biennial Conference of Research on the Colorado Plateau*, Flagstaff, AZ, October. 1999.

7) Predicting Animal Responses to Ecological Changes on the San Pedro River: A Spatial Model Incorporating Edge Effects. H.M. Hampton, L. Ries, T.D. Sisk and B.R. Noon. Poster presentation to the conference *Aguas Divididas*, *International Conference on the Future of the San Pedro River,* Canenea, Sonora, Mexico and Bisbee, AZ, Nov. 1999.

8) Predicting animal responses to ecological change on the San Pedro River: A spatial model incorporation edge effects. H.M. Hampton, L. Ries, T.D. Sisk and B.R. Noon (poster). *"Aguas Divididas/Divided Waters" Bi-national Conference on Management of the San Pedro Watershed,* November 1999.

9) The response of butterflies to structure edges in northern Arizona ponderosa pine forests. C. Meyer, T.D. Sisk, and W.W. Covington (poster). *Steps Towards Stewardship Conference.* May 2000.

10) Landscape change along desert riparian ecosystems: implications for butterflies and conservation. L. Ries and T.D. Sisk (oral). *Annual meeting of the Society for Conservation Biology*, June 2000.

11) The responses of microclimate and butterflies to structural edges in ponderosa pine forests. C. Meyer and T.D. Sisk (oral). *Annual meeting of the Society for Conservation Biology,* June 2000.

12) Effects of spatial heterogeneity on breeding bird abundance in the San Pedro Riparian National Conservation Area. A.L. Brand, S. Bayard de Volo, B.R. Noon, and T.D. Sisk (poster).*Annual meeting of the Society for Conservation Biology*, June 2000.

13) Assessing the impacts of landscape change on mobile animals**.** T.D. Sisk, B.R Noon, and H.M. Hampton (oral). *Annual meeting of the Ecological Society of America*, August 2000.

14) Predicting animal responses to ecological changes: A spatial model incorporating edge effects. T.D. Sisk, B.R. Noon, and H.M. Hampton (poster). *4th International Conference on Integrating GIS and Environmental Modeling.* September 2000.

15) A Spatial Model for Predicting Animal Responses to Ecological Changes. Haydee M. Hampton, Leslie Ries and Thomas D. Sisk (oral). *ESRI Users' Conference, Annual Meeting*, June 2001.

16) Impacts of Landscape Change on Mobile Animals: Effective Area Models for Conservation Planning. T.D. Sisk, H.M. Hampton, and B.R. Noon (oral). *Society for Conservation Biology, Annual Meeting,* July 2001.

17) Land Use Change, Landscape pattern, and the Conservation of Biological Diversity. T.D. Sisk (oral).*Colorado State University, invited lecture*, November 2001.

18) Assessing avian responses to ponderosa pine forest restoration. J. Battin (Invited talk) *Ecological Society of America,* Tucson, AZ, August 2002.

19) Placing Edge Responses in a Predictive Framework. L. Ries and T.D. Sisk (poster), *Ecological Society of America,* Tucson, AZ, August 2002.

20) Edge effects on bird abundance in a landscape undergoing ponderosa pine forest restoration. J. Battin and T.D. Sisk (poster), *North American Ornithological Congress,* New Orleans, LA, September 2002.

21) Landscape-scale modeling to link scales in restoration and conservation planning. T.D. Sisk (Invited seminar), *School of Forestry, Northern Arizona University,* November 2002.

22) Integrating Species-Level Biology and Ecosystem Management: The Role of Landscape-Scale Spatial Models. T.D. Sisk and L. Ries (Symposium presentation), *SERDP Symposium*. Washington, DC, December 2002.

23) Landscape-level management on military bases: Modeling the ecological consequences of alternative management scenarios. L. Ries and T.D. Sisk (Poster), *SERDP Symposium*, Washington, DC, December 2002.

24) A predictive model of edge effects. L. Ries and T. D. Sisk (oral), Cooper Ornithological Meeting, April 2003.

25) Multi-scale habitat selection and its reproductive consequences for the plumbeous vireo in a changing landscape. J. Battin (oral), Cooper Ornithological Meeting, Flagstaff, AZ, April 2003.

26) Ecological and life-history traits predict avian edge response: a meta-analysis. L. Arriana Brand (oral), Cooper Ornithological Meeting, Flagstaff, AZ, April 2003.

27) A predictive model of edge effects. L. Ries and T. D. Sisk (oral), Society for Conservation Biology Annual Meeting, July, 2003.

28) When good animals love bad habitats: theory and evidence for ecological traps. J. Battin (oral), Society for Conservation Biology Annual Meeting, July, 2003.

29) The effects of severe drought on the reproductive output of southwestern passerine birds. J. Battin (oral), Conference for Research on the Colorado Plateau. Flagstaff, AZ, November 2003.

30) Effective Area Models for Conservation Planning: Linking Species-Level Biology with Landscape Perspectives. T.D. Sisk, L.R. Ries, J. Battin, H.M. Hampton, A. Brand, B. Noon, & M.M. Howe (poster). *SERDP Symposium*, Washington, DC, December 2003.

31) The Ecological Impacts of Alternative Management Scenarios: An example of the use of the Effective Area Model on Ft. Benning in Georgia. L. Ries and T. D. Sisk (poster). *SERDP Symposium*, Washington, DC, December 2003.

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APPENDIX IV: Acknowledgements

We thank the many collaborators involved in this project: Semi-Arid Land-Surface-Atmosphere (SALSA), Fort Huachauca Department of Natural Resources (Particularly Sheridon Stone)**,** Dr. Tony King at Oak Ridge National Laboratory, Camp Navajo, the Bureau of Land Management's Arizona Strip Office, the Bureau of Land Management's Tucson Field Office and San Pedro Field Office (especially Bill Childress, Dave Krueper, & Jack Whetstone), Ecological Restoration Institute (ERI).

APPENDIX V: Related Projects

Spatial Analysis Workshop

On Oct. 4-5, 2001, Northern Arizona University (NAU) hosted a workshop organized by Carolyn Hunsaker to discuss coordination and collaboration in assessing uncertainty in spatial models developed SERDP-funded groups. In attendance were Carolyn T. Hunsaker (U.S.D.A Forest Service), Tony King, Tom L. Ashwood, and Henriette I. Jager (ORNL); John Radke (UC Berkeley), George Gertner (Univ. of Illinois), Tom Sisk and Haydee Hampton (NAU), and Marc Deconchat (INRA-URSAD-DYNAFOR France). Each team presented their SERDP work and associated uncertainty analysis methods. The outcome of the meeting was improved understanding and coordination among participants and the finalization of the report: "Uncertainty in Spatial Data Used in Ecology" by Marc Deconchat, Carolyn Hunsaker, and John Radke. The report is a literature review and synthesis submitted to Oak Ridge National Laboratory for the Strategic Environmental Research Program.

Forest Ecosystem Restoration Analysis (ForestERA)

The goal of the Forest Ecosystem Restoration Analysis Project is to provide a framework for assessing the impacts and implications of ponderosa pine restoration treatments at landscape and regional scales. This framework will provide a data-based means for analyzing cumulative effects of multiple restoration treatments, and a means of integrating consideration of fire and forest ecology with consideration of wildlife and biodiversity issues. The Forest Ecosystem Restoration Analysis (ForestERA) project will provide a landscape ecology framework to help guide the location and timing of restoration treatments in ponderosa pine forests across northern Arizona and in contiguous areas of adjacent states.

APPENDIX VI: Students and Project Titles

Brand, Arriana
(tentative) Predicting the impacts of fragmentation on bird populations on the San Pedro River

Battin, James
Habitats and the animals that love them: avian habitat selection in a post-restoration landscape

Ries, Leslie
Placing edge responses into a predictive framework

Meyer, Cecelia
Microclimatic changes and biotic effects across forest structural gradients associated with ponderosa pine restoration

Kelly, Shannon
Butterflies at Camp Navajo

APPENDIX VII: Thesis and Dissertation Chapters

EDGE EFFECTS IN PONDEROSA PINE FOREST PASSERINES IN A LANDSCAPE UNDERGOING FOREST RESTORATION TREATMENTS

By James Battin

Abstract

Throughout southwestern North America, efforts are under way to reduce the risk of large-scale, high intensity fires and improve forest health through the implementation of forest restoration, a process of timber harvesting and prescribed burns designed to return the ponderosa pine forest ecosystem to a state similar to that in which it existed prior to European settlement of the Southwest. Restoration treatments produce a novel type of habitat edge—the edge between treated and untreated forest patches—which has the potential to have profound effects on animal abundance in the post-restoration landscape. We studied the influence of the edge between ponderosa pine forest patches that had undergone restoration treatments and those that remained untreated on the abundance of seven passerine bird species. One species, the dark-eyed junco, showed an edge-exploiting response, occurring more frequently at the edge than in either neighboring habitat. Of the six remaining species, none changed in abundance near the structural edge in the treated forest, but four showed significant changes in abundance relative to the edge in the untreated forest. These responses did not conform to a simple null model based on birds integrating changes in habitat preference across the edge. On the other hand, the null model was correctly predicted the direction of all observed edge responses in the untreated habitat. Edge effects on bird abundance mirrored changes in microclimate across the edge. Like the avian responses observed in this study,

microclimate was found, in another study, to change with respect to edge in the untreated, but not in the treated, forest. Our results suggest that a consideration of edge effects will be especially important in areas where forest management objectives call for patches of untreated forest to be retained for the purpose of providing habitat for animals that prefer the unrestored forest type.

Introduction

In the American Southwest, a recent increase in the frequency of high-intensity wildfires, coupled with concerns about declining forest health, has led scientists and land managers to develop aggressive forest management strategies to return the ponderosa pine forests that cover large portions of the region to the more open condition in which they existed prior to European settlement (Allen et al. 2002, Friederici 2003a). This process, known as forest restoration, is based on the premise that the combined effects of fire suppression, logging, and cattle grazing have, over the course of more than a century, transformed what was once an open system characterized by frequent, low-intensity fires, into a closed-canopy forest that is subject to infrequent, high-intensity fires (Covington and Moore 1994, Covington et al. 1997). Restoration treatments designed to counter this trend involve the removal of over 50% of ponderosa pine basal area followed by a prescribed burn (Friederici 2003a; Fig. 5.1). Such treatments are scheduled to be applied to hundreds of thousands, if not millions, of hectares of forest lands over the coming decades (Allen et al. 2002), creating major habitat changes for a wide range of ponderosa pine forest animal species (Battin and Sisk 2003).

One effect of forest restoration treatments is to propagate a novel type of habitat edge across the landscape: the edge between treated and untreated forest tracts. These edges are likely to become long-lasting features of the post-restoration landscape for a

variety of reasons, including the presence of administrative boundaries (e.g., between private and public lands and between public lands managed by different agencies with opposing 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). Edges have been found to have wide-ranging effects on animal abundance (Lidicker 1999, Sisk and Battin 2002), productivity (Paton 1994, Andrén 1995, Hartley and Hunter 1998), and behavior (Haddad 1999, Meyer and Sisk 2001, Ries and Debinski 2001), as well as on abioitic factors and habitat features that are important to animals (Matlack 1993, Sisk et al. 1997, Kristan et al. 2003). Understanding how animals respond to habitat edges can be essential both to animal conservation (Lidicker 1999) and to efforts to predict animal distributions in fragmented landscapes (Sisk and Haddad 2002). Edges between treated and untreated forest thus have the potential to have a substantial effect on animal populations, and an understanding of edge effects in this landscape should help improve our ability to predict the effects of forest restoration activities on animal distributions (Sisk et al. 2002).

From the point of view of animal habitat selection, edges can be divided into two qualitatively different categories: those separating two habitat patches that differ in quality, and those dividing habitat from non-habitat. Of 38 avian studies reviewed by Sisk and Battin (2002) that examine changes in bird abundances relative to edges, all but six focused exclusively on edges between habitat and non-habitat. In these cases, few or no species inhabited the interiors of both of the adjoining habitats. Situations in which two neighboring habitats both serve as habitat for the same species are common in both

natural and anthropogenically altered systems, but the edges between such patches remain relatively unstudied. The edge between treated and untreated ponderosa pine forest is one such edge. Bird communities differ very little between treated and untreated forest, although large differences in bird abundance may exist between the two habitat types.

While numerous empirical studies have described patterns of change in animal abundances with respect to habitat edges, few studies have addressed the mechanisms driving edge effects or attempted to develop a theoretical underpinning for the study of edges (Murcia 1995, Lidicker 1999, Sisk and Battin 2002). Recently, however, several authors have begun to take a more mechanistic approach to the study of edges, both by measuring edge-associated environmental variables that may cause bird abundances to change near the edge (e.g., vegetation and microclimate) and by measuring aspects of bird behavior that may lead to edge effects (Fletcher and Koford 2003, Kristan et al. 2003). The increased interest in the mechanisms driving edge effects has pushed investigators to pursue two different strands of modeling work to elucidate further the mechanistic underpinnings of edge effects. The first is the development of null models, which are designed to isolate a single ecological process and test whether or not it explains observed changes in animal abundance near edges (King et al. 1997, Lidicker 1999, Kingston and Morris 2000). The second is the development of approaches for the prediction of edge responses based on general properties of ecological systems and animal life history traits (McCollin 1998, Brand 2003, Ries and Sisk *in review*). Here, we use both approaches, first developing and testing a null model appropriate to our system and then applying a recently developed predictive framework (Ries and Sisk *in*

review) to our data to gain additional insight into the possible mechanisms driving observed edge effects.

We examine changes in bird abundance across the edge between ponderosa pine forest stands that have undergone a restoration treatment and ones that have remained untreated. Restoration treatments provide an ideal, landscape-scale, replicated experimental system in which to study 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 (turnover of about two species) between treated and untreated forest, although some species differ substantially in abundance between the two (J. Battin & T. Sisk, unpublished data). Because the edges considered in this study were created experimentally quite recently (0-3 years prior to the beginning of the study), there was no time for many of the habitat changes often associated with edges (e.g., the formation of a transitional shrub layer) to develop. The uniformity of the treatment across the study area, coupled with the recency of treatments and the clearly defined nature of the edge eliminated many of the factors that confound other edge studies, including the uncertain location of the edge between two habitats and the presence of vegetation gradients across the edge. This allowed us to focus on a relatively small suite of possible mechanisms when attempting to understand the mechanistic basis of edge effects in this system.

Null models of edge effects

The general purpose of null models is "to generate an expected pattern in the absence of specific processes" (With 1997). For edge-abundance relationships, null models can be used to predict how animal densities should change near edges in the absence of many of the factors normally invoked to explain edge effects in animals,

including behavioral avoidance of, or preference for, the edge, gradients in habitat quality across the edge, preference for areas where animals can have access to multiple habitats, or any other more complex responses to habitat edges. Deviations from the null suggest the existence of a more complex response. The simplest null model of an edge-abundance relationship is, of course, no change in abundance with relation to the edge (Lidicker 1999); Fig. 5.2a). This model simply tests the hypothesis that animals do not change in abundance near the edge for any reason. In general, however, null models of edge effects simulate a single, simple edge response. These include, for birds, changes in abundance caused by territory selection rules (King et al. 1997); Fig. 5.2b) and nest site selection rules (Bollinger and Switzer 2002).

Here, we develop a null model for territorial forest passerines in a landscape containing two habitats, one of which is more densely populated than the other. It is based on the idea that the change in bird abundance near the edge should be proportional to the proportion of a bird's territory that overlaps the neighboring habitat. The model produces predictions that are qualitatively similar to those generated by a model developed for small mammals in which mammal densities in preferred habitats decrease as their surroundings include a larger proportion of the less preferred habitat, and vice versa (Kingston and Morris 2000). For a species that differs in abundance between two habitats, null model predictions are generated by calculating the proportion of a circular territory that lies in the less preferred habitat type as the center of a territory moves closer to, and eventually crosses, the edge and multiplying the result by a scaling factor parameter that reflects the magnitude of the abundance difference (Fig. 5.3). As in the mammal-based model of Kingston and Morris (2000), abundance in the less preferred

habitat increases near the edge, and abundance in the preferred habitat decreases near the edge. For species that do not differ in abundance between habitats, the null model predicts no edge effect on abundance.

We use this null model to examine the edge responses of nine species of territorial forest passerine at edges between restored and unrestored ponderosa pine forest in northern Arizona. We conduct a simple model test in which we predict the expected null edge response based on relative bird abundance in the two habitats. When bird abundance is higher in one habitat than the other, we expect an increase in abundance near the edge in the habitat in which abundance is lower and a decrease in the habitat in which abundance is higher. We then examine the actual change in bird abundance near the edge for each species and compare it to model predictions. When observed responses agree with the predictions of the null model on both sides of the edge (i.e., in treated and untreated forest), it suggests a simple response in which bird abundances transition slowly from the interior abundance in one forest type to that in the other. When observed responses deviate from model predictions, it suggests that other mechanisms are driving edge-abundance relationships.

Study area

Our 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 120 miles northwest of Flagstaff, Arizona, the Mt. Trumbull area represents the first large-scale application of the "Flagstaff model" (Friederici 2003a) of forest restoration treatments. Approximately 1200 hectares of ponderosa pine (*Pinus ponderosa*) and ponderosa pine-Gambel oak (*Quercus gambeli*) forest, ranging from

about 2050 to 2200 m in elevation, are slated for restoration at Mt. Trumbull (Friederici 2003b).

Methods

Bird Survey Methodology

We developed a transect-based methodology that sampled an equal area of habitat at all distances (out to 200 m) from the edge created by forest restoration treatments. We used mapped locations of individual birds as the basis for a fine-scale analysis of edge effects. Birds were surveyed each summer from 1999 through 2002 along 200 m transects running from the treated-untreated edge into the interior of one habitat or the other. When possible, transects were paired, with one transect running into the treated forest and another into the untreated from the same point at the edge. Because restoration treatments were in progress during the course of the study, many edges at which we had placed bird survey transects were destroyed between years, and new edges were created, where new survey transects were placed. Each year, therefore, we used a different set of edge transects. In each year we placed transects at all available treated-untreated edges. Transect numbers varied from 5 to 12 per habitat in any given year (Table 5.1). Over the course of the study, we placed transects in seven different treatment units and the untreated forest stands adjacent to them.

Morning surveys were conducted at each transect between 28 May and 10 July each year. Surveys were conducted between 0.5 hours before sunrise and 4.5 hours after sunrise. Due to logistical and personnel constraints, only three surveys per transect were conducted in 1999 and 2002, while four surveys were conducted in 2000 and 2001. Time

of day, direction in which transects were run, and observer were rotated in order to minimize bias.

Each transect was surveyed for 30 minutes. Transects were divided into four 50 m segments, each of which was surveyed for 7.5 minutes. Only birds within the 50 m segment currently being surveyed were recorded. Individual birds that were detected on more than one segment during a given survey were noted, and one observation was chosen at random for analysis. The division of the transect into 50 m segments, coupled with the random selection of a single observation for any individual sighted in more than one segment remove the spatial bias usually associated with transect surveys, i.e., that the center of the transect is surveyed more intensively than either end and that observations tend to be biased toward the end of the survey at which the observer begins. For all birds within 50 m of the transect segment being surveyed, species, detection method, and distance from the transect were recorded. The location of each bird along the transect was mapped and entered into a GIS.

Statistical Analysis

We used program DISTANCE (Research Unit for Wildlife Population Assessment, University of St. Andrews) to determine whether distance sampling-based estimates of detectability (Buckland et al. 1993) differed between habitats for each species. Akaike's Information Criterion (AIC) values were compared between a model of bird detectability that included habitat type and a global detectability function. Detectability differed between habitats for only one species, Grace's warbler. For all other species, AIC chose the detectability model without a habitat term. This finding was not surprising, as all species considered here could be detected easily, especially by ear,

to distances well beyond 50 m in both treated and untreated forest. We therefore did not employ any habitat-specific correction to our data on bird detections, but between-habitat differences in Grace's warbler abundance may have been underestimated, since detectability appeared to be higher in the treated areas, where Grace's warblers were found to occur at lower densities.

Determining whether species abundances changed near the edge in a way that was consistent with the null model was a two-part process. First, we made predictions of species edge responses based on the null model. If a species was found to be significantly more abundant in one habitat (e.g., treated forest) than the other (e.g., untreated forest), we predicted that it would increase in abundance near the edge in the habitat in which it was less abundant and decrease in abundance near the edge in the habitat in which it was more abundant. We then tested the edge response to see if it conformed to these predictions.

To assess between-habitat differences in abundance, we compared the interior portion of each transect (i.e., 100 m – 200 m from the edge) between 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. All species for which a significant ($p<0.10$) year by habitat interaction was detected were excluded from further analyses because the extremely low power of year-by-year tests of habitat differences and edge effects made it nearly impossible to generate meaningful predictions or tests of edge effects for these species. An alpha of 0.10 was chosen for this test to ensure that we were conservative about pooling data across years. Species showing no year by habitat interaction and a statistically significant ($p<0.05$) difference

in abundance between habitats were predicted to show evidence of an edge effect in abundance, while those in which no significant difference was detected were predicted to show no edge effect. For each species, we conducted a retrospective power analysis (Sokol 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 an alpha of 0.05. This allowed an assessment of the likelihood that a meaningful between-habitat difference in abundance might have gone undetected due to low power, leading to a spurious prediction of no edge effect.

Because bird abundances were low, there was rarely more than one observation for a given species in a given edge distance class on a single transect, 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. We chose to model each side of the edge 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 different occurrence probabilities in the two habitats.

We used random effects, mixed model, repeated measures logistic regression to determine whether bird abundances changed with respect to distance from the edge (SAS PROC MIXED with the GLIMMIX macro; (Fletcher and Koford 2003). We divided each transect into eight 25 m segments. For each segment 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. We specified year and transect as random effects and distance category as a repeated measure, using an autoregressive covariance structure (SAS AR(1)). 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 patterns observed in this analysis would not differ regardless of the method used to compute degrees of freedom.

Results

Model Predictions

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 5.2). These species were excluded from further analysis because year-by-year tests had very low power and showed substantial interannual variation in abundance patterns. Of the remaining seven species, three—western bluebird, chipping sparrow, and dark-eyed junco—were significantly more abundant in treated than in untreated forest. Our null model, therefore, predicted that, in forest areas that had undergone a restoration treatment, these three species would decrease in abundance near the edge, while they would increase near the edge in untreated forest. For the remaining four species, we found no significant between-habitat differences in abundance, which led us to predict no edge effect for those species. Power analysis revealed, however, that, with an alpha of

0.05, we would only be able to detect a between-habitat difference of between 76 and 100% (depending on species) eighty percent of the time (Table 5.2). This result suggests that substantial between-habitat differences in abundance could have gone undetected. Indeed, three of the four species for which no significant between-habitat difference in abundance was detected showed potentially meaningful differences in mean abundance between habitats. Mean abundance for the white-breasted nuthatch was 34% higher in the treated forest than in the untreated forest. For the western tanager, mean abundance was 41% higher in the treatment. Mean abundance of the Grace's warbler was 59% higher in the untreated forest than in the treated forest. For these species our model predicted no edge effect, although this prediction could be erroneous when between-habitat differences in abundance were not detected due to low statistical power.

Edge Effects

Of the three species for which edge effects were predicted, only one, dark-eyed junco, showed a change in abundance near the edge in the treated habitat, and that change was in the opposite direction from what was predicted (Fig. 5.4). In the untreated habitat, on the other hand, the probability of occurrence of two of the three species was found to increase near the edge, as predicted. The western bluebird was the only species for which an edge effect was predicted that showed no evidence of a change in the probability of occurrence near the edge in either habitat. All four of the species for which no edge effect was predicted behaved as expected in the treated forest (Fig. 5.5). Three, however, showed changes in the probability of occurrence near the edge in the untreated habitat, one (Grace's warbler) decreasing and two (white-breasted nuthatch and western tanager) increasing. All three of the changes were in the direction that would have been predicted

by the model if the observed between-habitat differences in abundance reported in Table 5.2 were statistically significant. The yellow-rumped warbler, for which mean abundance was very similar between habitats, showed no edge effect in either habitat.

Discussion

Edge-abundance relationships

Overall, of fourteen total edge responses modeled, our null predictions integrating bird densities in the two habitats across the edge predicted the correct edge response (or lack thereof) half of the time. Only one species, however, showed edge responses in both habitats that were consistent with the model. This was the yellow-rumped warbler, the species for which abundances were most similar between habitats and for which no edge response was predicted. With six of seven species departing from the model, it seems likely that something other than between-habitat differences in density is driving edge effects in most bird species in this system.

In the untreated habitat we observed three unpredicted positive responses. The fact that all three went in the direction that would have been predicted if observed between-habitat abundance patterns had been statistically significant suggests that low statistical power may have caused us to underpredict edge responses. Two species deviated from model predictions in both habitats. One, the dark-eyed junco, demonstrated an edge-exploiting response, reaching its peak abundance at the edge. The other, the western bluebird, did not respond to the edge at all, even though it differed substantially in abundance between habitats, showing a response like that in Fig. 5.2a.

In addition, two species, the mountain chickadee and the plumbeous vireo, showed substantial interannual variation in between-treatment abundance responses, suggesting that a modest percentage of species may show complex responses to the restoration treatment. For instance, other research at this site suggests that the plumbeous vireo responds much more strongly to the abundance of oak when selecting habitats than it does to the restoration treatment. Indeed, it may not take the restoration treatment into

account at all when selecting breeding habitat (see Chapter 4). Since we used different areas in different years for our edge surveys, year-to-year variation in between-habitat patterns of oak distribution may have resulted in large swings between years in between-habitat vireo abundance patterns. The mountain chickadee may also have been responding strongly to some habitat feature not associated with the restoration treatment, or it might have been especially sensitive to the considerable variability in climatic conditions at the site.

Mechanisms for edge-abundance relationships

A small number of general causative factors are thought to be responsible for edge effects on animal abundance. These include passive displacement (King et al. 1997, Ortega and Capen 1999, Fletcher and Koford 2003), resource availability (McCollin 1998, Ries and Sisk *in review*), and interspecific interactions (McCollin 1998, Fagan et al. 1999). Passive displacement only applies at edges between habitat and nonhabitat, which leaves resource availability and interspecific interactions as the two primary categories of mechanism potentially responsible for the edge effects in bird abundance observed here.

Ries and Sisk (*in review*) developed a conceptual model of edge effects based entirely on resource distribution, although they effectively include interspecific interactions as well by incorporating variables such as enemy-free space into their definition of resources. In this framework, resources in a two-habitat landscape can either be distributed so that some occur in one habitat and some in another (e.g., nest sites in one habitat and forage in another) or so that all necessary resources occur in each habitat, though possibly at different levels. When resources are divided between habitats,

animals are expected to occur at highest densities near the edge, where they can have easiest access to both habitats. When all resources occur in a both habitats, animals should display a "transitional" edge response, similar to that shown in Fig. 5.3, in which abundance changes gradually from the more preferred habitat to the less preferred one. Looking at our data in light of this framework, most species whose abundances changed near the edge showed responses consistent with a transitional response, although only in one habitat. The two exceptions were the dark-eyed junco and the western bluebird. The junco occurred most frequently at the edge, suggesting resource division. Of the seven species examined here, the junco was the only ground nester. It is also a ground forager. It is possible that the treatment areas, perhaps due to the burning of the understory, contain fewer suitable nest sites but a greater amount of forage than the untreated forest, causing juncos to seek out territories that encompass some treated and some untreated forest. The western bluebird displayed perhaps the most confounding pattern of edge effects, exhibiting no edge response in either habitat despite being over 2 ½ times more abundant in the treated area. It is unclear why this should be the case.

Animal responses to resources can be driven either by a simple integration of habitat preference across the edge (i.e., our null model) or by animals mapping onto changes in vegetation, microclimate, or the abundances of other animal species across the edge (McCollin 1998). Both our null model and Ries and Sisk's (*in review*) resource distribution model are based on an assumption that edge effects should be symmetrical—that is, when a species' abundance declines by a certain amount at the edge in one habitat, it should increase by a similar quantity at the edge in the other habitat. Actual abundance changes for most bird species at the edge between treated and untreated forest, however,

displayed a distinctly asymmetrical pattern. Five of seven species changed in abundance near the edge (four increasing and one decreasing) in the untreated habitat, while only one changed in abundance near the edge in the treatment, and that in the opposite direction from our prediction. It seems clear, then, that some force other than a simple "transitional" edge response is driving bird responses to edges in this habitat.

Working at the same site and using some of the same edge transects, Meyer et al. (Meyer et al. 2001) documented an asymmetrical pattern of microclimate change with respect to the edge that was quite similar to the pattern that we saw in birds. 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. Differences were especially pronounced in the morning, the period of maximum bird activity (and the period during which our surveys were conducted). The correspondence between microclimate and bird edge effects suggests that many species may have been responding to something associated with the microclimatic gradient—either microclimate itself or some resource (e.g., prey or cover) that was in turn responding to microclimatic changes. Microclimate in the untreated forest became more similar to that in the treatment the nearer to the edge it was measured. Birds seemed to respond to the microclimate gradient in the same way that they responded to the treatment. Most species that were more abundant in the treatment increased near the edge, and the one that showed a trend toward lower abundance in the treatment decreased. Because the edges used in this study were relatively young, the sort of understory vegetation gradient characteristic of many more established edges (e.g., (Cadenasso and Pickett 2001) was not apparent in this site. Indeed, given the relatively

low productivity of the ponderosa pine forest ecosystem, such gradients are likely to be slow to develop, if they do at all. Gradients in other resources (e.g., prey), however, might map onto the microclimatic gradient even in the absence of a vegetation gradient.

Implications for management and future studies

Ponderosa pine forest restoration treatments cause radical habitat changes for forest-dwelling animal species, among them the creation of a novel type of habitat edge. From our results, it seems clear that the edge between treated and untreated forest can have a substantial influence on avian abundance in the post-restoration landscape. The pattern of asymmetrical edge responses seen here suggests that, when considering the impact of forest restoration treatments on animal populations, it will be especially important to consider edge effects on birds inhabiting remnant unrestored patches. Conversely, edge effects would appear to be relatively unimportant in stands that have undergone a restoration treatment. The observed asymmetry in avian edge-abundance relationships paralleled an asymmetrical microclimatic gradient, suggesting that microclimatic changes associated with restoration may be a key factor in understanding animal responses both to the treatment and to the treated-untreated edge. The microclimatic gradient may also presage the establishment of a vegetational gradient as the restoration treatments age, a development that could further impact bird populations in the untreated forest.

Forest restoration plans often call for the maintenance of untreated patches and/or corridors (e.g., (Friederici 2003a) for the preservation of animal species dependent on dense forest stands. 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. Our

data suggest that it will be important to take edge effects into account when planning the location, size, and configuration of such patches in order to ensure that sufficient habitat is protected. Of the species studied here, only one, the Grace's warbler, showed a trend toward higher abundance in the untreated forest. It experienced a substantial decline near the edge, which may be duplicated in other species that favor untreated forest areas. This result suggests that it will be prudent to account for species declines near edges when planning the sizes of remnant unrestored patches and thus to preserve larger areas of untreated forest than might be retained if edge effects were not accounted for. Plans for corridors, habitat features that contain a large proportion of edge, should be scrutinized especially carefully to ensure that sufficient habitat is retained.

The null model developed here did not predict edge responses well in the treated forest, where only one species showed an edge response, but it predicted the direction of the edge response in the untreated forest for most species. Overall, it achieved its intended purpose: to point out cases where it was likely that more complex forces than simple differences in habitat preference were driving edge effects. We suggest that, as the study of edges continues to focus more on the mechanisms driving edge effects, the development of appropriate null models for a wide range of taxa will be helpful in differentiating among the mechanisms underlying observed patterns of edge effects.

The consistent asymmetry in edge effects reported here is relatively unusual in the edge literature, but this may largely be a function of most edge studies having examined only one side of the edge. Edges between distinct patches that both serve as habitat (though not necessarily of the same quality) for the same animal species have received considerably less study than those between habitat and non-habitat areas. Such edges are

common, however, and it is clear from this study that they can have relatively complex dynamics that are not easily predicted from simple models. A greater emphasis on the study of this type of edge may yield considerable insight into the mechanics of edge effects. Approaches that combine the use of null models with the measurement of relevant habitat gradients, together with the further development of predictive frameworks (Brand 2003, Ries and Sisk *in review*), are likely to provide the greatest insight into edge effects in this sort of landscape.

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Table 5.1. Number of transects surveyed in treated and untreated forest in each year of the study.

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

Table 5.2. 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 we found significant year*treatment interactions (labeled "I" in the P-value column).

Common Name	Latin Name	Treated	Untreated	P[1]	Detectable Diff. (%)[2]
Mountain Chickadee	*Poecile gambeli*	0.196 (±0.040)	0.337 (±0.083)	I	--
White-breasted Nuthatch	*Sitta carolinensis*	0.527 (±0.087)	0.394 (±0.086)	0.47	76
Western Bluebird	*Sialia mexicana*	0.797 (±0.119)	0.298 (±0.077)	0.001	68
Plumbeous Vireo	*Vireo plumbeus*	0.216 (±0.044)	0.125 (±0.044)	I	--
Yellow-rumped Warbler	*Dendroica coronata*	0.230 (±0.045)	0.269 (±0.054)	0.64	91
Grace's Warbler	*Dendroica graciae*	0.176 (±0.044)	0.279 (±0.058)	0.31	95
Chipping Sparrow	*Spizella passerina*	0.331 (±0.066)	0.058 (±0.032)	0.001	91
Dark-eyed Junco	*Junco hyemalis*	0.277 (±0.056)	0.125 (±0.037)	0.01	93
Western Tanager	*Piranga ludoviciana*	0.284 (±0.062)	0.202 (±0.046)	0.52	100

[1]P-value for between-habitat differences from ANOVA, I = significant interaction effect (year-by-year results reported in table 2).
[2]From retrospective power analysis, the minimum between-treatment difference detectable 80% of the time at an alpha of 0.05, expressed as a percentage of the mean abundance in the habitat in which the species is more abundant.

FIGURE LEGENDS

Figure 5.1. Photographs of untreated forest (left) and a forest patch ~150 m away on which a restoration treatment was completed less than two years prior to the date on which the photograph was taken. Note the more open canopy and greater understory development that results from the restoration treatment.

Figure 5.2. Two null models of changes in animal abundance relative to a habitat edge: (a) no edge effect, and (b) edge effects on bird abundance in a habitat patch bordering non-habitat based on how circular territories fit into a patch. Dotted line represents the edge, with the area to the left of the line representing the less-preferred habitat and the area to the right representing the more-preferred habitat.

Figure 5.3. Null model of bird abundance change across an edge between two habitats, one preferred over the other. Bird abundance is proportional to the proportion of an average-sized territory that overlaps the poorer habitat. Dotted line represents the edge, with the area to the left of the line representing the less-preferred habitat and the area to the right representing the more-preferred habitat.

Figure 5.4. The relationship between the probability of bird occurrence and distance from the edge between treated and untreated forest stands for the three species for which an edge effect was predicted. Graphs on the left half of the figure represent treated habitat and those on the right untreated. Points represent observed probabilities of occurrence (from four years of data) 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.

Figure 5.5. The relationship between the probability of bird occurrence and distance from the edge between treated and untreated forest stands for the four species for which no edge effect was predicted. Graphs on the left half of the figure represent treated habitat and those on the right untreated. Points represent observed probabilities of occurrence (from four years of data) 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.

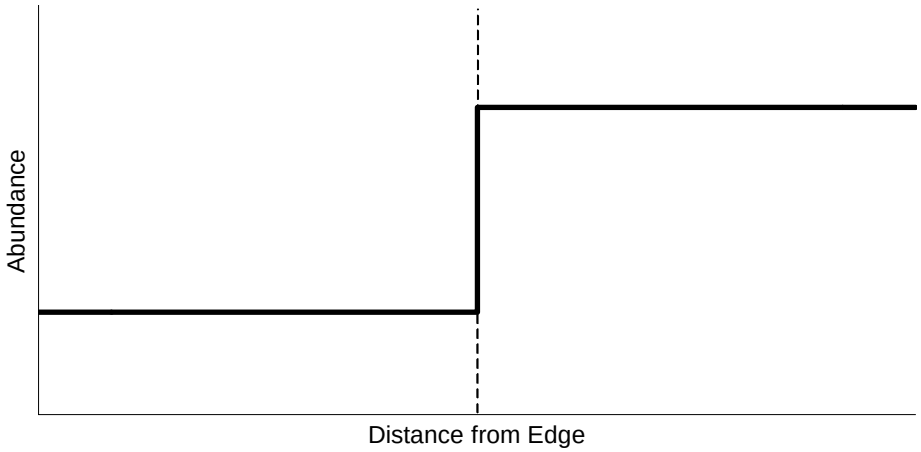
Fig. 5.1

Untreated

Treated

Fig. 5.2

a. Lidicker 1999



b. King et al. 1997

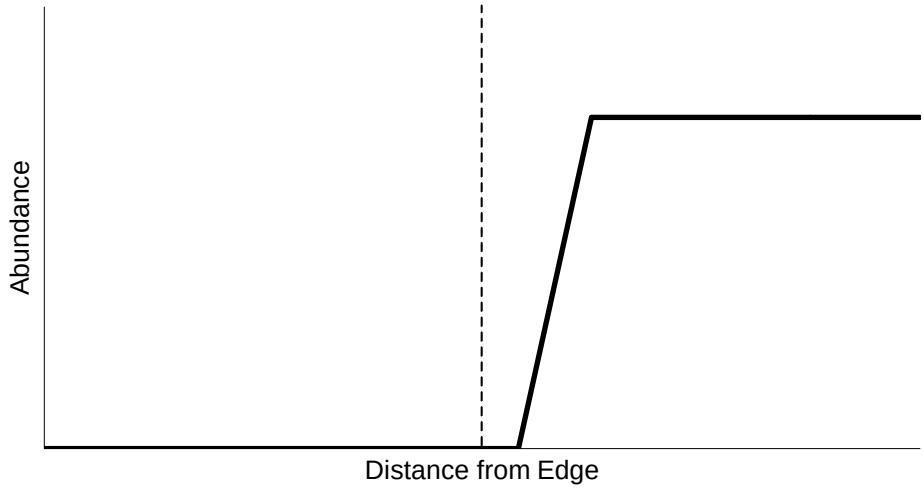


Fig. 5.3

Fig. 5.4

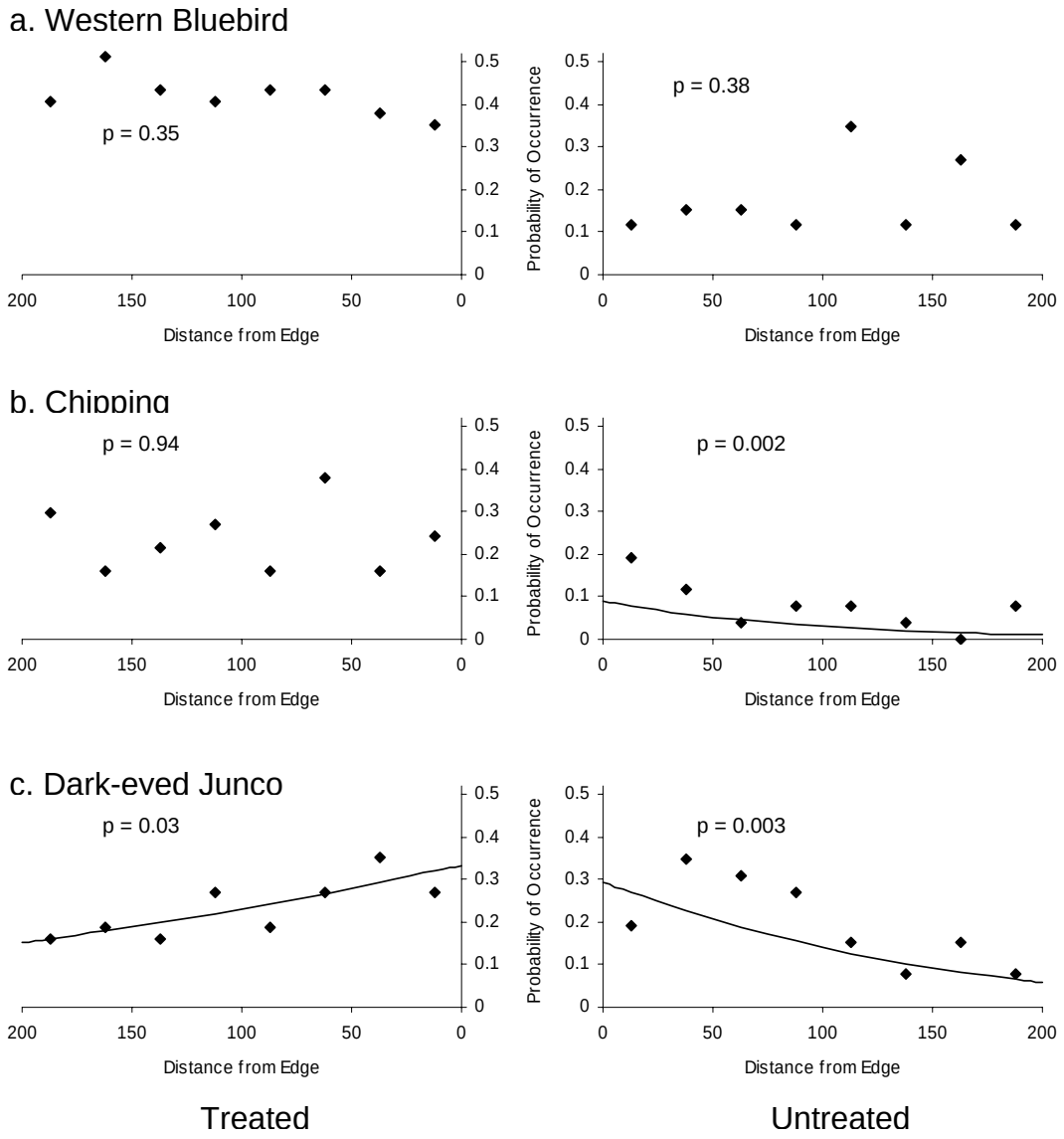
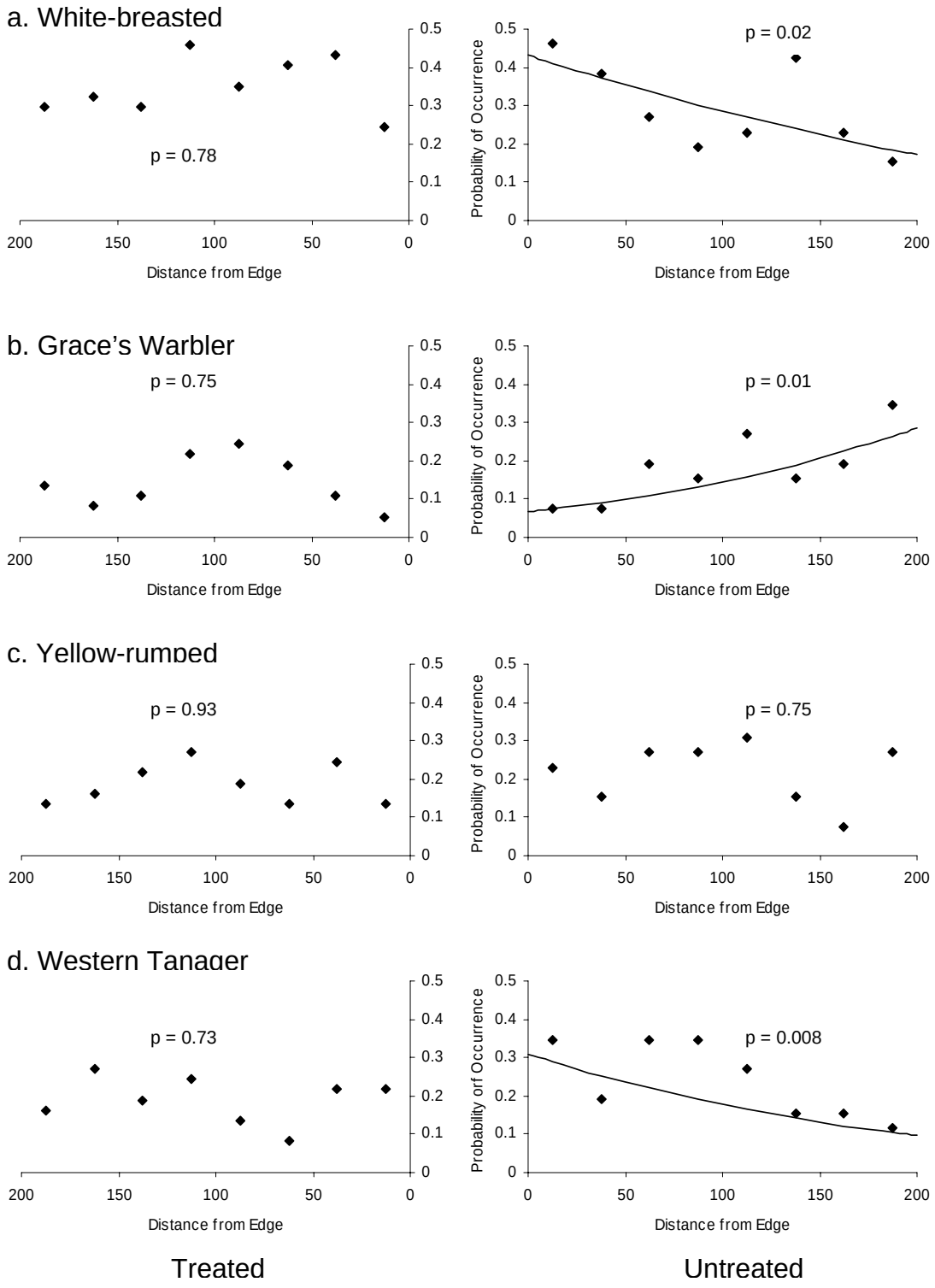

a. Western Bluebird
p = 0.35
p = 0.38
b. Chipping
p = 0.94
p = 0.002
c. Dark-eved Junco
p = 0.03
p = 0.003
Probability of Occurrence
Distance from Edge
0
0.1
0.2
0.3
0.4
0.5
200
150
100
50
Treated
Untreated

Fig. 5.5


a. White-breasted
p = 0.78
p = 0.02
b. Grace's Warbler
p = 0.75
p = 0.01
c. Yellow-rumped
p = 0.93
p = 0.75
d. Western Tanager
p = 0.73
p = 0.008
Probability of Occurrence
Distance from Edge
Treated
Untreated

THE RELATIONSHIP BETWEEN HABITAT SELECTION AND HABITAT QUALITY FOR THE PLUMBEOUS VIREO IN A CHANGING LANDSCAPE

By James Battin

Abstract

We document a mismatch in the scales at which habitat selection occurs and those at which habitat quality is determined in a migratory bird species selecting breeding habitat in a landscape undergoing ponderosa pine forest restoration. Restoration treatments, which involve a radical thinning treatment coupled with prescribed fire, present birds with a novel habitat selection conundrum: to nest in treated forest or nearby untreated patches. Our data indicate that plumbeous vireos (*Vireo plumbeus*) do not take treatments into account in selecting habitat, even though they experience higher nest success in the treatments, especially in drought years. Instead, vireos appear to select habitat on the basis of preferred nest tree and nest site characteristics, even though these appear to have little or no effect on nesting success. In particular, the birds favor areas in which Gambel oak is relatively abundant. Indeed, the distribution of plumbeous vireos between treated and untreated areas can be predicted remarkably well based solely on the distribution of oaks. It appears that habitat selection in this bird in this landscape is driven primarily by relatively small-scale processes, while habitat quality is determined primarily by the restoration treatment, a relatively large-scale phenomenon. Our findings reinforce the importance of studying the relationship between habitat selection and habitat quality in measuring the effects of landscape change on animal populations, and they demonstrate the utility of a multi-scale approach in elucidating this relationship. This study represents the first investigation of avian habitat selection and its relationship to habitat quality under ponderosa pine forest restoration, and the results are encouraging

for plumbeous vireos. Although plumbeous vireos do not appear to recognize the treatment as a higher-quality habitat, it does benefit them. It is unclear, however, how well these conclusions will generalize to other species. For the western bluebird (*Sialia mexicana*), the only other bird species for which the effect of restoration treatments on habitat quality has been studied, the restoration treatment may not be beneficial. Because restoration-like fuels reduction treatments are likely to be implemented across large areas of western North America, it is essential to investigate further the effects of restoration treatments on avian population dynamics.

Introduction

An understanding of the relationship between habitat selection and habitat quality is essential to the conservation of sensitive animal populations (Schlaepfer et al. 2002, Battin *in review*). In recent decades, the study of animal populations inhabiting landscapes containing multiple habitats that differ in quality has been dominated by the source-sink paradigm, in which animals are assumed to occupy superior habitats preferentially. A growing number of studies (e.g., Gates and Gysel 1978, Purcell and Verner 1998, Boal and Mannan 1999, Remeš 2003) suggest, however, that, in rapidly changing landscapes, animals may experience "ecological traps", habitats of poor quality that, due to some mismatch between the cues that animals use to select habitats and actual habitat quality, they select over superior habitats that are readily available. In rapidly changing landscapes, especially where anthropogenic habitat alteration presents animals with novel habitat types with which they have no evolutionary experience, ecological traps can have severe consequences for animal populations and have the potential to drive them to extinction (Delibes et al. 2001, Donovan and Thompson 2001, Kokko and

Sutherland 2001, Kristan *in press*). Other combinations of habitat selection and habitat quality can also have a substantial impact on populations (Kristan *in press*). For example, animals may fail to distinguish between habitats of different quality (Doak 1995, DiMauro and Hunter 2002). When seeking to understand how animals respond to rapid changes in habitat quality, such as those brought on by most forms of human landscape alteration, it is therefore essential to understand not only how habitat quality changes but how animals perceive and respond to the changed landscape.

While great strides have been made in understanding how landscape change affects habitat quality and animal fitness (Paton 1994, Robinson et al. 1995, Hartley and Hunter 1998, Steffan-Dewenter and Tscharntke 2002), much less study has been devoted to understanding how animals select habitats in changing landscapes. For most species, it is unclear what cues have the greatest influence on their habitat selection decisions. We also know very little about the scales at which habitat selection decisions are made and how selection at one scale affects selection at other scales.

Habitat selection in birds is generally thought to be a hierarchical process, with selection at larger scales constraining selection at smaller scales (Block and Brennan 1993). Johnson (Johnson 1980) identified four scales of resource selection by birds. With respect to nest site selection, these scales are as follows: the geographic range of the species (first order selection), home range or territory (second order), nest site (third order), and the actual location of the nest (fourth order). Very different factors may drive selection at different scales. For example, red-winged blackbirds (*Agelaius phoeniceus*) choose nest sites in aquatic vegetation growing in deeper water, but nest placement within the nest site is determined by vegetation density (Pribil and Picman 1997). An

additional constraint on habitat selection for migratory birds, especially those breeding in arid regions and at high latitudes and altitudes, where breeding seasons tend to be short, is the need to select territories rapidly at the beginning of the breeding season (Orians and Wittenberger 1991). Because birds must select a breeding territory for the entire summer based on information available to them when they arrive in the spring, they must rely on indirect cues such as vegetation structure as surrogates for the factors such as prey availability and predation risk that actually determine habitat quality. The necessity of making rapid habitat selection decisions based on indirect cues may make migratory birds more prone than other taxa to making habitat selection mistakes if, due to habitat change, those indirect cues become decoupled from actual habitat quality (Battin *in review*).

Many studies of avian breeding habitat use have failed to take into account the hierarchical nature of habitat selection (Jones 2001), but assessments of habitat use at multiple scales are becoming increasingly common. The methodology for conducting multi-scale habitat selection studies is still being developed. Jones (2001), in a review of avian habitat selection studies, pointed out that, in many such studies, flaws in design and methodology have made their results difficult to interpret. One factor that has, to our knowledge, not yet been noted in the literature, but that has the potential to complicate the interpretation of multi-scale habitat selection studies is the issue of cross-scale correlations in habitat variables. In general, multi-scale studies treat the measurement of habitat selection at each scale as entirely independent processes except inasmuch as selection at coarser scales constrains selection at finer ones. While this approach maps well onto hierarchical habitat selection theory (Johnson 1980, Cody 1985), it ignores the possibility that patterns of habitat selection at smaller scales can generate spurious

conclusions of habitat selection at larger scales. For instance, if a bird selects a particular tree species in which to place its nest (Johnson's fourth-order selection), and that tree species occurs in clumps, the bird may wind up with a disproportionate amount of that tree species in its nest site (third-order selection), making it appear that the bird is selecting that species at the nest site scale when, in reality, it is not exercising any selection for tree species at the nest site scale. Spurious conclusions of selection can result at any scale whenever a variable selected at a smaller scale is correlated with features at a larger one.

Here, we examine habitat selection in the plumbeous vireo (*Vireo plumbeus*) and its relationship to factors that drive habitat quality, measured in terms of reproductive success, in a forested landscape undergoing a dramatic change in structure and heterogeneity due to ponderosa pine forest restoration treatments. Restoration is a process of tree thinning and prescribed burning designed to return ponderosa pine forests to a condition resembling the conditions that predominated prior to European settlement of southwestern North America. The rationale for restoration is that the combination of fire suppression, logging, and cattle grazing has, over the course of the past century, transformed what was once an open system characterized by a dense herbaceous understory and frequent, low-intensity fires, into a closed-canopy forest with a sparse understory that is subject to infrequent, high-intensity fires (Covington and Moore 1994, Covington et al. 1997). Restoration aims to turn the clock back by removing most of the smaller trees and returning fire to the system in the form of regular prescribed burns. In practice, the restoration treatment involves the removal of over 50% of ponderosa pine basal area followed by a prescribed burn (Friederici 2003a). Restoration treatments

similar to those studied here have been proposed for millions of hectares of forest lands (Allen et al. 2002), making it especially important to understand how treatments affect the animals of the ponderosa pine ecosystem (Battin and Sisk 2003). Restoration treatments represent a novel landscape-scale experiment and provide an unusual opportunity to study animal responses to landscape change under relatively controlled conditions.

To identify the cues used by plumbeous vireos in selecting breeding habitat and to assess whether vireos select habitat optimally in the post-restoration landscape, we examine habitat selection and reproductive success of plumbeous vireos at four scales in areas that have undergone restoration treatments and in nearby untreated areas. Because breeding habitat selection decisions are made by vireos in mid- to late April, presumably using indirect cues, and because we were especially interested in the effect of forest restoration treatments on habitat selection and quality, we focused on the indirect cues most likely to be altered by restoration: vegetation composition and structure. We asked the questions:1) at what scale do we see evidence for habitat selection in this landscape, and 2) what is the relationship between habitat selection and reproductive success at each scale? The four scales examined were: (1) landscape (treated vs. untreated forest), (2) territory, (3) nest site, and (4) nest tree (Table 4.1). In addition, we used correlation analysis and a simulation model to examine whether apparent patterns of habitat selection at larger scales could be explained by selection at smaller scales, asking the additional question, can between-treatment differences in bird distribution be explained by habitat selection at finer scales?

Study organism and study site

Study organism

The plumbeous vireo (*Vireo plumbeus*) is a Neotropical migratory passerine bird. Our study site in northern Arizona lies near the southern edge of its breeding range, which reaches its northern limit in southern Montana. Plumbeous vireos winter from Central America north to southern Arizona. (Curson and Goguen 1998). At our study site, the first males arrive and begin establishing territories in mid-April, with female arrivals beginning 1-2 weeks later. Nesting usually begins around 1 May and continues through late June. We have never seen evidence of pairs attempting to renest after fledging young, but birds typically will attempt to renest after failure.

Study site

Our 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 120 miles northwest of Flagstaff, Arizona, the Mt. Trumbull area represents the first large-scale application of the "Flagstaff model" (Friederici 2003a) of forest restoration treatments. Approximately 1200 hectares of ponderosa pine and ponderosa pine-Gambel oak forest, ranging from about 2050 to 2200 m in elevation, are slated for restoration (Friederici 2003b). We worked in four treatment units that ranged from less than one year to four years old at the inception of the study and totaled approximately 126 hectares. We used between 246 and 310 ha. (depending upon the year) of untreated forest as our untreated study area. In 2000, our study area included three blocks of untreated forest, but, between 2000 and 2001, we had to abandon one untreated control area and expand another to take its place after the area used in 2000 was

partially logged. This left us with two untreated blocks, one of them very large, in 2001 and 2002.

Methods

Nest searching and monitoring

During the years 2000, 2001, and 2002, we searched our treated and untreated study areas intensively in order to locate all breeding pairs of plumbeous vireo and find all of their nests. Nests were located by following birds and using behavioral cues (Martin and Geupel 1993). Once a pair was located, we spent as much time as needed to find its nest. Most nests (86-97% in a given year) were found before the onset of incubation.

Nests were monitored, on average, every 3 days (range 1-6 days) to determine nest fates. We used pole-mounted video cameras and mirrors to examine nest contents. Nest contents were checked to confirm clutch size and hatch date. In order to minimize the chances that nest monitoring activities would attract predators, we checked nest contents as few times as possible. Between the inception of incubation and hatching, and between hatching and fledging, nests were monitored by observers with binoculars in order to determine nest status. Only if no bird activity was detected at a nest were cameras or mirrors used to check nest contents.

Vegetation measurements

We measured vegetation on 0.04 ha. square plots centered on trees of three different types. 1) Plots were surveyed at each nest tree. 2) A random non-nest tree near each nest tree was chosen by walking 35 m from each nest tree in a randomly selected direction and selecting the nearest tree as the plot center. This tree was assumed to

represent a tree lying within a pair's territory that could have been used for nesting but was not. 3) In each study area, we placed a grid of vegetation survey plots. Each grid had a 200 m spacing, and the grid starting point was determined by generating a random latitude and longitude. These were used for the assessment of territory-scale habitat selection (described in more detail below).

At each plot we established a 20 m X 20 m square survey plot centered on the nest tree, non-nest tree, or the tree nearest to a grid point. Within the boundaries of the plot, we counted and identified all trees, classifying each tree as belonging to one of the six U.S. Forest Service Vegetational Structural Stage (VSS) classes based on diameter at breast height: <2.5 cm, 2.5-12.5 cm, 12.5-30.0 cm, 30.5-45.0 cm, 45.0-61.0 cm, >61.0 cm. We measured canopy cover by the point-intercept method using a vertical projection scope (Rosenstock 1996) at 2 m increments around the perimeter of the plot and along a transect through the plot center. We measured shrub cover, also by the point-intercept method, at the same points at which canopy cover was measured. For each plot, we estimated basal area of ponderosa pine, Gambel oak, and all trees combined by multiplying the median basal area value for each VSS class by the number of trees in that class and summing the results.

Statistical analyses

Due to high interannual variability and a lack of independence due to an unknown proportion of birds returning to the study area each year, all analyses were conducted separately for each of the three years of the study. SAS software (SAS Institute, Cary, North Carolina) was used for all analyses, except where otherwise stated. Only nests in which at least one egg was laid were included in analyses.

To compare habitat use between treated and untreated areas (the landscape scale), we compared the observed distribution of vireo pairs between treated and untreated areas to a uniform distribution using a chi-square test (SAS PROC FREQ). Likewise, we used chi-square tests to compare the proportion of pairs producing a successful nest in treated vs. untreated areas. We used program MARK (G. White, Colorado State University) to generate Mayfield estimates of daily nest survival rate for each habitat (Mayfield 1975). We used MARK to fit models of nest success with and without a habitat term and used Akaike's Information Criterion for small sample sizes (AICc) to choose which model best fit the data. In cases where AIC selected the model with the habitat term, we concluded that there was a habitat effect on nest survival rate.

A number of different analytical approaches have been used by different investigators to assess breeding habitat selection. We chose to employ logistic regression because it has the most well-developed theoretical foundation for the measurement of resource selection (Manly et al. 2002). At the territory scale, we used multiple, stepwise logistic regression (SAS PROC LOGISTIC) to determine which combination of five vegetation variables (Table 4.2) best differentiated territories from non-territory areas. We set $p<0.20$ for the score chi-squared value as the threshold for entry into the model and a Wald chi-squared value of $p<0.10$ as the condition for retention (Hosmer and Lemeshow 1989). Before fitting the model, we assessed the degree of correlation among predictor variables (SAS PROC CORR). For any variables showing a high level of correlation ($R \geq 0.70$), the variable deemed less biologically relevant was dropped from the analysis. At the nest site scale, our analytical approach was the same except that, due to the paired nature of the data (nest site vs. neighboring non-nest site), we used case-

control logistic regression (Hosmer and Lemeshow 1989) (SAS PROC PHREG with nest site name as the stratifying variable).

At the nest tree scale, we also used multiple, stepwise, case-control logistic regression, again stratified on the nest site to assess which variables associated with the nest tree (Table 2.3) could be used to distinguish nest from non-nest trees. For this analysis, we compared the nest tree to all other trees within the 0.04 ha. plot around the nest. Tree species was transformed into a set of binary dummy variables, and diameter for each tree was recorded as the median diameter for its VSS class. In all other respects, this analysis was conducted in the same manner as those at the territory and nest site scales.

At all three scales, we modeled the vegetation variables affecting nest success using stepwise, multiple logistic regression. To examine whether nest site selection at smaller scales might produce vegetation differences at larger scales, we examined correlations among vegetation variables at the nest site and territory levels. To look at potential effects of nest tree selection on larger scales, we used multiple analysis of variance (MANOVA) to compare vegetation at nests in oak trees to nests in other species (SAS PROC GLM). We chose this approach because oak was by far the most frequently used nest tree. We also used MANOVA and univariate tests to compare vegetation between treated and untreated forest areas, comparing vegetation grid points in the treated area to those in the untreated area. For these analyses, percent cover data were arcsine-square-root transformed. Data were then back-transformed for display in figures and tables.

Simulation model

To examine the potential effects of nest site selection on the distribution of birds between treated and untreated areas we developed an individual-based, spatially explicit simulation model of avian habitat selection. The model simulated a landscape of 0.04 ha. grid cells containing two adjacent habitat patches, one treated and the other untreated. We populated each habitat with clumps of oak trees of varying basal area according to their actual distribution in each habitat, as determined from vegetation grid points in each habitat. To determine the distribution of oak basal area values in each habitat, we divided our vegetation survey plots in each habitat into seven basal area categories (0 cm^2, 1-1290 cm^2, 1291-2580 cm^2, 2581-3871 cm^2, 3872-5161 cm^2, 5161-6452 cm^2, and >6452 cm^2). We then determined the proportion of patches that fell into each of these categories and used those in the model as the probability of a given grid cell containing a given level of oak. Each grid cell was assigned the mean level of oak basal area for the category to which it was assigned. For instance, 31% of patches in the treated area had a basal area of 1-1290 cm^2, so patches in the treated area had a 31% chance of being assigned an oak basal area value of 645 cm^2.

Once the landscape was populated with oak, we "released" a number of vireos into the landscape one by one. Each bird appeared on the landscape at a randomly assigned starting location, moved through the landscape, selected a nest site, and defended a 100 m radius (3.14 ha) territory around its nest site (described in more detail below). Because the size of the study area and the vireo population varied among years, we conducted separate model runs for each year of the study, using empirical data to parameterize the simulations. For each year, we created a landscape the size of the

landscape sampled that year with an appropriate proportion in treated and untreated habitat. We then populated the landscape with a number of vireos equal to the total number of vireo pairs detected on our treated and untreated study areas during that year.

Because the process by which migratory birds select habitats after arriving on their breeding grounds is little understood, we modeled five different scenarios of vireo movement and habitat selection, four of which were intended to bracket possible values of habitat selection and movement parameters, and one of which ("mid-move, oak threshold") represented a combination of parameters that we believed most actually represented vireo habitat selection activity (Table 4.3). The scenarios differed only in the maximum number of grid cells that the vireos could sample before selecting a nest patch and in the criteria by which they selected nesting habitat. Birds either sought to maximize the amount of oak in their territories, or they exhibited a threshold response, settling in the first patch they encountered that exceeded a threshold of oak basal area (3200 cm^2) representing the 75th percentile of basal areas of nest sites. The choice of the 75th percentile was based on the assumption that the threshold would be greater than the mean oak abundance at nests (assuming that some birds wound up settling in nest sites that contained less than their preferred amount of oak). In two models, the birds sampled only 25 grid cells, a number that is almost certain to be an underestimate, while in two other models they sampled 300 cells, which approximated full knowledge of the habitat.

At the beginning of each simulation, the first bird arrived at a random location on the grid. It then compared the oak basal area in that cell to its oak threshold value (if it had one). If attractiveness was greater than the threshold, the animal settled in the patch. Otherwise it moved across the landscape seeking a patch that exceeded the attractiveness

threshold. At each movement step, the bird moved a distance of between 1 and 20 grid cells, selected at random from a uniform distribution, in one of the four cardinal directions (selected at random). A bird was not allowed to return to a patch that it had already visited. The bird settled in the first patch it found that exceeded the attractiveness threshold. If it did not find such a patch by its final move, it settled in the patch with the highest oak basal area. When there was no threshold, birds moved the maximum number of steps and then settled in the patch with the highest oak basal area. Subsequent birds followed the same steps, except that they were assumed to know the location of, and avoid, all patches that were already occupied. In order to avoid edge effects, we employed periodic boundary conditions (Wilson 2000)—that is, patches at one edge of the grid were considered to be neighbors of those at the opposite edge.

For each scenario, we ran 100 repeated simulations on each of 100 randomly generated landscapes, for a total of 10,000 model runs for each simulation for each year. To examine the sensitivity of model predictions to variation in model parameters, we compared predictions from our five model runs. We then compared the results of the simulation with the parameter values that we believed to be most realistic to the actual number of birds found in the treated area in each year. We used chi-squared analyses to compare our observed values to a model of vireo distributions based on the assumption that vireo density was proportional to oak basal area in each habitat, and to a null model assuming a random distribution of birds between habitats.

Results

Landscape Scale

In all three years, there were approximately three times as many vireos in the treated areas as in untreated control areas (Fig. 4.1). In each year, this difference was statistically significant ($\chi^2<0.01$ for each year) During the three years of the study we found between 16 and 18 pairs in the treated areas and between 13 and 14 in the substantially larger untreated area. Some pairs (1-3 per year) had to be excluded from territory-scale analyses because they were found outside the areas covered by vegetation grids.

We found between 38 and 43 vireo nests each year. Both the magnitude and pattern of nest success varied among years (Fig. 4.2). Overall nest success was highest in 2001, with over 50% of pairs successfully fledging at least one young, and lowest in 2002, a record-setting drought year in which only one of the 38 monitored nests succeeded, and some pairs apparently never even managed to lay an egg. In 2000, a year of moderate drought, significantly more pairs fledged young in the treated area than in the untreated. There was no significant difference in the number of successful nests per pair between treated and untreated areas in 2001, when nest success was high in both habitats or in 2002, when statistical analysis was not possible due to the fact that only a single nest fledged.

Because we were able to find the vast majority of nests before the onset of incubation, and because we were able to find pairs' post-failure renests, the number of pairs successfully fledging young more accurately reflects the actual fitness experienced by birds nesting in a given habitat than would the more commonly used Mayfield

estimate of daily nest survival rate. Because nest success was so low in 2002, however, the proportion of pairs fledging young provides very little information about the relative qualities of the two habitats. For this reason, we also calculated Mayfield nest survival probabilities for each year.

In 2002, daily nest survival rate was much higher in the treated forest (0.89) than in untreated (0.81). Extrapolated out over the 28 day nesting period of the plumbeous vireo, these estimates yield a 4% probability of a nest fledging young in the treatment and a 0.3% chance in untreated forest (Fig. 4.3). AICc chose the model that included a habitat term over the one without (ΔAICc = 0.3), suggesting that the treatment did have an effect on nest success in that year. In 2001, nest survival rates were similar between the two treatments, with the rate in untreated forest (0.97) being slightly higher than that in treated forest (0.96). AICc strongly selected the model with no treatment term for 2001 (ΔAICc = 1.9). In 2000, nest survival rates in the treated forest were substantially higher (0.97) than those in the untreated forest (0.94), leading to a more than two-fold difference in nest success rates (Fig. 2.4). AICc did not choose the model with a treatment effect, although the difference between models was small (ΔAICc = 0.2). It should be noted that, in 2000 and 2001, pairs in treated areas tended to produce more successful nests relative to pairs in untreated forest (Fig. 2.3) than their nest survival probabilities (Fig. 2.4) would suggest. This pattern was due to a larger proportion of pairs in treatments renesting after failure.

Territory scale

We measured vegetation on a total of 28 grid points in the treated areas and 60 in the untreated. Vireo territories were more likely to occur in areas with relatively low tree

densities and canopy cover, but with high oak basal area. In 2000, total basal area was the only significant predictor of territory selection (Table 4.4). Its negative coefficient (β) indicates a negative relationship between territory occupancy and total basal area. In 2001 and 2002, logistic regression indicated a negative relationship between territory occupancy and canopy cover and a positive relationship with oak basal area (Table 4.4). None of the vegetation variables were significant predictors of nest success at the territory scale in either 2000 or 2001, the only two years in which such analyses could be conducted.

Nest site scale

Nest sites had higher oak basal area and, in one year, higher canopy cover, than nearby non-nest sites (Table 4.5). In 2000 and 2001, oak basal area was the only variable entered into the logistic regression model for nest site selection. In 2002, percent canopy cover was the only variable entered into the model. All were positively associated with nest sites. Only in 2001 was any variable associated with nest success (Table 4.6). In that year, higher ponderosa pine basal area was significantly associated with successful nest sites.

Nest Tree Scale

Vireos nested disproportionately in junipers and Gambel oaks, and nests were located disproportionately in trees with larger diameters (Table 4.7). Gambel oak and tree diameter were significant positive predictors of nest placement in all three years, while juniper was significant in 2 years (in the 2002 it produced an unstable model and had to be excluded). Oak snags appeared in the model in 2000 only. This was the result

of birds nesting in clumps of dead leaves in oaks recently killed by prescribed fire in the treatment area. Neither nest tree species nor size was associated with nest success in either 2000 or 2001.

Between-treatment vegetation comparisons

Vegetation at grid points in the treated and untreated forests differed significantly The MANOVA comparing the two was highly significant ($F=14.26$, $df=87$, $p<0.0001$). As might be expected, pine basal area ($F=39.72$, $df=91$, $p<0.0001$) and canopy cover ($F=8.54$, $df=91$, $p=0.004$) were much lower in the treated area than the untreated (Fig. 4.4). Oak basal area, on the other hand, was almost three times higher in the treated area than in the untreated forest ($F=43.13$, $df=91$, $p<0.0001$), which was entirely a result of pre-existing between-site variation, since the restoration treatment does nothing, at least in the short term, to increase oak densities. Shrub cover was also higher in treatments ($F=10.25$, $df=91$, $p=0.002$). Only total basal area of all tree species combined did not differ significantly between habitats ($F=1.25$, $df=91$, $p=0.27$), apparently the result of high variability in this variable in the treated area.

Correlations across scales

Many nest site variables showed strong correlations with territory-scale variables Table 2.7). Oak basal area, the main predictor of nest locations at the nest site scale, was strongly correlated with oak basal area at the territory scale. The fact that oak basal area was a significant predictor of territory locations may therefore simply be a byproduct of selection at the nest site level. Percent canopy cover, the other strong predictor at the territory scale, was highly correlated with nest site-scale ponderosa pine basal area. The

large number of correlations among nest site and territory variables suggests that nest site selection has the potential to have a substantial impact on the measurement of territory-level selection, but these correlations could also be the result of selection for similar vegetation characteristics at both scales.

Because the main predictor of nest tree selection was tree species, a categorical variable, we were unable to use correlation analysis to assess the potential influence of nest tree selection on habitat selection at both the nest site and territory scales. Instead, we compared nest site and territory vegetation at nests in oak trees to that at nests in other tree species. Our MANOVA analyses found no significant differences at the nest site or territory scales, except in 2001 at the territory scale ($F=3.06$, $df=15$, $p=0.043$), where univariate tests found marginally significant differences in canopy cover ($F=3.77$, $df=1$, $p=0.067$) and oak basal area ($F=3.28$, $df=1$, $p=0.086$).

Modeling results

Different levels of habitat selection and movement parameters had a noticeable effect on model predictions of bird population levels in the treated habitat (Fig. 4.5a). The threshold models were sensitive to variation in movement parameters, while the models in which birds sought the maximum amount of oak they could find were insensitive to variations in movement parameters. Our chosen scenario of mid-level movement and selection for a threshold amount of oak produced predictions that were higher than three of our four parameter testing scenarios.

Observed between-treatment distributions in vireo abundance corresponded very well to a model of bird distributions in which bird distributions were proportional to oak distributions (Fig. 4.5b). The simulation model of vireo nest site selection based on oak

basal area also did a good job of predicting between-treatment variation in bird distributions, although it overpredicted populations in the treated area by about three pairs in 2000. There was no statistically significant difference between observed vireo numbers, numbers predicted by the oak proportion model, and numbers predicted by the simulation model in any year (χ^2>0.10 in all cases). Both the simulation model and the proportion of oaks were much better at predicting vireo abundance than was a random distribution of animals across the landscape. Both observed and modeled bird numbers differed significantly from the random model (χ^2<0.05 in all cases).

Discussion

Habitat Selection at Multiple Scales

We found strong evidence of habitat selection by plumbeous vireos at all scales, with Gambel oak figuring in habitat selection decisions at all of the scales at which it was measured. At the coarsest scale examined, the landscape scale, we consistently found about three times as many vireos in the treated as in the untreated forest. Vireo territories contained more oak but had lower overall tree basal area and/or canopy cover than non-territory areas, suggesting a preference for oaky, open areas. Nest sites tended to have more oak, or, in 2002, higher canopy cover, than non-nest sites. The strongest, most consistent evidence of selection was found at the nest tree scale, where vireos consistently favored oaks, junipers, and trees with larger diameters. But what does this really tell us about vireo habitat selection in this landscape?

It seems clear that vireos do prefer certain tree species for nesting. At larger scales, however, the picture becomes somewhat murkier. Because Gambel oak tends to grow in clumps, an apparent preference for oaks at the nest site scale could simply result

from most nests being placed in oak trees. This, however, was not the case, as nest sites in which nests were placed in oak trees did not differ in oak basal area from nest sites in which nests were placed in other tree species, except marginally so in 2001. At the territory scale, and especially at the landscape scale, it is unclear that any selection was exercised at all. With treated areas containing almost three times as much oak as untreated areas, vireo densities in the treated vs. untreated areas were almost exactly proportional to relative oak densities in the two habitat types, and a mechanistic model of vireo habitat selection based solely on a preference for oaky nest sites predicted observed patterns of between-treatment abundance very well. At the territory scale, oak basal area at nest sites was strongly correlated with oak basal area at the territory scale. It is therefore impossible to tell whether apparent selection for oak at the territory scale is a spurious pattern driven by nest site-scale selection or if it reflects selection for territories containing a high number of good nest sites (Jones and Robertson 2001). While territory-scale canopy cover, the other territory-scale variable that came out as significant in the logistic regression analysis, was not positively correlated with variables selected at the nest site, lower canopy cover at the territory scale could also have been caused by selection at the nest site scale. If selection for oaky nest sites caused more vireos to settle in the treatment, then canopy cover in territories would be lower than that in non-territory areas, since most territories would be in the treatment, where canopy cover was lower. It seems clear that some habitat selection must occur at the territory scale—birds choose to defend territories in some areas and not in others—but it is impossible to tell from our data what factor or factors drive selection at this scale.

The picture of plumbeous vireo habitat selection that emerges from this analysis is one of strong selection for nest trees and nest site characteristics, and apparent selection for territories that is driven either by factors at the nest site scale or by a preference for more open areas. The apparent pattern of preference for restoration treatments likely driven by finer-scale selection for a particular habitat feature (oak) that is not related to the restoration treatment itself. Our results suggest that it is important not only to evaluate habitat selection in a hierarchical context but also to consider explicitly the linkages among the different levels of the hierarchy. Failing to do so may lead to spurious conclusions about habitat selection at coarser scales.

In other bird species, evidence of nesting habitat selection has been found at all scales that have been studied, from nest placement within a tree (Hardy and Morrison 2001, Kershner et al. 2001, Luck 2002) to landscape-scale features (Huhta et al. 1998, Luck 2002, Martinez et al. 2003). There is little consistency among studies of multi-scale habitat selection regarding which scales show evidence of selection and which do not. Some studies have found strong evidence of selection at the finest scales and little at coarser scales (e.g., Kershner et al. 2001) while others have found no selection at fine scales but selection at coarse scales (e.g., Esely and Bollinger 2001). In some cases, birds appear to select very different habitat components at different scales (Orians and Wittenberger 1991, Pribil and Picman 1997), while, in others, they appear to select similar features at different scales (Bergin 1992, Sedgwick and Knopf 1992, Jones and Robertson 2001). Despite a number of studies suggesting selection of similar features at different scales, we are aware of no study that has explicitly examined cross-scale

correlations in variables that determine nest site selection or any studies that assess the possibility that patterns of selection at finer scales are driving those at coarser scales.

The relationship between habitat selection and reproductive success

Our results suggest a mismatch between the scale at which habitat selection occurs and the scale that determines habitat quality. By far the most important factor governing habitat quality for plumbeous vireos in this landscape was the restoration treatment. In two of the three years of the study, reproductive success was substantially higher in treated than in untreated forest. There appeared to be an interaction between climatic conditions and the treatment effect on reproduction. The one year in which there was no difference between treatments (2001) was the wettest year of the study (Fig. 4.6), while in 2002, a record drought year, there was a greater than tenfold difference in the probability of nest survival. In 2000, a year of less severe drought, nest success was about twice as high in treated as in untreated forest.

In 2001, the one year in which nest success was not affected by the restoration treatment, nest sites with a higher basal area of ponderosa pine, a factor not selected for at any scale, were more likely to produce successful nests. Otherwise, none of the variables measured at the territory, nest tree, or nest site scales had any effect on reproductive success. This contrasts sharply with habitat selection measures, which showed evidence of strong selection at smaller scales.

Other studies that have examined the relationship between avian habitat selection and reproductive success at multiple scales have found everything from a strong correspondence between the factors affecting selection and success (Huhta et al. 1998, Jones and Robertson 2001) to evidence of selection that appears to have no effect on

success (Esely and Bollinger 2001). Several single-scale studies have documented a mismatch between selection and success at one scale or another (Schmidt and Whelan 1999, Misenhelter and Rotenberry 2000).

In plumbeous vireos, there appeared to be no relationship in any year between the variables responsible for nest success and those used to select habitat. No variable related to Gambel oak, which appeared to be the main driver of habitat selection, affected nest success. Vireos appear to wind up disproportionately in the superior habitat by pure happenstance. They choose habitat based on oak density, there are more oaks in the area that has been treated, and the treatment, through mechanisms that are unclear, decreases the risk of nest predation.

Implications for Management

This study represents the first study of avian population biology under ponderosa pine forest restoration. To date, only one other study has been completed on any aspect of avian response to the restoration treatment (Germaine and Germaine 2002). It is likely that forest restoration treatments similar to those studied here will be implemented across large areas of the Southwest in order to curb the growing risk of large, high-intensity wildfires (Allen et al. 2002). Several factors suggest that the ponderosa pine zone is likely to be transformed into a mosaic of treated and untreated areas and will remain so for the foreseeable future: 1) the restoration process is liable to take decades, 2) many areas will be difficult or impossible to restore, and 3) different landowners and agencies have different attitudes about the desirability of restoration (Battin and Sisk 2003). Given the large scale of proposed restoration treatments and the likely persistence of a

landscape mosaic such as that studied here, it is essential to gain an understanding of how this novel landscape affects wildlife.

The short-term effect of the restoration treatment on plumbeous vireos appears to be positive, even if the vireos do not take full advantage of it due to their propensity to nest in oak, apparently regardless of treatment status. Western bluebirds at the same site also experienced higher nest success in the treated areas, but this was, to some extent, counterbalanced by much higher rates of blowfly (*Protocalliphora* sp.) parasitism (Germaine and Germaine 2002), a factor that has the potential to decrease fledgling survival substantially (Loye and Carroll 1995). Plumbeous vireos, on the other hand, experience extremely low blowfly parasitism rates (one or two nests per year, J. Battin & T. Whitworth, unpublished data). The bluebird example, however, suggests that we must exercise caution in extrapolating the results of this study to other species.

The lack of selection by vireos for restoration treatments means that the impact of restoration on vireo populations will largely depend on whether the habitat being restored is preferred (e.g., oaky) or non-preferred habitat. Restoration of preferred habitat areas will have a much greater impact on population size.

Our results reinforce the importance of considering the relationship between habitat selection and elements of habitat quality (e.g., reproductive success) when evaluating the impacts of landscape change on animal populations. They also demonstrate the importance of a multi-scale approach to assessing the factors influencing both habitat selection and habitat quality. A traditional assessment of the response of a bird species to this sort of landscape change would involve a comparison of bird densities or reproductive success, or, at best, both between treated and untreated areas. This would

lead to a conclusion of optimal habitat selection in this landscape. A more detailed understanding of the scale at which habitat selection occurs and habitat quality is determined shows a different picture that is likely to be more generalizable across treatments within and among management units and biogeographic regions.

This study highlights another important management issue: climate. Our data suggest that restoration treatments may serve as a buffer against drought, which can have extremely negative effects on reproduction (Smith 1988, Morrison and Bolger 2002). Indeed, there was no between-treatment difference in reproductive success in the one year of relatively normal rainfall. With the southwest in a period of extended drought and climate change models predicting a long-term drying trend in the region, restoration treatments may have substantial benefits for the persistence of populations of this, and perhaps other, bird species.

Clearly, information on more species in more experimental treatment areas is needed before any firm conclusions can be drawn about the effects of restoration on bird populations. In particular, it is unclear whether the positive effect documented in this study is a short-term phenomenon or whether it will stand up over the long term. The vast majority of treatment areas used in this study were four years old or less by the end of data collection. Continued vegetational succession at these sites may alter habitat quality, changing the relationship between habitat selection and reproductive success. Climate may also play a role in the observed mismatch between habitat selection and habitat quality. If birds select habitats based on cues developed during a wetter climatic period, they may not settle in the habitats that will serve them best under drought conditions. This suggests a potentially unrecognized danger of climate change: a lag

between environmental change and the learning or evolutionary change needed for organisms to adapt to the new environmental conditions, particularly in terms of their habitat preferences.

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TABLES

Table 4.1. Scales of analysis used in this study, showing the name of the scale and a description of the habitat selection question addressed at that scale.

Scale	Question	Analytical Approach
Landscape	Do vireos choose areas that have undergone a restoration treatment over those that have not?	Bird densities in treated areas compared to those in untreated areas.
Territory	What vegetation features influence where vireos place their territories?	Vegetation within territories compared to that outside territories.
Nest Site	What vegetation features influence where, within a territory, vireos place their nest?	Vegetation in immediate vicinity of nest compared to equal-sized nearby plot where no nest was placed.
Nest Tree	What tree species do vireos favor for nesting?	Trees in immediate vicinity of nest compared to nest tree.

Table 4.2. Vegetation variables used in multiple logistic regression analysis at each scale.

Territory & Nest site:
- Basal area of ponderosa pine
- Basal area of Gambel oak
- Total basal area (all tree species)
- Percent canopy cover
- Percent shrub cover

Nest tree:
- Tree species:
  - ponderosa pine
  - Gambel oak
  - juniper (multiple species)
  - other species
  - pine snags
  - oak snags
  - snags of other species
- Tree diameter

Table 4.3. Parameter values for five simulations of bird habitat selection based on between-habitat distribution of oak. # of moves = number of movement steps an animal takes while searching for suitable habitat. Threshold = the threshold level of oak basal area (cm^2) in a patch that would elicit a settling response. In the case of oak maximizers, there was no threshold; birds sampled as many patches as they could based on the number of moves they were allowed and settled in the one with the most oak.

	Model Name				
Parameter	Short move, oak maximizer	Short move, oak threshold	Long move, oak maximizer	Long move, oak threshold	Mid-move, oak threshold
# of moves	25	25	300	300	50
Threshold	none	none	3200	3200	3200

Table 4.4. Ordinary logistic regression models for habitat selection by plumbeous vireos at the territory scale for each year of the study. Positive β indicates selection for a higher value of a variable.

Year Variable	β	SE	Wald χ^2	P
2000				
Total Basal Area	-0.0015	0.0006	7.07	0.008
2001				
% Canopy Cover	-4.282	1.568	7.45	0.006
Oak Basal Area	0.0027	0.0012	5.19	0.023
2002				
% Canopy Cover	-3.326	1.340	5.81	0.016
Oak Basal Area	0.0018	0.0010	2.95	0.086

Table 4.5. Case-control logistic regression models for habitat selection by plumbeous vireos at the nest site scale for each year of the study.

Year Variable	β	SE	Wald χ^2	P
2000				
Oak Basal Area	0.0015	0.0008	3.35	0.067
2001				
Oak Basal Area	0.0021	0.0009	5.57	0.018
2002				
% Canopy Cover	6.9161	2.9324	5.56	0.018

Table 4.6. Ordinary logistic regression models of the relationship between nest site vegetation and nest success for 2000 and 2001. In 2002 only one nest succeeded, making logistic regression analysis impossible.

Year Variable	β	SE	Wald χ^2	P
2000				
None				
2001				
Ponderosa Pine Basal Area	0.0010	0.0005	3.93	0.047

Table 4.7. Case-control logistic regression models of plumbeous vireo nest tree selection.

Year Variable	β	SE	Wald χ^2	P
2000				
Gambel Oak	6.992	1.581	19.57	0.001
Juniper	7.723	1.840	17.61	0.001
Tree Diameter	0.286	0.082	12.08	0.001
Gambel Oak Snag	2.449	1.409	3.02	0.082
2001				
Juniper	2.502	0.721	12.04	0.001
Gambel Oak	1.014	0.459	4.87	0.027
Tree Diameter	0.432	0.185	5.44	0.020
2002[a]				
Tree Diameter	0.883	0.206	18.34	0.001
Gambel Oak	1.617	0.476	11.56	0.001

[a] Juniper excluded from analysis because it produced an unstable model.

Table 4.8. Correlations between territory vegetation and nest site vegetation. Numbers in the body of the table indicate the number of years (out of 3) in which a significant ($p<0.05$) correlation was detected for a given pair of variables. Symbol in parentheses indicates whether correlation was positive or negative.

		Territory Scale				
		Ponderosa Pine B.A.	Gambel Oak B.A.	Total Basal Area	% Canopy Cover	% Shrub Cover
Nest Site	Ponderosa Pine B.A.	2 (+)	0	1 (+)	3 (+)	1 (-)
	Gambel Oak B.A.	0	2 (+)	0	0	0
	Total Basal Area	0	0	1 (+)	2 (+)	0
	% Canopy Cover	2 (+)	0	1 (+)	3 (+)	0
	% Shrub Cover	1 (-)	0	1 (-)	1 (-)	0

FIGURE LEGENDS

Figure 4.1. Plumbeous vireo abundance, expressed as the number of vireos pairs per hectare, was significantly higher (about 3X higher) in treated than in untreated forest in each year of the study.

Figure 4.2. Plumbeous vireo nest success (number of successful nests per pair $\pm$ 1 SE) in treated and untreated forest in each year of the study. Only in 2000 was the between-habitat difference in nest success significant (statistical analysis was not possible in 2002 due to there being only one successful nest).

Figure 4.3. Plumbeous vireo nest success, projected from Mayfield estimates, in treated and untreated forest for each year of the study. Bars represent the Mayfield estimate of daily nest survival multiplied out across the vireo's 28-day nesting cycle.

Figure 4.4. Comparison of vegetation structure variables between treated and untreated forest (mean $\pm$ 1 SE), using data from vegetation survey grids in treated and untreated study areas. All variables show significant between-habitat differences except for total basal area.

Figure 4.5. Results of a simulation model in which birds select nest sites based solely on the amount of oak present at a site. Oak levels in treated and untreated areas are simulated based on the distribution of oaks between treated and untreated study areas at the Mt. Trumbull Resource Conservation Area. (a) Results of five different scenarios are shown. Parameter values for each simulation are shown in Table 4.4. "Short, max" = short move, oak maximizer, "Long, thresh" = long move, oak threshold, etc. (b) Comparison of observed numbers of vireo pairs in treated habitat to three models of vireo distributions: (1) a model of vireo distributions in which vireo numbers are proportional to mean oak basal areas in the two habitats ("oaks"), (2) the "mid, thresh" simulation run ("simulation"), and (3) a random distribution of birds between habitats ("random").

Figure 4.6. December-May rainfall for Flagstaff, Arizona for 2000-2002, expressed as a percentage of mean rainfall during this period for the past 50 years. Data provided by Southwest Regional Climate Center.

Fig. 4.1

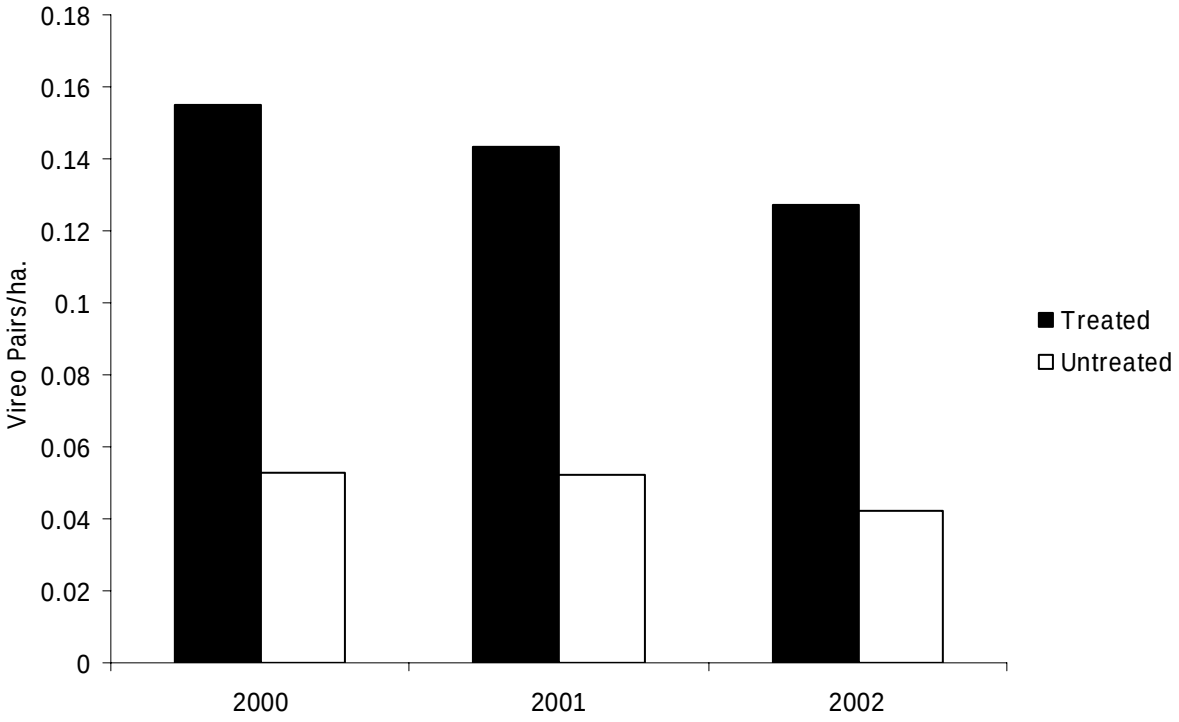

0.18
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
Vireo Pairs/ha.
2000
2001
2002
Treated
Untreated

Fig. 4.2

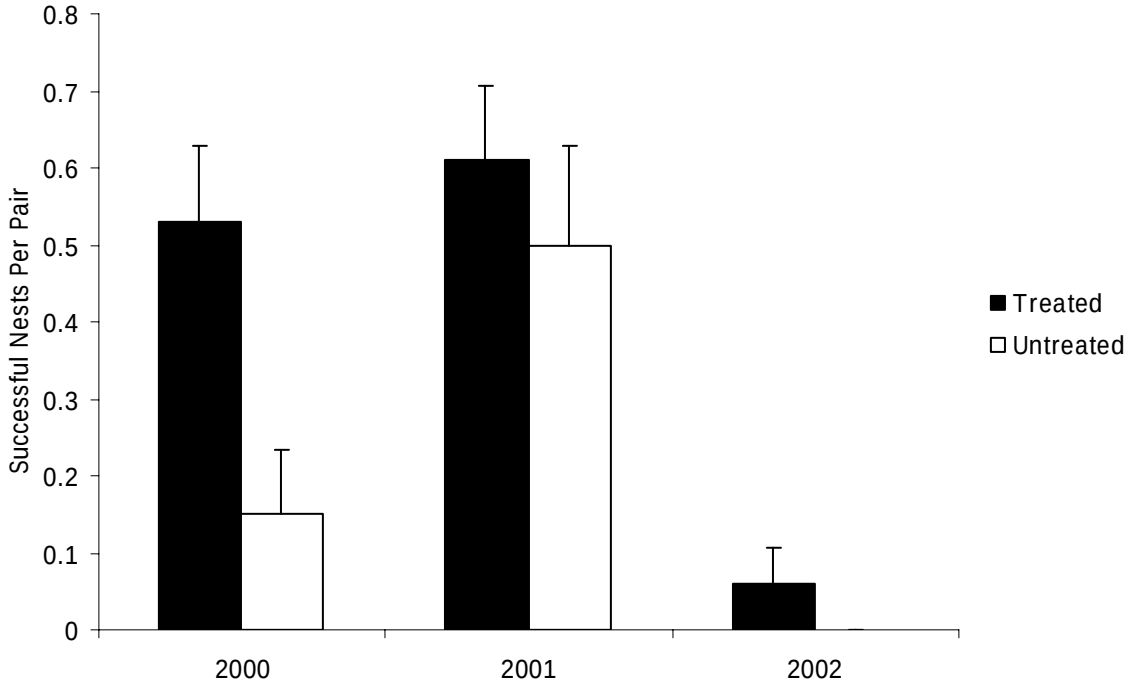

0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Successful Nests Per Pair
2000
2001
2002
Treated
Untreated

Fig. 4.3

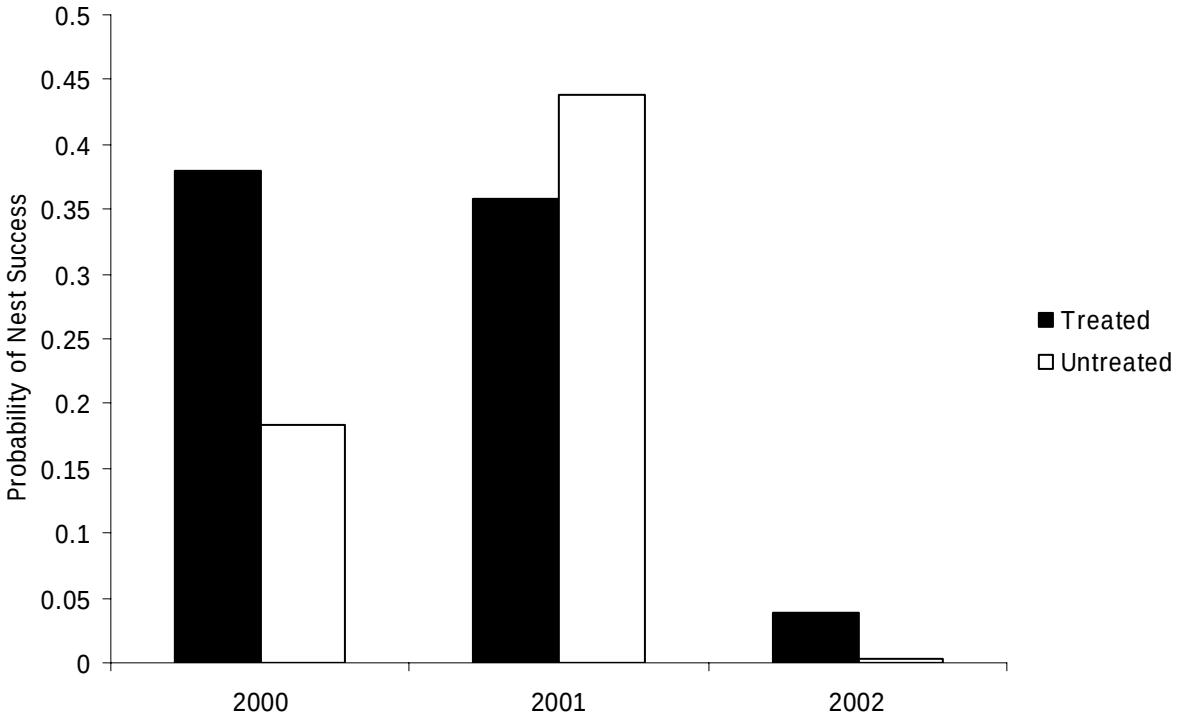

0.5
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Probability of Nest Success
2000
2001
2002
Treated
Untreated

Fig. 4.4

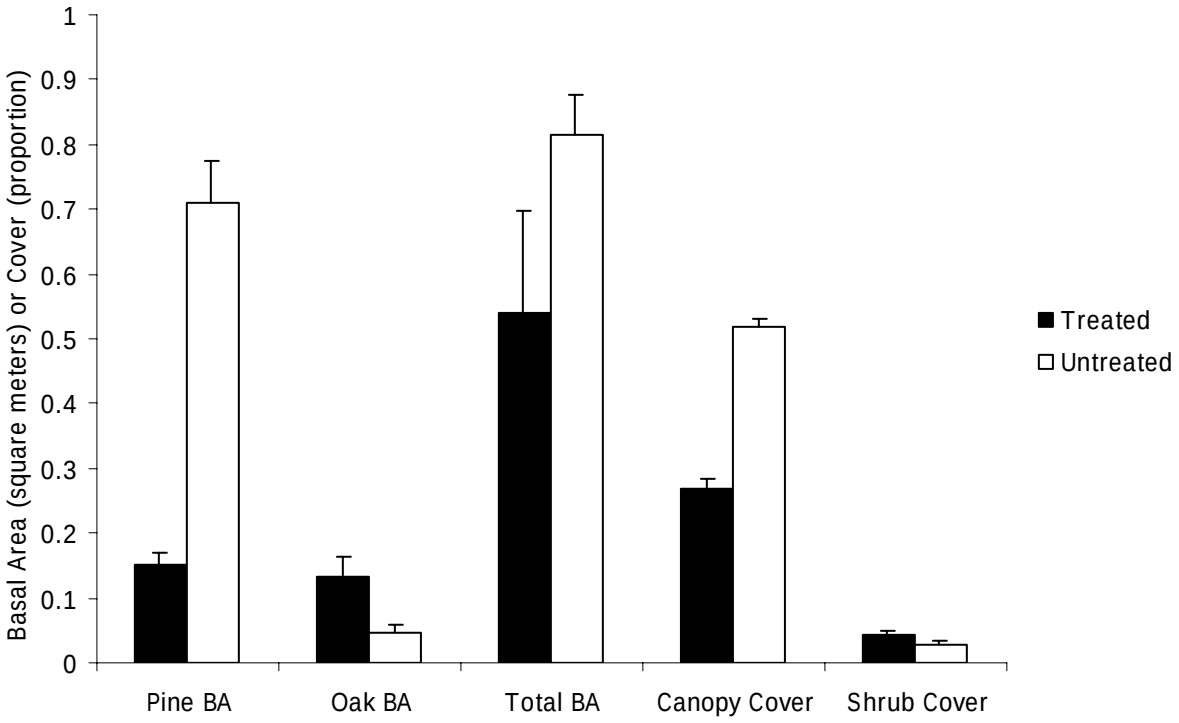
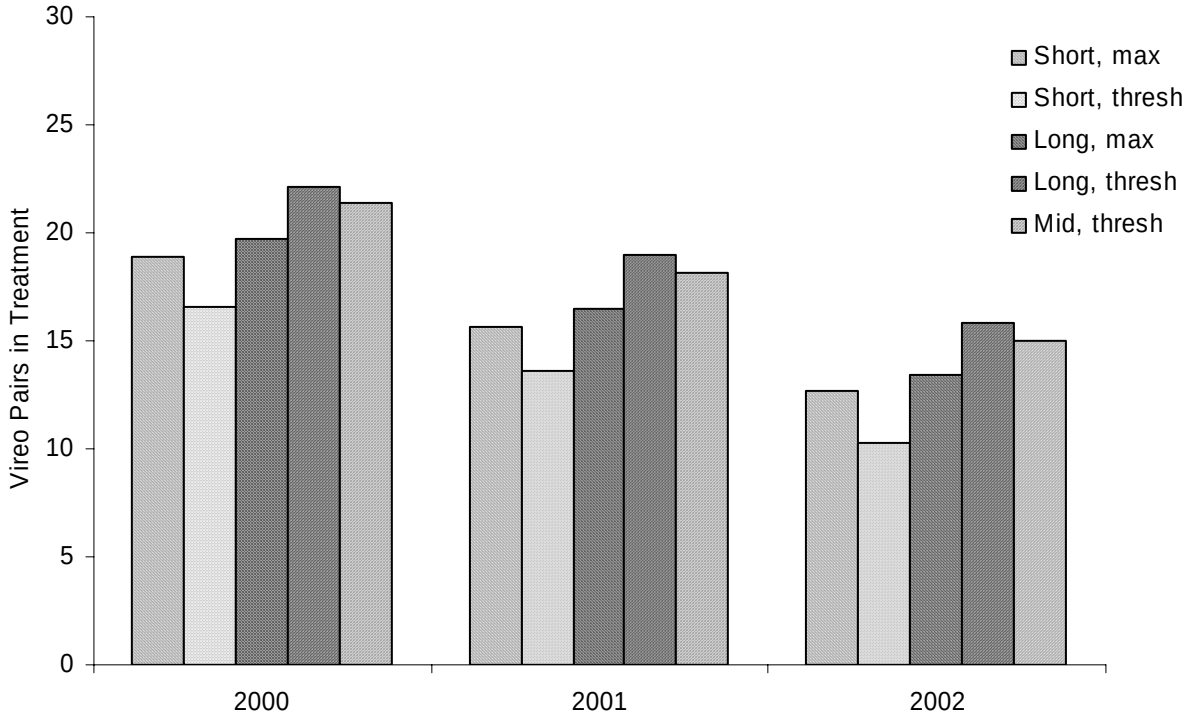

Basal Area (square meters) or Cover (proportion)
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Pine BA
Oak BA
Total BA
Canopy Cover
Shrub Cover
Treated
Untreated

Fig. 4.5


30
25
20
15
10
5
0
Vireo Pairs in Treatment
2000
2001
2002
Short, max
Short, thresh
Long, max
Long, thresh
Mid, thresh

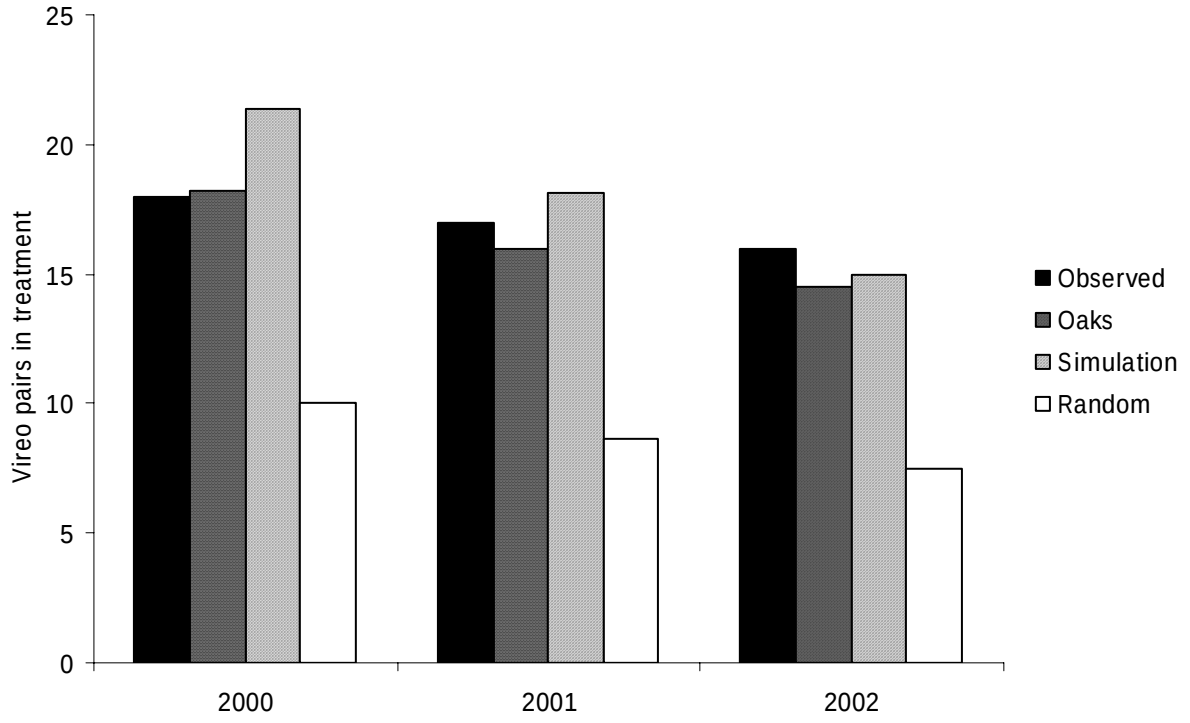
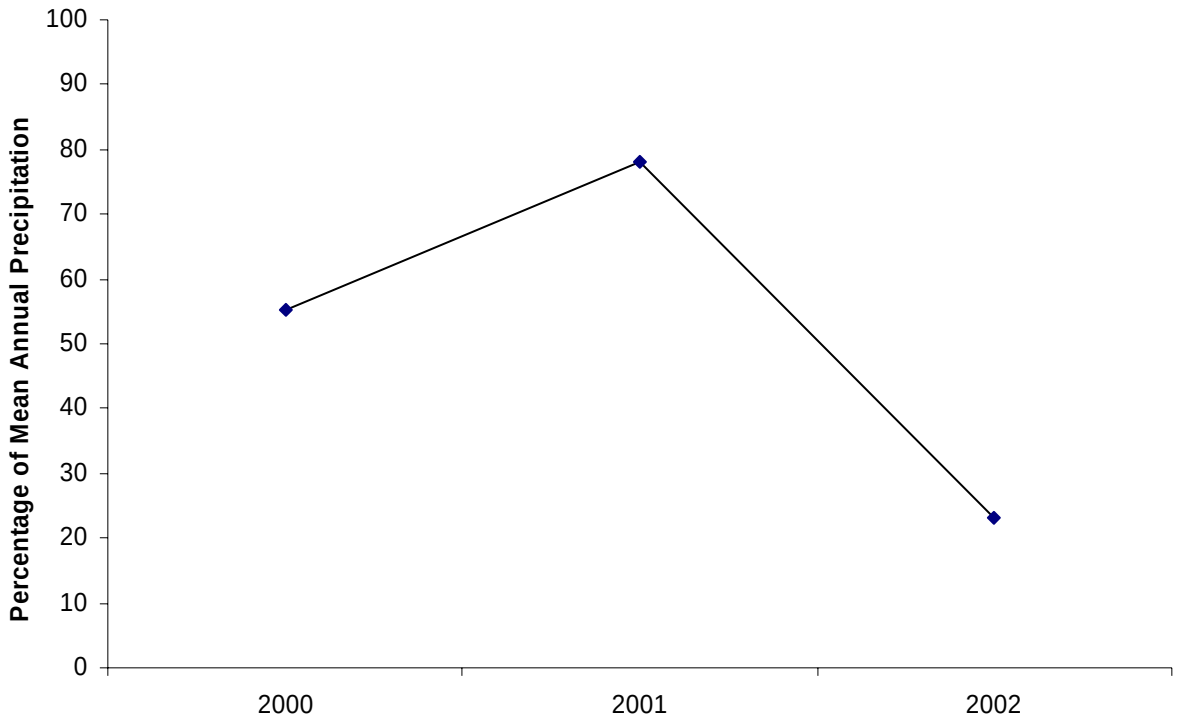

25
20
15
10
5
0
Vireo pairs in treatment
2000
2001
2002
Observed
Oaks
Simulation
Random

Fig. 4.6


Percentage of Mean Annual Precipitation
100
90
80
70
60
50
40
30
20
10
0
2000
2001
2002

TESTING THE EFFECTIVE AREA MODEL FOR PONDEROSA PINE FOREST BIRDS

By James Battin

ABSTRACT

We tested the predictions of the Effective Area Model (EAM) against a null model that did not include edge effects in areas undergoing restoration-like forestry treatments. We measured edge effects on the abundances of the eleven most frequently observed bird species at the Mt. Trumbull Resource Conservation Area, where forest restoration treatments are currently being implemented. We used the edge responses measured at Mount Trumbull to parameterize the EAM. We tested the model at two sites: the Kaibab Plateau and the Fort Valley Experimental Forest. To test the model, we measured the abundances of our eleven target species in seedtree cuts (Kaibab) and restoration areas (Fort Valley) and compared observed bird densities to those predicted by the model. In general, both the EAM and the null model faired poorly at predicting animal abundances at our model test sites. There was considerable between-site variation in model performance. Both the EAM and the null model performed equally poorly at the Fort Valley site. At the Kaibab site, both models fit the observed data better than at Fort Valley, but it was unclear which model performed better. In 2000, the EAM was superior to the null, but in 2001, the null was superior to the EAM. Between-year variability in model fit was greater than between-model variation. We conclude that, due to a lack of suitable model test sites, we were unable to develop a robust test of the EAM for ponderosa pine forest restoration. We chose the best two sites available for model testing, but large difference between Mt. Trumbull (our model development site) and our two model test sites in habitat type, treatment type and age, and/or local bird community

structure caused site-specific factors to overwhelm any possible benefit gained from including edge effects in our model. We continue to believe that the inclusion of edge effects is likely to improve our predictions of bird community responses to restoration and suggest that, because, as we show elsewhere, birds appear to show a stronger response to habitat edges in untreated areas, a greater emphasis should be placed on modeling edge effects in this habitat type.

INTRODUCTION

We tested the accuracy of the Effective Area Model (EAM), a model that predicts animal densities in heterogeneous landscapes based on information about animal responses to habitat edges, in predicting the distributions of eleven ponderosa pine forest bird species. Specifically, we focused on predicting bird abundances in areas undergoing ponderosa pine forest restoration treatments. We compared the predictions of the EAM to a null model that predicted species abundances based solely on their measured abundances in habitat interiors.

Forest restoration is based on the premise that the combined effects of fire suppression, logging, and cattle grazing have, over the course of more than a century, transformed what was once an open system characterized by frequent, low-intensity fires, into a closed-canopy forest that is subject to infrequent, high-intensity fires (Covington and Moore 1994, Covington et al. 1997). Restoration treatments designed to counter this trend involve the removal of over 50% of ponderosa pine basal area followed by a prescribed burn (Friederici 2003). Such treatments are scheduled to be applied to hundreds of thousands, if not millions, of hectares of forest lands over the coming

decades (Allen et al. 2002), creating major habitat changes for a wide range of ponderosa pine forest animal species (Battin and Sisk 2003).

One effect of forest restoration treatments is to propagate a novel type of habitat edge across the landscape: the edge between treated and untreated forest tracts. These edges are likely to become long-lasting features of the post-restoration landscape for a variety of reasons, including the presence of administrative boundaries (e.g., between private and public lands and between public lands managed by different agencies with opposing 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). In attempting to predict the impacts of restoration treatments on bird communities, a consideration f edge effects is therefore likely to be important.

METHODS

Development of Edge Response Functions

We developed a transect-based methodology that sampled an equal area of habitat at all distances (out to 200 m) from the edge created by forest restoration treatments. We used mapped locations of individual birds as the basis for a fine-scale analysis of edge effects. Birds were surveyed each summer from 1999 through 2002 along 200 m transects running from the treated-untreated edge into the interior of one habitat or the other. When possible, transects were paired, with one transect running into the treated forest and another into the untreated from the same point at the edge. Because restoration treatments were in progress during the course of the study, many edges at which we had

placed bird survey transects were destroyed between years, and new edges were created, where new survey transects were placed. Each year, therefore, we used a different set of edge transects. In each year we placed transects at all available treated-untreated edges. Transect numbers varied from 5 to 12 per habitat in any given year. Over the course of the study, we placed transects in seven different treatment units and the untreated forest stands adjacent to them.

Morning surveys were conducted at each transect between 28 May and 10 July each year. Surveys were conducted between 0.5 hours before sunrise and 4.5 hours after sunrise. Due to logistical and personnel constraints, only three surveys per transect were conducted in 1999 and 2002, while four surveys were conducted in 2000 and 2001. Time of day, direction in which transects were run, and observer were rotated in order to minimize bias.

Each transect was surveyed for 30 minutes. Transects were divided into four 50 m segments, each of which was surveyed for 7.5 minutes. Only birds within the 50 m segment currently being surveyed were recorded. Individual birds that were detected on more than one segment during a given survey were noted, and one observation was chosen at random for analysis. The division of the transect into 50 m segments, coupled with the random selection of a single observation for any individual sighted in more than one segment remove the spatial bias usually associated with transect surveys, i.e., that the center of the transect is surveyed more intensively than either end and that observations tend to be biased toward the end of the survey at which the observer begins. For all birds within 50 m of the transect segment being surveyed, species, detection method, and

distance from the transect were recorded. The location of each bird along the transect was mapped and entered into a GIS.

Because, for any given species, most transect segments contained 0 individuals, our data were not amenable to linear regression techniques. To develop edge response functions, we pooled observations between 0 and 50 m from the edge to generate an abundance estimate for the edge and pooled observations between 125 and 200 m to generate an estimate of interior abundance. We assumed a linear change in abundance between edge and interior.

Testing the Effective Area Model

To test the Effective Area Model, we conducted bird surveys in two model testing study areas, one located on the Kaibab Plateau, approximately 95 km east of our Mt. Trumbull study area, and one located at the Fort Valley Experimental Forest near Flagstaff, AZ, about 190 km southeast of Mt. Trumbull. At the Kaibab study area, we conducted model testing surveys in 15-20-year-old seed tree cuts. These areas were cut to a somewhat different prescription than the restoration areas at Mt. Trumbull. Seed tree cuts contained fewer standing live trees and snags than the restoration areas, and the trees left in the seed tree cuts were, on average, smaller than those left in restoration cuts. The restoration areas used at the Fort Valley site were all < 1 year old and were cut either to a similar prescription as at Mount Trumbull or to a prescription that involved the retention of a greater number of standing trees.

We surveyed five seed tree cuts in 2000 and nine in 2001 at the Kaibab site. We surveyed three restoration areas at the Fort Valley site in 2001. Counts were carried out between 5 June and 19 July. Between three and seven point count locations were placed in each patch (seed tree cut or restoration area). At each point we conducted two 10 minute, 50 m radius point counts over the course of the summer. At each point we recorded the same information as was recorded in the transect surveys described above. Points were located at least 50 m from an edge to avoid counting birds in the adjacent habitat.

We used GIS coverages of seed tree cut and restoration area boundaries to generate base maps for the Kaibab and Fort Valley sites, respectively. We applied the Effective Area Model to each patch (seedtree cut or restoration unit), using the edge and interior densities described above to generate EAM density estimates for each species for each patch. We also generated density estimates using a null model that projected the interior density across the entire patch for each species. For all species, we used a Dmax value of 125.

To compare the predictions of the EAM to those of the null model, we ranked species according to their relative abundance at each site (all patches combined) in each year. We then compared these ranks to the ranked abundances predicted by the EAM and the null model using Kendall's tau (Sokol and Rohlf 1995).

RESULTS

We computed edge and interior abundance values for the 11 most frequently observed species at the Mt. Trumbull Resource Conservation Area (Table 1). For four

species, abundances were higher at the edge than in the interior. Edge abundances for the rest were similar to or lower than those in the interior.

At model test sites we recorded a total of 278 detections of our 11 target species (Table 2). For most species, there was considerable variation both between sites and between years in the numbers of birds detected. Three species were never detected at the Fort Valley site. These were excluded from our model testing analysis.

We conducted three model tests: 1) Kaibab 2000, 2) Kaibab 2001, 3) Fort Valley 2001. In 2000, the EAM predictions were more strongly correlated with observed abundances ($\tau = 0.42$, $p>0.1$) than were the null model predictions ($\tau = 0.37$, $p>0.1$). In 2001, however, we observed the opposite pattern, with the null being more strongly associated with observed abundances ($\tau = 0.78$, $p>0.05$) than was the EAM ($\tau = 0.61$, $p<0.1$). At the Fort Valley site, correspondence between both models and observed abundances was low and was the same for both models ($\tau = 0.29$, $p>0.2$).

DISCUSSION

The effectiveness of the EAM relative to the null model varied considerably between sites and years. We documented one case in which the EAM was superior to the null, one in which it was inferior, and one in which both models made the same prediction. At the Kaibab site, where we collected data in two years, the between-year difference in model fit for both models was greater than the difference in fit between models in either year.

There are several possible explanations for the relatively poor performance of both the EAM and the null model. The model test sites that we chose, while they

represented the closest match available to the forest restoration treatments at Mt. Trumbull, differed in important ways from our model development site. In the case of the Kaibab sites, our study units had undergone a forestry treatment that differed in important ways from restoration treatments. These sites were, on average, considerably more open than restoration treatments and contained younger pine trees. They were also considerably older than the restoration treatments at Mt. Trumbull, meaning that succession had proceeded considerably further than at Trumbull. In some areas, thickets of young pine trees had become established. The land use histories of the Mt. Trumbull and Kaibab areas also differ substantially, and other local differences in physical characteristic of the landscape probably caused there to be substantial differences in habitat quality between the areas. All of these factors have the potential to alter local bird communities and/or the responses of birds to forestry activities.

While the restoration treatments used at Fort Valley and Mt. Trumbull were fairly similar, the two areas differed in other important ways. The Fort Valley site was located nearly 200 km from Mt. Trumbull, raising the possibility that local bird communities at the two sites might differ as a result of regional variation in species abundances. The sites also differed in that the Mt. Trumbull restoration treatments were located primarily in ponderosa pine/Gambel oak forest while the Fort Valley treatments were carried out largely in pure ponderosa pine forest. Gambel oak is an important habitat component for many species, and its presence appears to lead to increased abundances of a number of bird species, including several of our target species (Rosenstock 1998). Of the eleven most frequently observed species at Mt. Trumbull, three—chipping sparrow (3rd most abundant species in Mt. Trumbull restoration treatments), plumbeous vireo (8th), and

Grace's warbler (11th)—were not detected even once on our Fort Valley surveys, suggesting that the bird communities in the two areas do differ to markedly.

Our ability to conduct a rigorous test of the Effective Area Model was clearly hampered by a lack of suitable model test sites. Because the implementation of forest restoration treatments has only recently begun, and because the process of restoration is a slow one, restoration treatments of the size required for avian studies had been completed in only one area (Fort Valley) by 2001, the final year of our study. This area was, unfortunately, a long way from Mt. Trumbull and was situated in a somewhat different forest type. We also encountered difficulties when we attempted to test the model in seedtree cuts at a site nearer to Mt. Trumbull (though still almost 100 km away). In this case, differences in the treatment type and age, as well as differences in habitat and local bird communities, made a valid model test difficult.

It should also be noted that most species studied showed relatively weak edge effects in the areas that had undergone restoration treatments (see our chapter on edge effects in ponderosa pine forest birds). In contrast, the same species tended to show stronger edge effects in untreated forest areas, suggesting that it will be more important to parameterize the Effective Area Model untreated than for treated forest areas. Due to the difficulty of finding patches of unlogged forest surrounded by seedtree cuts or restoration treatments, we did not attempt to test the model in untreated forest, but it is likely that further work on the EAM in landscapes undergoing restoration treatments should focus more on this habitat type. The increased strength of edge effects in the untreated forest suggests that a consideration of edge effects in this habitat is more likely to lead to improved predictions of animal density.

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Table 1. Relative abundances of each bird species used in model tests at edge and interior. These are the values that were used as model parameters for the test of the Effective Area Model.

	Relative Abundance	
Species	Edge	Interior
Hairy Woodpecker	0.216	0.296
Steller's Jay	0.144	0.237
Mountain Chickadee	0.338	0.213
White-breasted Nuthatch	0.720	0.654
Western Bluebird	0.733	0.915
Plumbeous Vireo	0.221	0.228
Grace's Warbler	0.117	0.162
Yellow-rumped Warbler	0.238	0.213
Chipping Sparrow	0.270	0.351
Dark-eyed Junco	0.598	0.321
Western Tanager	0.297	0.336

Table 2. Total numbers of detections of each of our 11 target species at two model test sites.

	Site		
Species	Kaibab 2000	Kaibab 2001	Ft. Valley 2001
Hairy Woodpecker	9	5	11
Steller's Jay	0	10	5
Mountain Chickadee	7	1	3
White-breasted Nuthatch	11	11	15
Western Bluebird	24	17	8
Plumbeous Vireo	7	11	0
Grace's Warbler	9	4	0
Yellow-rumped Warbler	1	4	8
Chipping Sparrow	26	3	0
Dark-eyed Junco	20	13	9
Western Tanager	6	15	5

ECOLOGICAL AND LIFE-HISTORY TRAITS PREDICT AVIAN EDGE RESPONSE: A META-ANALYSIS

CHAPTER 1. Ph.D. Dissertation

DRAFT 2 (includes revisions by Barry Noon)

Submitted to Ken Burnham, Ken Wilson, and John Wiens

by Arriana Brand

9/22/03

Abstract

Despite 70 years of research addressing avian abundance in relation to distance from habitat edges, no general relationship exists that will allow *a priori* predictions of the expected abundance response of a given species. A predictive approach is needed because conservation decisions often need to be made when appropriate data are unavailable. In an effort to predict how birds will respond to edges, a meta-analysis was used to identify ecological and life-history traits of species that may allow *a priori* predictions. From the published literature, a database was developed for avian edge response in forest edge studies conducted in North America from 1937 to the present, consisting of 513 replicates of 132 bird species from 30 families. A database consisting of ecological and life-history traits was then developed for species included in the above dataset. Edge types and regions were incorporated in the models as adjustment factors. Four predictive models were developed to separately model positive and negative edge responses on both sides of the forest edge. Candidate models with different combinations of traits as well as adjustment variables were ranked with AICc criteria, and the best model in each set was used to predict the edge response of birds. Each of the four predictive models was used with traits alone, traits plus species as a random effect, and traits plus family as a random effect, yielding a total of 12 predictive models. This approach enables assessment of the value of incorporating the random effects for predictive purposes. To internally validate the predictive edge models, ROC analysis was used to compare observed versus predicted edge response by calculating the area under the ROC curve as well as to calculate the % correctly classified, sensitivity, and specificity. The area under the ROC curves for the 12 models ranged from 79-93% and

the number of observations correctly classified ranged from 76-89%. This approach has the potential to enable land managers to identify species that may be vulnerable to habitat fragmentation by having information on life-history and ecological traits of birds which are often available in the literature, rather than by conducting detailed, time-consuming studies of edge responses for each species in each habitat.

Introduction

Land use / land cover change has transformed one-third to one-half of the Earth's ice-free, terrestrial surface (Vitousek 1994). Given the concern of the scientific community and general public over the impacts of habitat loss and fragmentation there has been an enormous effort to document the effects of habitat fragmentation on vertebrate, invertebrate, and plant populations. The investigation of "edge effects" for birds was one of the first questions addressed by ecologists, and since then a plethora of fragmentation studies have been published in the scientific literature documenting the requirements of certain species for a given patch size or distance from habitat edges. Yet, despite 70 years of research addressing avian abundance in relation to distance from habitat edges, no general relationship has emerged that will allow *a priori* predictions of the expected edge response of a given species. Virtually all papers addressing bird response to edges are exploratory and few have developed a carefully selected set of candidate models based on hypotheses of the mechanisms that may be structuring how different bird species respond to edges. Further, there seems to be a general perception that predicting how unstudied species will respond to edges is not possible (Mac Nally et al. 2000).

Growing criticism has been directed at ecology for the paucity of predictive approaches to fundamental ecological problems (Peters 1983, Côté and Reynolds 2002, Lens et al. 2002, Burnham and Anderson 2002). In order to be useful for conservation, research on habitat fragmentation needs to move away from the piecemeal documentation of effects of fragmentation for each species in each landscape and move toward more general predictions. A predictive approach pertaining to the effects of habitat fragmentation is especially needed because there is not sufficient time and resources to study each species in each habitat for which conservation decisions need to be made (Côté and Reynolds 2002).

A number of different approaches have been attempted in the effort to use one or a small suite of surrogate species whose status and trends provide insights into the state of the larger ecological system to which it belongs (Noon et al. 1997). These include the umbrella, indicator, keystone and focal species concepts (Landres et al. 1988, Mills et al. 1993, Lambeck 1997). However, attempts to utilize these concepts for predictions across ecological systems have been fundamentally limited because a new representative species or set of species needs to be identified in each new location or system that one is interested in studying or managing. For example, while a focal species may serve as an indicator for the particular system in which the data were collected, it is not necessarily predictive for species in other regions. Furthermore, the attempt to identify indicator or focal species in a particular ecosystem is difficult – no strong ecological theory currently exists to guide the selection of such species (Noon et al. 1997, MacNally and Fleishman 2002).

With these various approaches at prediction, the focal species approach stands out in its identification of an indicator for a larger suite of species in regards to a specific threat (Lambeck 1997). If my goal is to predict beyond a particular location in which the data were collected, then it seems useful to focus on a particular stressor, or threat, which may be affecting many different regions and in turn, may apply to many different species occupying diverse ecosystems.

Further, if my goal is to predict beyond a particular location in which the data were collected, then it seems useful to focus on aspects of species life history or ecology that can be inferred beyond a particular location. This is a different goal from predictions based on indicator, keystone, or focal species approaches that attempt to identify a suite of species that represent other unmeasured species. Rather, I propose to use basic characteristics of species described by their life history and ecological traits in an attempt to identify a set of traits that enables general predictions across species and regions. The use of a suite of traits, rather than a suite of species, enables one to move from one system to another or to novel species in the goal of predictive ecological modeling.

Assuming that habitat fragmentation is a stressor that affects population persistence (Fahrig 2002), I can consider how best to identify predictive traits for this threat. Habitat fragmentation studies typically measure patch size, patch shape, or distance from edge (George and Brand 2002, Flaspohler et al. 2001). I chose to focus on edges because they have a number of important advantages over studies of patch size. Edge studies are fundamentally less confounded than patch size studies because they isolate the effect of edge, whereas patch size studies confound the effect of edge along

with patch size and shape. On a patch or landscape sclae, effects of edge can also be used in a predictive capacity more readily than patch size (Sisk et al. 1997). Given the apparent interest in both positive and negative results in edge studies in numerous habitat types since the late-1930's, edge studies are also unlikely to show a publication bias (Lay 1938, Johnston 1947, Ferris 1979, Kroodsma 1982, Germaine et al. 1997).

Given a focus on edges, I began by identifying mechanisms operating at edges that may select for particular ecological and life-history traits. The term "edge effect" has been used to include a wide variety of different biotic and abiotic phenomena. Put into an evolutionary context, the environment may select for a specific set of traits for species adapted to exploit edges. Conversely, the environment may select for a different set of traits for species that are adapted to exploit forest interior habitat and /or that respond negatively to edges. If I view the edge as a selective environment arising from a unique set of physical and biological drivers that occur at the edge, we would expect traits associated with edge species to differ from interior species to the extent the two selective environments differed. The environment at the edge is characterized by a particular set of mechanisms such as changes in microclimate, inter-specific interactions, intra-specific interactions, vegetation structure and competition, resource availability, and disturbance processes. Based on the assumption that habitat edges result in unique selection regimes, these various biotic, abiotic, and stochastic factors that occur at the edge environment differently from the interior environment serve as the mechanisms of edge habitat selection or avoidance, and in turn, shape the evolutionary history of an organism through the process of natural selection. My assumption is that higher abundance at the edge is generally due to higher fitness at the edge, based on the idea that

traits that increase an organisms' fitness are more likely to increase in the population (central tenant of natural selection).

While I would ideally like to understand the selection regimes or mechanisms operating on birds at edges, I recognized that a given mechanism may influence multiple traits. For example, increased predation could impact both clutch size and nest substrate. Thus traits that may predict how species respond to edge cannot be unambiguously associated with a specific mechanistic explanation (Wiens 1989). However, a focus on mechanisms provides the basis for informed hypotheses regarding a predictive suite of traits and allows predictions of which species will be affected by edges and how they will respond.

A number of authors have attempted to relate one or a small set of ecological and life-history traits with sensitivity to habitat fragmentation. Most often these have been based on qualitative observations, but there have also been a few attempts to identify traits related to vulnerability to fragmentation based on statistical analyses. For example, Brittingham and Temple (1983) conjectured that bird species vulnerable to fragmentation tend to be forest habitat specialists, long-distance migrants, have inadequate defense against brood parasitism, low reproductive output, and are most common in warblers (*Parulidae*), vireos (*Vireonidae*), flycatchers (*Tyrannidae*), tanagers (*Thraupidae*), and thrushes (*Turdidae*). De Graaf (1992) used statistical analyses and found that territory size, foraging substrate, and nesting substrate were associated with edge response. Best et al. (1990) found a relationship between edge response and diet, foraging substrate, and nesting substrate. To date, Whitcomb et al. (1981) have done the most comprehensive investigation of traits related with fragmentation, concluding that breeding habitat type

and migratory status most accurately predict vulnerability to forest fragmentation. Previous attempts to relate traits with sensitivity to fragmentation provide a useful starting point. Yet none of the previous studies has attempted to identify a comprehensive set of traits that allows predictions across assemblages of species occupying diverse ecosystems.

Given the goal of prediction to previously unstudied species and locations, I have explored a diverse set of ecological and life-history traits in order to identify those traits that allow us to predict how species will respond to edges. I have used the following basic approach: given a particular stressor such as habitat fragmentation and the creation of edges, identify mechanisms or selective pressures operating as a result of the threat, develop candidate explanatory models by identifying traits that seem related / predictive for the mechanisms, identify predictive trait models by use of model selection, and validate the predictive models. Recent attempts to predict species responses to novel threats (e.g. invasive species) have highlighted the importance of using quantitative analyses that are ecosystem and taxon specific (Kolar and Lodge 2002). In similar fashion, I focus here on birds in forest ecosystems of North America. I believe this approach has the potential to enable land managers to predict a previously unstudied species' edge response by making use of readily available information on life-history and ecological traits of birds from the literature. As a result, when detailed studies of edge response are not possible, reliable conservation decisions can still be made.

Methods

Selection of Papers

The selection of papers to include in the meta-analysis was based on reviews of the literature done by Sisk and Battin (2002) as well as additional literature searches I conducted. Sisk and Battin (2002) reviewed 90 studies that presented original research addressing avian response to edges in primarily forested landscapes. Response variables included bird density and abundance, and nest success based on real or artificial nests. From this process, I identified 71 potential papers that estimated bird density or abundance or nest density in relation to distance from the forest edge.

A number of criteria were used for the selection of papers included in the meta-analysis. Papers were limited to breeding bird species in North America, where the response to edge was species-specific and the outcome variable was relative or absolute density, abundance, or nest density. To estimate the nature of a species' response to the edge, the distance from edge was used as a predictor variable and at least one interior location had to have been measured. Papers meeting my criteria studied abrupt edges, regardless of whether they were human-caused or naturally occurring, and presented original data analysis published in peer-reviewed literature. The response to edge was viewed as occurring from the edge boundary into a single interior habitat type (focal habitat). In order to standardize methodology, results were split up into separate focal and matrix habitats if density or abundance was recorded on both sides of edge. Either the focal or matrix habitat was restricted to forest since the purpose was to investigate avian ecological and life-history traits on both sides of the edge in forested landscapes. Thirty papers from 15 states met my criteria (Table 1).

Data Collection from edge response papers

While a meta-analytic approach ideally transforms the data from multiple studies into effect size (Arnqvist and Wooster 1995), determining what to consider the appropriate effect size is difficult with edge studies because of differences in methods of data collection and analysis, and because information contained in the studies vary substantially. For example, some studies density and some report abundance, and some report only relative measures estimated without a detection function. Some studies used distance from edge as a binary variable (edge vs. interior) and some used distance from edge as a continuous measure with from 2 to 15 different classes. Other researchers only provided general categorizations of birds as "edge" or "interior" birds but did not report their findings quantitatively. Aspects of the sampling design, such as the number and size of plots sampled, whether or not the plots were selected randomly, and how many times the plots may also affect data quality. These issues were resolved in the best way possible by using a qualitative measure of edge response. For each species, edge response was categorized as positive, neutral, or negative, where positive edge response indicates an increase in abundance or density near the edge, neutral indicates no change in abundance or density near the edge, and negative indicates a decline in abundance or density near the edge.

The categories of positive, neutral and negative were then collapsed into binary response variables. Positive (versus non-positive) and negative (versus non-negative) edge responses were modeled separately due to potential differences in traits operating for different edge responses. In attempting to predict negative versus neutral / positive edge response, I used traits expected to be predictive of a negative edge response. In

attempting to predict positive vs. neutral / negative edge response, I used traits expected to predict positive edge response.

Edge response information was gathered for each bird species for each edge type addressed in the literature. There are numerous cases where a particular paper investigated the edge response of the same species in multiple edge types, and those were recorded separately. Independent observations were considered to be species by edge type within each journal article. As such, the same species may have been investigated in different edge types in the same study, as well as in different studies. This potential lack of independence in the data is accounted for in the analysis methodology (see below).

For each edge response record, I recorded the focal habitat type (e.g. coniferous forest), the matrix habitat type (e.g. powerline corridor), and region (e.g. eastern U.S.). These variables were recorded in order to categorize species with respect to possible confounding variables, such as edge type, matrix type, and region, and to gain insights to intra-specific variability in edge response in addition to inter-specific response to edges.

My goal was to identify traits over a large regional scale, and to generalize across different habitat types. Therefore, two edge-types were identified – "forest-open" and "open-forest" – which represented both sides of the edge between forest and open focal habitats respectively (Figure 1). The focal and matrix habitat were categorized as forest-open or open-forest habitat, where the type of edge for each data record was a) forest focal habitat surrounded by open matrix habitat, or b) open focal habitat surrounded by matrix forest habitat. Forest habitat included coniferous, deciduous, and mixed forests and woodlands. Open habitat included clearcut, agriculture, meadow, powerline, pine barren savanna, and chaparral.

Candidate Model Development

My goal in the development of candidate models was to identify those ecological and life-history traits that could be used to predict positive or negative response to edge. Based on hypothesized patterns and processes occurring at edges, candidate models with different combinations of traits as well as adjustment variables were developed for each of four candidate model sets. The four candidate model sets were used to predict both positive and negative edge response for both forest-open and open-forest edge types. Forest-open vs. open-forest edge type was used to subset all analyses because I expected, *a priori*, the traits that enable prediction of the abundance response of species in the forest interior compared with the edge, and the open habitat compared with the edge, to be quite different based on ecology and biology of species. Additionally, I modeled positive vs. negative predictions separately due to potential differences in traits operating for different edge responses.

Prior to constructing statistical models, I attempted to decrease the number of traits as much as possible based on *a priori* thinking as well as by minimizing collinearity between trait variables. For example, nest height and substrate are likely to be collinear so were not included in the same models. While some previous papers have shown territory density to be related with edge response (De Graaf 1992), I did not include territory density as a trait in the candidate models because much of the information contained in territory density was probably contained in body mass (Peters 1983). In the interest of parsimony and minimizing the number of models considered in model selection, I collapsed variables where possible, such as lifetime reproduction with annual reproduction and longevity (Anderson and Burnham 2002). However, certain variables

that have shown inconclusive evidence of collinearities were allowed to remain in the same models, such as migratory status with lifetime reproduction and cowbird host frequency (Whitcomb et al. 1981).

A total of 12 traits were used in the four candidate model sets (Table 2), with four traits categorized in two ways (depending on the specific candidate model set) for a total of 16 traits (Table 3). Subsets of the 16 traits were included in each of the four candidate model sets. Some of the traits were used in all four sets. Some were included in only forest-open edge type, some in only open-forest edge type, some in positive and some in negative, and some in combinations of the above. Traits were included in a given candidate model set where I expected, *a priori*, changes between the interior and edge environment for a particular edge type based on the mechanisms thought to be occurring at the edge. I expected fewer traits to distinguish open focal habitat from the edge than forest focal habitat from the edge.

Mechanisms (selective agents) potentially operating on birds at habitat edges can be characterized as environmental factors, biotic interactions, and stochastic processes each hypothesized to be related to a set of trait variables (Table 2). Additionally, selection or avoidance of the edge environment may have fitness consequences that operate as a selective agent. Generally, I expected traits to be different to the extent that selective agents at the edge differ from those in the interior. The following paragraphs discuss the logic for including various traits in the different candidate model sets as well as the parameterization of the different trait variables.

Environmental Factors

Environmental factors include changes in abiotic conditions, vegetative structure, and prey availability at edges compared with the forest interior. Bird traits that may respond to environmental factors include the degree of mesic habitat selection, nest substrate, foraging substrate, and diet changes caused by varying amounts of resources at edges. Habitat utilization also represents a response to changes in environmental factors. Each of the traits will be addressed below.

While numerous abiotic conditions such as wind speed and incident radiation have been found to differ between edges and interior (Chen et al. 1992, 1995, Newmark 2001), I hypothesized decreased humidity at edge compared with the forest interior to be particularly important for forest birds. Birds may preferentially select the forest interior if they require higher humidity directly or indirectly through effects on prey or vegetation (Brand and George 2001, Whitcomb et al. 1981). To reflect the effects of relative humidity, I used habitat descriptions to categorize whether species demonstrate obligate mesic habitat selection, that is depend only or primarily on moist, humid habitat (Erlich et al. 1988, National Geographic 1992). I expected species with obligate mesic habitat selection to have a more negative edge response in the forest-open edge type (Table 3, 4).

Change in vegetation structure between edge and interior locations is an environmental factor hypothesized to affect nest substrate availability in forest edge versus interior. Shrubs as well as shrub nesting birds often attain higher density at the edge compared with the forest interior (Lopez de Casenave et al. 1998, De Graaf 1992). The abundance of ground and tree nest site locations are similar between edge and interior locations, and both ground and canopy nesting birds have shown mixed results with respect to abundance at edges (De Graaf 1992, Gates and Gysel 1978, Germaine et

al. 1997, Marini et al. 1995). Thus in the forest-open edge type I hypothesized that birds that nest or forage in shrub foliage will preferentially select edges over forest interior habitats. I categorized nesting substrate as shrub vs. non-shrub (Trait: NS, Table 2; Erlich et al. 1988) to predict positive edge response for the forest-open edge type.

Differences in vegetation structure between edge and interior locations were hypothesized to affect nest height in open habitat versus forest edge. The categorization of nest substrate for forest habitat is less clear for open habitat because shrub nesters are often equally abundant in edge versus open habitat (De Graaf 1992). However, the height of the vegetation is usually lower in open habitat than in the forest edge where trees are present. Therefore, I used nest height to predict both positive and negative edge response in the open-forest edge type based on published average nest heights (Ehrlich et al. 1988, Trait: NH, Table 2).

Differences in environmental factors between edge and interior locations affect prey populations and may influence avian diet. I categorized diet in two ways. For forest habitat, insectivores often show higher abundance in forest interior locations (e.g., Restrepo and Gomez 1998, Whitcomb et al. 1981). As a result, I hypothesized that insectivores would show a negative edge response in the forest-open edge type and categorized the diet contrast as insectivore vs. non-insectivore (Ehrlich et al. 1988, Trait: DI 1, Table 2). I also predicted that omnivores may be more abundance at the edge because they may benefit from cross-boundary subsidies (Fagan et al. 1999, Cantrell et al. 2001) in both the forest-open and open-forest edge types and contrasted diet as omnivore vs. non-omnivore (Ehrlich et al. 1988, trait DI 2, Table 2). I did not use diet as

a trait to predict negative edge response for open-forest since no clear patterns were apparent in published studies.

Foraging substrate may differ between edge and interior locations as a result of changes in prey abundance, prey availability, and vegetation structure and composition. Abundance of foliage prey as well as foliage predators has shown inconsistent patterns between forest edge and interior in different studies (Yahner 1995, De Graaf 1992, Van Wilgenburg et al. 2001, Jokimaeki et al. 1998). For example, bark foragers were more abundant in the forest interior than at the edge (Yahner 1995), but ground-shrub foragers tended to be more abundant near the edge than interior (Yahner 1995, De Graaf 1992). As such, I expected bark foragers to show a negative edge response in forest-open edge type and categorized foraging substrate as bark vs. non-bark (Ehrlich et al. 1988, Trait: FS 1, Table 2). To predict positive edge response in forest-open edge type I categorized foraging substrate as ground vs. non-ground (Ehrlich et al. 1988, Trait: FS2, Table 2). Due to similar abundance of ground foragers in open and edge habitat, inconsistent results for foliage foragers, and the general lack of bark foragers in open habitat, foraging substrate was not used as a trait in the open-forest edge type.

Habitat utilization is considered to be a particularly important trait and is used in all four candidate model sets. While certain authors have considered habitat use an important determinant of sensitivity to habitat fragmentation, they have also used circular reasoning when investigating the relationship between habitat utilization and sensitivity to fragmentation (Whitcomb et al. 1981 and Germaine et al. 1997). Both Whitcomb et al. (1981) and Germaine et al. (1997) categorized habitat utilization in terms of sensitivity to fragmentation in order to test for sensitivity to edges. Here I consider habitat utilization

to be a predictor of edge response, but define it separately from aspects of sensitivity to fragmentation. I categorized habitat utilization according to whether a species used forest habitat, open habitat, or both forest and open habitats (National Geographic 1992, Ehrlich et al. 1988). For the forest-open edge type, I characterized habitat utilization as forest vs. open or both (Trait: HU 1, Table 2). For the open-forest edge type I characterized habitat utilization as open vs. forest or both (Trait: HU 2, Table 2). Birds that use only forest habitat may avoid forest edges (have a negative edge response) because there is no appropriate habitat on the other side of the edge. Birds that use open or both habitats may have positive or neutral responses to edge because the edge and interior environments do not differ greatly. Likewise, birds that use only open habitat may avoid edges (have a negative edge response) because no adequate habitat occurs on the other side of the edge. I also expected a positive edge response in open habitats for birds that use forest or both habitats.

Biotic Interactions

Numerous inter- and intra-specific interactions could differ between the edge and interior environments, but increased predation and parasitism at edges has been most frequently observed across edge types and regions (Brittingham and Temple 1983, Chalfoun 2002, Donovan et al. 1997). Bird traits that may respond to increased predation and parasitism at the edge include nest height, nest type, duration of the incubation and nesting period, as well as behavioral response to cowbird parasitism. I expected birds to avoid edges (show a negative edge response) if nest substrate or height, nest type, or duration of nesting makes them more susceptible to predation or parasitism.

Nest substrate may be influenced by biotic interactions in addition to the environmental factors discussed above. Flaspohler et al. (2001) found that ground nests close to edges had lower nest success than canopy nests, which they attributed to increased predation at edges. A hypothesized negative edge response for ground nesters who experience higher rates of predation at edges, combined with the categorization based on environmental factors, supports the hypothesis of positive edge response for shrub nesters and neutral or negative edge response for ground or canopy nesters in the forest-open edge type.

Like nest substrate, a species' nest height distribution may be responding to multiple factors. Based on vegetation structure in the open-forest edge, I hypothesized a positive edge response for higher nesting birds and a negative or neutral edge response for birds with lower nests. However, increased predation at edges for lower nests (Flaspohler et al. 2001) may interplay with the selection pressure for the vegetation structure. Based on both mechanisms, I hypothesized a net negative edge response for lower nest sites and a net positive edge response for higher nests.

Nest type may be related to vulnerability to predation and parasitism, and in turn, may influence whether birds will respond positively or negatively to edges. Nest type was categorized as open (cup, platform) versus closed (cavity, sphere, pendant; Ehrlich et al. 1988, trait: NT, Table 2). Open nesting birds are generally at higher risk to predation and parasitism since their nests are more accessible than birds that nest in cavities or in partially closed nests (Wilcove 1985, Germaine et al. 1997). Nest type was only used to predict edge response in the forest-open edge type since open habitats provide no closed

nests. I hypothesized that species with closed nests would have a more positive edge response than those with open nests based on the expected cost to reproduction.

The length of the incubation + nestling period has been shown to be associated with vulnerability to predation (Martin 1995). The number of days for incubation and nesting were obtained from Ehrlich et al. (1988) and supplemented by Pool and Gill (editors) for 12 species (Trait: IN, references in Table 2). Martin (1995) found that a decreased nestling period is associated with increased rates of predation. Assuming higher predation rates at the edge than the interior of both forest and open habitats, the length of time should be a useful predictor of both positive as well as negative edge response.

Another biotic interaction well documented to occur at edges is increased parasitism by
Brown-headed Cowbirds (Hobson and Villard 1998, Brittingham and Temple 1983, Evans and Gates 1997). I categorized a species cowbird host frequency as common vs. rare based on Ehrlich et al. (1988) (Trait: CH). Based on fitness consequences, I hypothesized a negative edge response for more frequent cowbird hosts in both edge types.

In general, while I expect traits to have evolved to improve fitness of birds at edges, decreased fitness at edges associated with certain traits may indicate vulnerability to an ecological trap (Gates and Gysel 1978). Ecological traps are typically defined as evidence of habitat selection (such as increased abundance) coupled with negative fitness consequences (such as low nest success; Gates and Gysel 1978, Pidgeon et al. 2003, Woodward et al. 2001). We expect birds to show a negative edge response if the nest

substrate, height, or type, or the length of the nesting period, makes them more susceptible to predation or parasitism. If observed results are counter to the expected predictions for certain traits, such as a more positive edge response for species with increased exposure of nest contents to predators due to longer length of the nesting period, then species with that trait may be vulnerable to an ecological trap at edges.

Migratory status may be an important predictor of response to edge. I defined migratory status based on Whitcomb et al. (1981) definitions of permanents resident, short-distance, and long-distance migrants based on descriptions in Ehrlich et al. (1988), National Geographic (1992) and Whitcomb et al. (1981). A number of authors have suggested that forest-nesting Neotropical migrants possess a particular set of characteristics that increase their susceptibility to fragmentation: open cup nests, ground nest location, and lack of defense against brood parasitism (Rich et al. 1994, Whitcomb et al. 1981, Galli et al. 1976, Crawford et al. 1981). While the relationship between Neotropical migration and increased sensitivity to habitat fragmentation has mostly been investigated in relation to forest habitats (Whitcomb et al. 1981, Rich et al. 1994), it is possible a similar relationship occurs in non-forested habitat interior such as grassland and meadows. Based on previous studies, I hypothesized a negative edge response for long distance migrants for both forest-open and open-forest edge types.

Stochastic Processes

Stochastic processes at edges can be characterized by increased variability of conditions on a daily or seasonal time scale. Various studies have shown increased variability of microclimatic conditions operating at edges over a daily time scale (Chen et

al. 1995, Newmark 2001). A more variable microclimate may also influence other factors such as prey abundance and availability or nest site heterogeneity occurring over longer time scales. I considered traits related with stochastic processes to be most pronounced between the forest edge and interior, rather than for the open-forest edge type, since I expect the degree of variability of conditions occurring within open habitats to be similar to that at the edge. Bird traits that may respond to stochastic processes include ecological plasticity (generalist vs. specialist) and body mass.

A larger body size may improve the ability of birds to deal with more variable conditions. For example, increased body mass has been found to improve survivorship in the presence of unpredictable feeding conditions (Lima 1986). Body mass has also been found to be strongly related with allometric relationships such as metabolic rate and home range size that may pertain to the ability to deal with variable conditions (Peters 1983). Body mass estimates were obtained from Dunning (1993) and in cases where body mass was distinguished for males and females I took the average value. I hypothesized that larger birds will be better able to buffer variable conditions at edges than smaller birds and thus show a more positive edge response, whereas smaller birds will be more affected by stochastic processes and show a more negative edge response.

I expected generalist species to be better able to cope with increased variability of conditions at the edge, whereas specialists should be less able to cope with variable conditions. Various authors have proposed that generalist bird species, such as those that are flexible in habitat use or nest placement, are adapted to have higher abundance at edges and thus may respond positively to edges whereas specialist species are negatively associated with the edge (Chasko and Gates 1982, Johnston 1947, Gates and Giffen 1991,

Kroodsma 1987, O'Connell et al. 1998, Whitcomb et al. 1981). I defined an index of ecological plasticity to represent the degree to which a species was an ecological generalist or specialist. The index ranged from 4-13 equal to the sum of the number of common nest substrates, prey items, and foraging methods (Ehrlich et al. 1988) added to the number of habitat types ranging from 1-4 (Ehrlich et al. 1988, National Geographic 1992). I hypothesized that species with greater placticity would be more likely to show a positive edge response and less plastic species a more negative edge response.

Fitness Consequences

In addition to the above ecological traits that may respond to the unique environmental conditions at edges, there may also be direct fitness consequences expressed as changes in survival and / or reproduction in edge habitats. These may be viewed as the ultimate consequences of changes in environmental factors, biotic interactions, and stochastic processes at edges. Negative fitness consequences at the edge may result from increased predation and parasitism, fewer resources such as prey and nesting sites, or greater environmental variation. However, since some species do nest preferentially at edges, there may also be a fitness advantage of nesting at the edge such as increased nesting substrate or prey availability for some species. I defined a species' fitness trait in terms of potential lifetime reproductive success equal to the number of broods per year x average clutch size x longevity (clutch size and brood estimates in Ehrlich et al. 1988 supplemented by Pool and Gill (editors) for 17 species; longevity obtained from bird banding longevity records; Trait: LR, references in Table 2). While this measurement greatly simplifies the many life-history traits of birds (Stearns 1977), it

is nonetheless a useful synthetic trait combining annual reproductive effort with longevity. Gates and Gysel (1978) and Whitcomb et al. (1981) found lower reproductive output near the edge, however Whitcomb et al. (1981) found no relationship between longevity and sensitivity to habitat fragmentation. Based on these published results, I hypothesized that species with lower potential lifetime reproductive success would show a more negative edge response, and that species with higher potential lifetime reproductive success would show a more positive edge response. This trait was used to predict edge response in both forest and open habitats.

Adjustment Factors

Many factors may confound the study of edge response in birds. Potentially confounding factors, such as edge orientation and forest age, are often not reported in avian edge response studies. Edge type and geographic region are additional potentially confounding variables that often are reported and can be incorporated as a covariate in the analysis. I hypothesized that three variables in addition to trait variables may be important for predicting edge response: geographic region, agricultural vs. non-agricultural edges, and anthropogenic vs. natural edges. While trait variables enable evaluation of inter-specific variability in edge response, these adjustment factors enable estimation of the degree of variation within species in different edge types or different geographic regions. As such, edge type and region may improve the ability to predict how a given species will respond to edges.

Anthropogenically induced edges vs. natural edges were included as covariates in the analysis. Anthropogenic edges arising from habitat fragmentation may generate a

different adaptational response than natural edges. Traits associated with natural edges may have evolved in response to threats occurring over thousands of generations, and thus, natural selection would be expected to select for traits that increase fitness. Anthropogenically induced edges have many similarities to natural edges (e.g., abrupt transition from one habitat to another) but may have distinct adaptational consequences. I classified edges as anthropogenic based on focal or matrix open habitats adjacent to forest including clearcuts, powerline corridors, and agricultural fields. Focal or matrix open habitats consisting of rivers, prairies, or meadows adjacent to forest were classified as natural edge.

Region was included as an adjustment factor. I defined region as eastern and midwestern U.S. vs. western U.S. separated by the Great Plains. There are probably some overarching differences between regions in terms of the levels of predation, availability of prey, and rates of parasitism by Brown-headed Cowbirds for example, that may improve prediction of edge response in addition to the trait variables. I hypothesized that birds in the midwestern and eastern U.S. undergo greater predation and parasitism rates and thus show a more negative edge response than western bird species (Brand and George 2000).

Recent studies have shown higher predation rates in agricultural vs. non-agricultural habitat (Chalfoun et al. 2002). I defined agricultural edge as focal or matrix open habitats consisting of agricultural fields adjacent to forest habitat. I hypothesized that birds may experience higher predation rates in agricultural edges and thus would more likely show a negative edge response than birds in non-agricultural edges.

Analytic Methods

Results presented in the published studies included in this meta-analysis were used to classify the edge response for a given species within a given edge type as positive, neutral, or negative. An ordered, categorical outcome variable is appropriate for analysis with the proportional odds model (Brant 1990). The primary assumption of the proportional odds model is that the regression coefficients are the same regardless of whether one compares positive edge response with neutral / negative, or positive / neutral with negative edge response (Brant 1990). However, based on a Likelihood Ratio Test of my data, this assumption was not met. As such, I used a binary outcome to compare positive vs. non-positive and negative vs. non-negative edge response with separate logistic regression analyses. The most important benefit of using separate logistic regressions was the ability to model different coefficients (and thus different traits) in the prediction of positive and negative edge response.

Even if a species' edge response varied for different edge types and in different studies, this species would have the same set of species-level traits. As a consequence, there was a lack of independence in the trait data used to predict edge response. I accounted for this dependence in the trait data by using a random effects model. I used logistic regression with species as a random effect to select the best predictive models for positive and negative edge response in forest-open and open-forest edge types.

In order to assess the importance of each trait, I first considered each trait and adjustment variable as a predictor for edge response individually. In addition to the analysis with each trait considered one-at-a-time, I also incorporated multiple traits and adjustment variables in order to develop four, multi-trait predictive models. All results

are interpreted in terms of the odds ratio, which is the standard means by which to interpret the coefficients in logistic regression analyses.

The identification of traits to include in the four 'best' predictive models was achieved by the information-theoretic approach for model selection (Burnham and Anderson 2002). Model selection criteria based on Akaike's Information Criterion (AIC) was used with the small sample correction to yield AICc (Burnham and Anderson 2002). Though AICc analysis is not yet worked out for use with random effects, one remedy is to use QAICc rather than AICc when there is evidence of overdispersion in the data (Burnham and Anderson 2002). To test whether QAICc was the appropriate criterion to rank models, I ran the global model under all four scenarios: negative and positive edge response in forest-open and open-forest edge types to calculate the overdispersion parameter constructed as Chi square GOF test / df. The mean ± sd = 0.98 ± 0.11 showed no evidence of overdispersion and thus I used AICc rather than QAICc.

For each candidate model set I selected traits for possible inclusion in the global model for that set based on previous literature and a priori thinking about he mechanisms operating on birds at edges (Table 4). From an original list of 26 traits, I narrowed the list to 11 and 10 traits to include in the negative and positive edge response in the forest-open edge type, and 6 and 5 traits to include in the negative and positive edge response for the open-forest edge type (Table 4). From the four global models, I included habitat utilization (HU) in every candidate model, then added every possible combination ranging from 1 to 5 traits in the forest-open edge type and 1-3 traits in the open-forest edge type. This yielded a total of 381 and 218 candidate models in the forest-open edge

type and 30 and 15 candidate models in the open-forest edge type for negative and positive edge response respectively.

Once the prediction equation with traits and species as a random effect was selected based on AICc, I included adjustment variables to assess their importance in the prediction equation. I separately added each of the three adjustment variables in candidate models with delta AICc values < 2, and used AICc criteria on the larger candidate model set to assess which traits and adjustment variables may be used to predict edge response.

While species random effects were used in candidate models for the purpose of model selection, prediction beyond the species included in the meta-analysis data set is desirable. In order to enable predictions to previously unstudied species, I applied the best model (containing traits and adjustment variables) in each candidate model set to use with both taxonomic family as a random effect as well as with trait and adjustment variables alone. For example, to model the edge response of a previously unstudied species, prediction may be improved by including family membership for species included in the meta-analysis data set. In cases where neither the species nor family was included in this meta-analysis, it is still possible to predict the edge response using traits alone.

In summary, I developed separate predictive models depending on edge responses (positive and negative) and edge types (forest-open and open-forest) to yield four multi-trait predictive models. Each predictive model can subsequently be used with traits plus species random effects, traits plus family random effects, or traits alone. This yields 12 predictive models that can be used by managers to predict a species' edge response based

on taxonomic information (whether the species or family has been studied previously), species' traits (drawn from the literature), and information about the study area (edge type and region).

In order to quantify the accuracy of a diagnostic test, I used non-parametric Receiver and Operating Characteristic (ROC) analyses to compare predicted edge response with what was observed (DeLong et al. 1985, DeLong et al. 1988). The observed value indicates the true state of the observation (positive or negative edge response) and the result of the diagnostic test indicates the predicted value (positive or negative edge response). I conducted ROC analysis on each of the 12 predictive models to calculate the area under the ROC curve along with the associated standard error and confidence intervals, as well as to calculate the maximum % correctly classified, sensitivity, and specificity associated with a particular cut-point. Sensitivity is the fraction of positive edge responses that are correctly classified by the predictive models (true-positive rate), and the specificity is the fraction of negative edge responses that are correctly classified by the predictive models (true-negative rate).

Keeping the traits contained within the predictive models regardless of whether we use traits + species random effect, traits + family random effect, or traits alone enables us to evaluate whether added predictive ability is gained with use of species or family information as a random effect in comparison with using predictive models containing traits alone. This analysis approach enables assessment of a model's predictive ability based on edge response, edge type, and whether or not the species has been studies previously.

Results

Descriptive Results

Out of the 30 papers included in this analysis, there were a total of 513 observations of edge response from 133 species representing 32 families. The number of times each of the 133 species was observed in the literature ranged from once (30 species) to 16 times (1 species). Of the 513 edge response observations, 158 were negative, 133 were neutral, and 222 were positive.

The data showed a wide range of inter-specific as well as intra-specific variability. Inter-specific variability was most pronounced when a species showed a consistent edge response. For example, the Brown-headed Cowbird showed positive edge response for 11 of 13 observed edge responses, and the Wood Thrush showed negative edge response for 10 of 13 observations. In contrast, some species showed extensive intra-specific variability. For example, of 12 edge response observations, the Blue Jay showed 3 negative, 5 neutral, and 4 positive responses to edge.

To gain general biological insights, it is informative to consider the importance of each trait variable as a predictor individually. This enables an evaluation of the relationship between a given trait and edge response. The trait variables considered individually had large explanatory power. I observed a significant result ($p < 0.1$) for 8 of 10 and 7 of 9 trait variables for negative and positive edge response respectively in the forest-open edge type, and for 4 of 6 and 5 of 6 trait variables for negative and positive edge response respectively in the open-forest edge type (Table 5).

In forest-open edge type, a negative edge response is 29.7 times more likely for specialist birds, 17 times more likely for birds that utilize forest habitat, 4.9 to 5.7 times more likely for insectivores, bark foragers, and for birds with lower lifetime reproduction,

and 2.5 to 3.7 times more likely for obligate mesic habitat selection, long distance migrants, and species with smaller body mass (Table 5, Figure 1). In forest-open edge type a positive edge response is 24 to 32 times more likely for generalist birds, omnivores, and birds that that utilize open or both open and forest habitat, 11.7 times more likely for shrub nesters, and 4.3-6.7 times more likely for birds with higher lifetime reproductive output, open cup nests, and ground foragers (Table 5, Figure 1).

In the open-forest edge type, a negative edge response is 55.4 times more likely for birds that nest low to the ground, and between 4.4 - 4.8 times more likely for birds that have low lifetime reproduction, utilize open habitats, have shorter incubation + nesting period, and are common cowbird hosts (Table 5, Figure 1). In the open-forest edge type, a positive edge response is 39 times more likely for birds that nest high above the ground, and between 5.3-6.5 times more likely for bird that utilize forest or both open and forest habitat, have larger lifetime reproductive output, and have longer incubation + nesting period (Table 5, Figure 1).

I also considered each adjustment variable individually as a predictor. For the forest-open edge type, none of the adjustment variables considered were significantly related with a negative edge response, though both region and agricultural matrix habitat were related with a positive edge response (Table 6). For the open-forest edge type, a negative edge response was 15.4 times more likely with a non-agricultural focal habitat, and a positive edge response was 6.8 times more likely with an agricultural focal habitat (Table 6).

Multi-Trait Predictive Model Selection Results

In order to develop models to predict edge response, I considered different combinations of traits in 4 candidate model sets with model selection based on AICc criteria (Burnham and Anderson 2002).

For the forest-open edge type, I considered 381 and 218 candidate models for negative and positive edge response respectively. Given this large number of models, I expected to observe model selection uncertainty in the top set of models selected with AICc criteria (Table 7). The best prediction model for negative edge response had an Akaike weight w_i = 18.2%, and the best model to predict positive edge response had an Akaike weight w_i = 28.3% (Table 7). Model selection uncertainty was also observed with ΔAICc value < 2 for 5 models in both candidate models sets (Table 7). Despite model selection uncertainty, there was an important increase in ΔAICc and w_i values between the first and second modles for positive and negative edge responses (Table 7).

For the open-forest edge type, I considered 30 and 15 candidate models for negative and positive edge response, respectively. Given a smaller set of candidate models, I observed less model selection uncertainty (Table 8). The best model to predict negative edge response had an Akaike weight w_i = 96.7 %, and the best model to predict positive edge response had an Akaike weight w_i = 95.3% (Table 8). A large jump can be seen in the ΔAICc values between the first and second best models used to predict both positive and negative edge response (Table 8).

Multi-trait Predictive Edge Models

We developed 8 predictive models using either species or family random effects within each of the 4 candidate model sets to predict both positive and negative edge response in forest-open and open-forest edge types.

Forest-Open Edge Type

The predictive models for negative edge response in forest-open edge type included 6 traits of which five traits were significant (p-values< 0.1). Similar results were observed using both species and family random effects. In both cases, the odds of a negative edge response was 9.7 times greater for forest habitat birds, and between 2.0 to 4.9 times greater for species that require mesic habitat, species with longer incubation and nestling periods, lower ecological plasticity, and smaller body mass (Table 9). Lifetime reproductive effort was included in the best models selected by AICc criteria for negative edge response in forest-open edge types with both species and family random effects, but was insignificant (Table 9). When considered individually, lifetime reproductive effort was significant (Table 6, Figure 2), and thus is probably redundant with other variables included in the muti-trait model.

The predictive models for positive edge response for the forest-open edge type contained 6 traits and an adjustment variable. For the species random effect, a positive edge response is 22 times more likely for omnivores, 14.7 times more likely for species that utilize open or both forest and open habitat, and 3.7 – 4.2 times more likely for shrub nesting species with shorter incubation plus nesting period (Table 9). A positive edge response is also 2.3 times more likely in the east than in the west (Table 9). For the model with family as a random effect, a positive edge response is 3.8 times more likely for omnivores and 7 times more likely for birds that utilize open or both forest and open habitats (Table 9). A positive edge response is also 2.2-2.7 times more likely for shrub nesting species with open cup nests (Table 9). Similar to negative edge predictive models, lifetime reproductive effort was included in the positive edge response models

but was not significant. In the family random effect positive models the duration of the incubation and nesting period as well as region were insignificant in contrast to the models using species as the random effect.

Open-Forest Edge Type

The most important trait and adjustment variables in the open-forest predictive models were nest height and agricultural edge. The model for negative edge response was identical for open-forest edge type for both species and family random effects. In both cases, the odds of a negative edge response was 172.1 times higher for nests 3 m off the ground than for nests 15 m off the ground (10th versus 90th percentile). The odds of a negative edge response was 36.9 times more likely for non-agricultural focal habitat, and 4.6 times more likely for birds that utilize just open habitat rather than forest or both forest and open habitat. Common cowbird hosts was in the best model but was not significant (P = 0.432) though it was significant when considered individually (Table 5).

The predictive models for positive edge response for the open-forest edge type were similar for species or family as the random effect. A positive edge response was 9.3-10.9 times more likely for nests 15 m off the ground than for nests 3 m off the ground (90th versus 10th percentile) and for agricultural edges in comparison with non-agricultural edges. Lifetime reproduction and habitat utilization were both non-significant in the multi-trait models but significant when considered individually (Table 5).

Validation of Predictive Edge Models

Receiver Operating Characteristic (ROC) analysis was used to compare observed with predicted edge response in order to assess the predictive ability of the models. ROC

analysis provides the area under the ROC curve along with the S.E. and Confidence Intervals. Additionally, I calculated the sensitivity, specificity, and percent correct classification associated with a particular cut point (Table 11). Cut points along the logistic function were determined by maximizing the percent correctly classified.

ROC analyses indicated that the multi-trait models predict both positive and negative edge response in forest-open and open-forest edge types. The estimated area under the ROC curve ranged from 78.9-93.1% for the forest-open edge type, and between 87.3-89.9% for the open-forest edge type (Table 11, Figure 3, Figure 4). The percent of observations correctly classified for positive and negative edge predictive models ranged from 76-87% for the forest-open models to 82-89% for the open-forest models.

For the forest-open edge type, the species random effect contributed strongly to both positive and negative edge response models (Table 11). The models ranged from 81.5 to 86.7 % correct classification using species as a random effect, 77.9 to 78.2 % using family as a random effect, and 76.0 to 77.5 % using traits alone (Table 11). For the open-forest edge type, use of species and family random effect provided virtually identical results with the models including traits alone. That is, species and family information provides no added predictive ability in the open-forest edge type (Table 11).

Discussion

A number of previous studies have attempted to identify diagnostic features of species sensitive to habitat fragmentation and induced edges. However, this is the first attempt to model species' traits in a unified framework in order to develop *a priori* predictive models. The percent of observations correctly classified for the four

predictive, multi-trait models ranged from 75-86% and 82-89% for the forest-open and open-forest edge types respectively. As a result, these models may have the potential to provide general predictions how a given species will respond to edges without the need to document the effect of fragmentation for each species in each novel landscape.

To assess the efficacy of various traits for predicting positive and negative edge response, I evaluated traits as predictors individually as well as in combination with other traits to select the best predictive model. Many similarities were observed between these two approaches, the primary differences arising from redundant information when these traits are considered together. It is possible to assess the relative importance of each of the 12 traits using both of these approaches in order to judge which traits most accurately predict edge response for unstudied species in novel locations.

Habitat utilization was a significant predictor of edge response when considered by itself as well as in each of the four predictive models. Birds that are restricted to a focal habitat (whether forest or open) are more likely to show a negative edge response. For example, I found forest birds to show a more negative edge response in the forest-open edge type, similar with what has been found in other studies (Whitcomb et al. 1981, Germaine et al. 1997). Birds that use matrix habitat or use both matrix and focal habitat are more likely to show a positive edge response. For example, birds that utilize the open habitat, or both open and forest habitat, show more positive edge response in forest-open edge type.

Other studies have found species related with mesic habitat more likely to show a negative edge response (Whitcomb et al. 1981, Brand and George 2001). Similarly, I

found species that demonstrate obligate mesic habitat selection in the forest-open edge type more likely to show a negative edge response.

A number of studies have also shown foraging substrate to be predictive of edge response (Yahner 1995, DeGraaf 1992). I found similar relationships in the forest-open edge type, with bark foragers more likely to show a negative edge response and ground nesters more likely to show a positive edge response when included as a trait by itself. However, foraging substrate was not included in the multi-trait models.

Avian diet had some predictive ability with respect to edge response. Similar to other studies (Restrepo and Gomez 1998, Whitcomb et al. 1981), I found insectivores to show a more negative edge response in the forest-open edge type when considered individually, but diet was not included in the best model based on AICc criteria. I expected omnivores to show a more positive edge response in both edge types due to cross boundary subsidies (Fagan et al. 1999, Cantrell et al. 2001). I found this relationship in both edge types, but it was only statistically significant in forest-open edge.

A number of traits related with biotic interactions also were important predictors. I expected, a priori, a species to show a negative edge response if its nest substrate or height, nest type, duration of incubation and nesting period, or cowbird host frequency makes it more susceptible to predation or parasitism. While I expected evolved traits to generally improve fitness of birds at edges, decreased fitness at edges from certain traits related with biotic interactions may indicate vulnerability to an ecological trap (Gates and Gysel 1978).

The expected predictions for certain traits allow us to assess whether species with particular traits may be at greater risk of an ecological trap. For example, nest type was significantly related with edge response when used as a trait by itself (P=0.005), and marginally significant (p=0.126) in the predictive model – open nesting species were more likely to show a positive edge response than closed nesting species in the forest-open edge type. This observation was counter to what I hypothesized, and may result from increased shrub density at the edge that may provide greater nesting opportunities. However, since there is greater predation risk to open cup nests than closed nests, this may be an example of a trait that increases a species' susceptibility to an ecological trap at induced edges, and at agricultural edges in particular, where predation has been found to increase (Chalfoun et al. 2002).

The incubation plus nesting period was considered in each of the four candidate model sets. In the forest-open edge type, the duration of incubation + nesting period was not significant when considered by itself, but was highly significant when included with other traits in the predictive models based on AICc. In the multi-trait models, birds with longer incubation + nesting period were more likely to show a negative edge response. This result is consistent with other studies that have found decreased nesting period associated with higher predation/parasitism (Martin 1995). Since duration of the incubation and nesting period was not a significant predictor when considered individually, it seems to represent a secondary effect that becomes important only when the variability related with other traits is removed. In the open-forest edge type, the opposite result occurred – duration of incubation + nesting period was significant when considered individually but was not selected based on AICc criteria. When considered by

itself in the open-forest edge type, birds with shorter incubation and nesting period were more likely to show a negative edge response, and birds with a longer incubation and nesting period were more likely to show a positive edge response counter to previous studies (Martin 1995). Because increased exposure of eggs and young in the nest is expected to increase vulnerability to predation and parasitism, species with a positive edge response coupled with longer duration of the nesting period may be vulnerable to an ecological trap in the open-forest edge type.

I hypothesized that species that frequently serve as cowbird hosts would show negative edge response in both forest-open and open-forest edges. However, there was no relationship between cowbird host frequency and edge response in the forest-open edge type. When considered as a trait by itself in the open-forest edge type, common cowbird hosts were four times more likely to show a negative edge response than infrequent cowbird hosts. Cowbird host frequency was also included in the model predictive negative edge response in the open-forest edge type but was not significant.

Although migratory status has been found in other studies to be strongly related with sensitively to habitat fragmentation (Whitcomb et al. 1981), I did not find a strong relationship. I included migratory status in the global models for negative edge response in both edge types. When included as a trait by itself, I found that long distance migrants were 3 times more likely to show a negative edge response in the forest-open edge type. However, migratory status was not predictive as a trait by itself in the open-forest edge type and was not included in either of the multi-trait models.

I expected shrub nesters to show a net positive edge response in forest-open edge type based on environmental factors as well as biotic interactions (Flaspohler et al. 2001,

De Graaf 1992). Similarly, we found shrub nesters were more likely to show a positive edge response than ground and tree nesters both when considered as a trait by itself as well as in the predictive model.

I hypothesized a relationship between nest height edge response in the open-forest edge type. When included as a trait by itself as well as in the multi-trait models, I found higher nesting species more likely to show a positive edge response when compared with open habitat, and lower nesting species more likely to show a negative edge response when compared with the open habitat. This makes a lot of sense based on the available nesting substrate being higher in the forest edges than in the open habitat.

I hypothesized that two traits related with environmental variability, body mass and ecological plasticity, would be related to edge responses in the forest-open edge type. As expected based on previous studies (Lima 1986, Peters 1983, O'Connell et al. 1998, Whitcomb et al. 1981), I found smaller, more specialist species more likely to show a negative edge response both when considered as traits by themselves as well as in the multi-trait model. However, body mass was not found predictive of positive edge response. When considered as a trait by itself, more ecologically generalist birds were significantly more likely to show a positive edge response, but the trait was not included in the multi-trait model.

In terms of fitness consequences, I saw a different result with lifetime reproductive potential than expected. Previous studies found lower reproductive output near the edge (Gates and Gysel 1978, Whitcomb et al. 1981). In contrast, I found a higher probability of positive edge response for birds with greater lifetime reproduction. Conversely, birds with lower reproductive output in their lifetime were more likely to

show a negative edge response. It is possible that this result reflects compensation for the negative fitness consequences of nesting at the edge. It seems likely that there is some fitness advantage of nesting at the edge for particular species (increased nesting resources, increased food) but it is possible that across species, birds have evolved a positive edge response if their lifetime reproductive output is large enough to compensate for the increased predation / parasitism risk at the edge. As such, edges may play an important role in the life-history evolution of birds, possibly including variation in the nestling period, clutch size, number of broods, longevity, and in turn, lifetime reproductive output.

Traits hypothesized to be related with environmental factors, biotic interactions, environmental variability, and fitness consequences were important predictors of edge response. Traits related to positive and negative edge response in the forest-open edge type represent each of the four factors both when considered individually as well as in multi-trait models. In the open-forest edge type, I did not consider environmental variability to be a dominant factor, but the other three factors were represented in the positive or negative multi-trait models as well as in single-trait models. Though it is not possible to relate traits to specific mechanisms, these results suggest that multiple mechanisms are operating at edges.

Suding et al. (2003) classified traits according to two selection regimes: genetically hardwired traits resulting from selection over long time scales, and secondary, more plastic traits evolved over shorter time scales. Genetic and physiological constrained traits proposed by Suding et al. (2003) included morphology and physiology. Traits included in this category include lifetime reproductive effort, body mass, duration

of incubation and nesting period, migratory status, habitat utilization, and nest type. Traits proposed by Sudding et al. (2003) to be more plastic include response to biotic and abiotic constraints such as predators, parasites, microclimate, diet, and response to vegetation structure. Traits that fall under this category include cowbird host frequency, mesic habitat selection diet, nesting substrate or height, foraging substrate, and ecological plasticity. My predictive models include traits from both of these categories, implying that edge response is a function of both genetic hardwiring as well as secondary, more plastic traits, for which selection pressure probably occurs over both short and long times scales.

I considered three adjustment factors to account for intra-specific variability in edge response. None of the adjustment variables improved prediction of negative edge response in forest-open edge type. Both region and agricultural edges were significant when considered by themselves as predictors for positive edge response, but only region was included in the multi-trait model. In the open-forest edge type, agricultural edge was included both as a trait by itself as well as in the multi-trait model for both positive and negative edge response. Birds in non-agricultural matrix habitat were more likely to show a negative edge response, and birds in agricultural focal habitat were more likely to show a positive edge response. This may be due to higher habitat quality for most species in non-agricultural versus agricultural habitat, or to higher predation rates in forest/agriculture edges (Chalfoun et al. 2002).

I included random effects in order to account for the lack of independence in the edge response with respect to a given species' traits. Additionally, I wanted to determine whether the use of species or family random effects increases model fit compared with

models containing traits alone. I found that species generally improved model fit better than family, and family better than using traits alone in the forest-open edge type. In the open-forest edge type, there was no improvement in predictive ability by including the random effect.

Previous attempts to predict species' responses to habitat fragmentation based on easily parameterized models have been largely unsuccessful (Mac Nally and Bennett 1997, Mac Nally et al. 2000). The ability to make a priori predictions of a species likely response to edge habitats based soley on life-history and ecological traits of birds is a very powerful tool because these data are readily available in the literature, rather than requiring detailed, time-consuming studies of edge responses for each species in each habitat. This approach is useful for well studied taxa such as vertebrates where much background information is already available. I believe my results indicate the utility of a trait-based approach to modeling edge response in birds. The models I have developed should help prioritize conservation efforts where the time or resources to study each species in each habitat are lacking.

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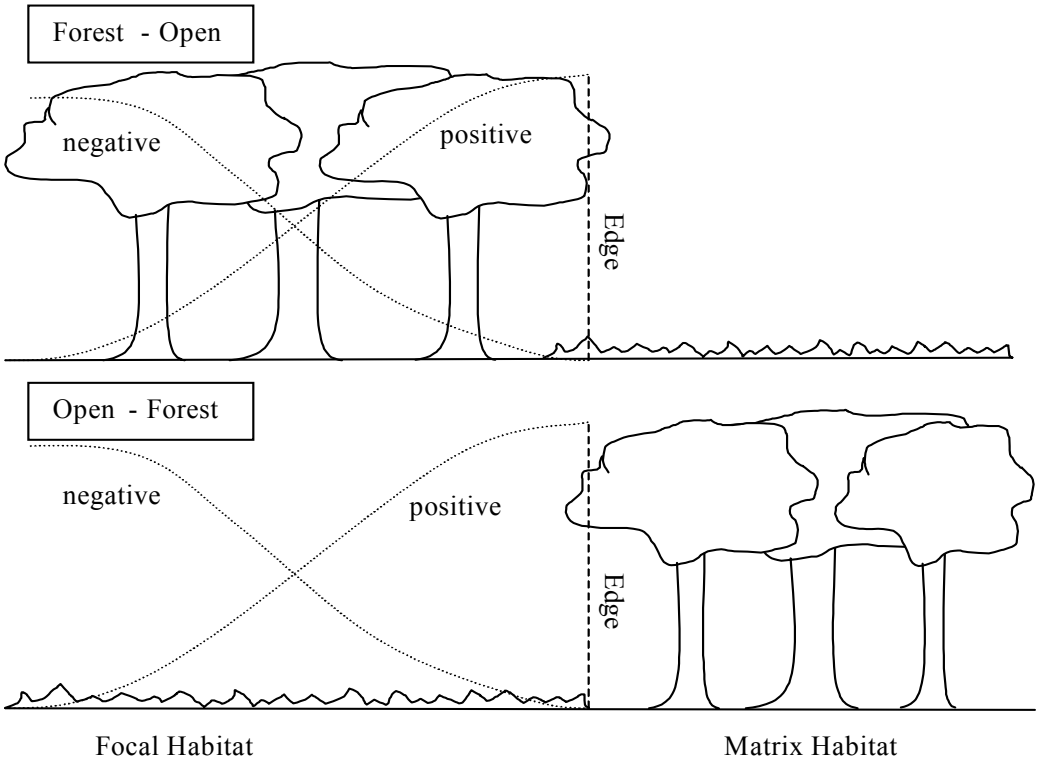
Forest - Open
negative
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Edge
Focal Habitat
Matrix Habitat

Figure 1. Positive and Negative Edge Response in Forest-Open and Open-Forest Edge Types

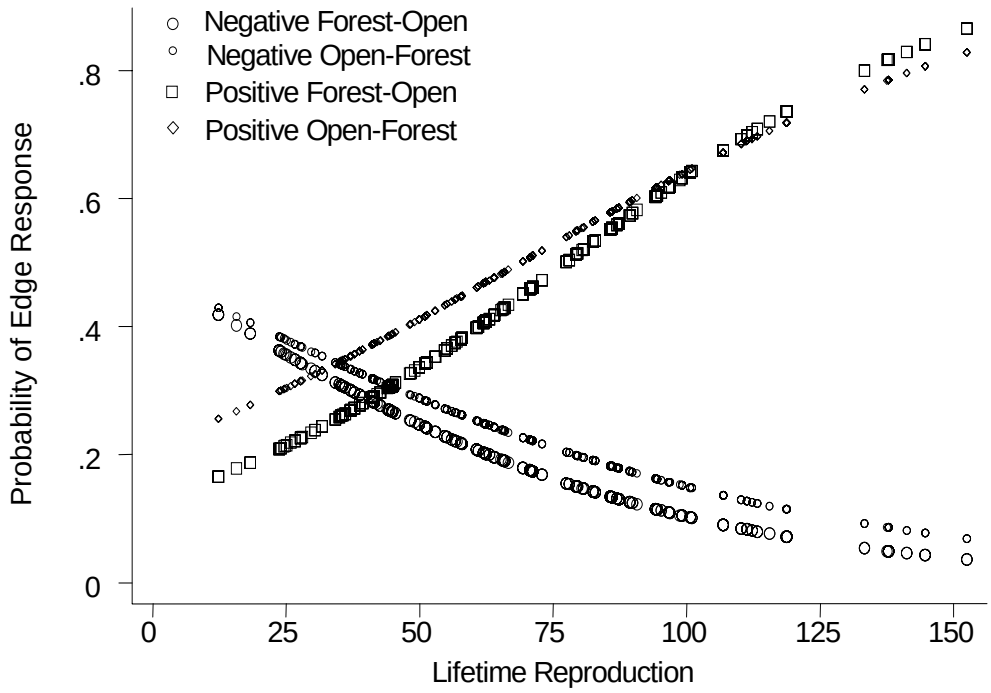

Figure 2. Probability of negative and positive edge response as a function of lifetime reproductive output in forest-open and open-forest edge types.

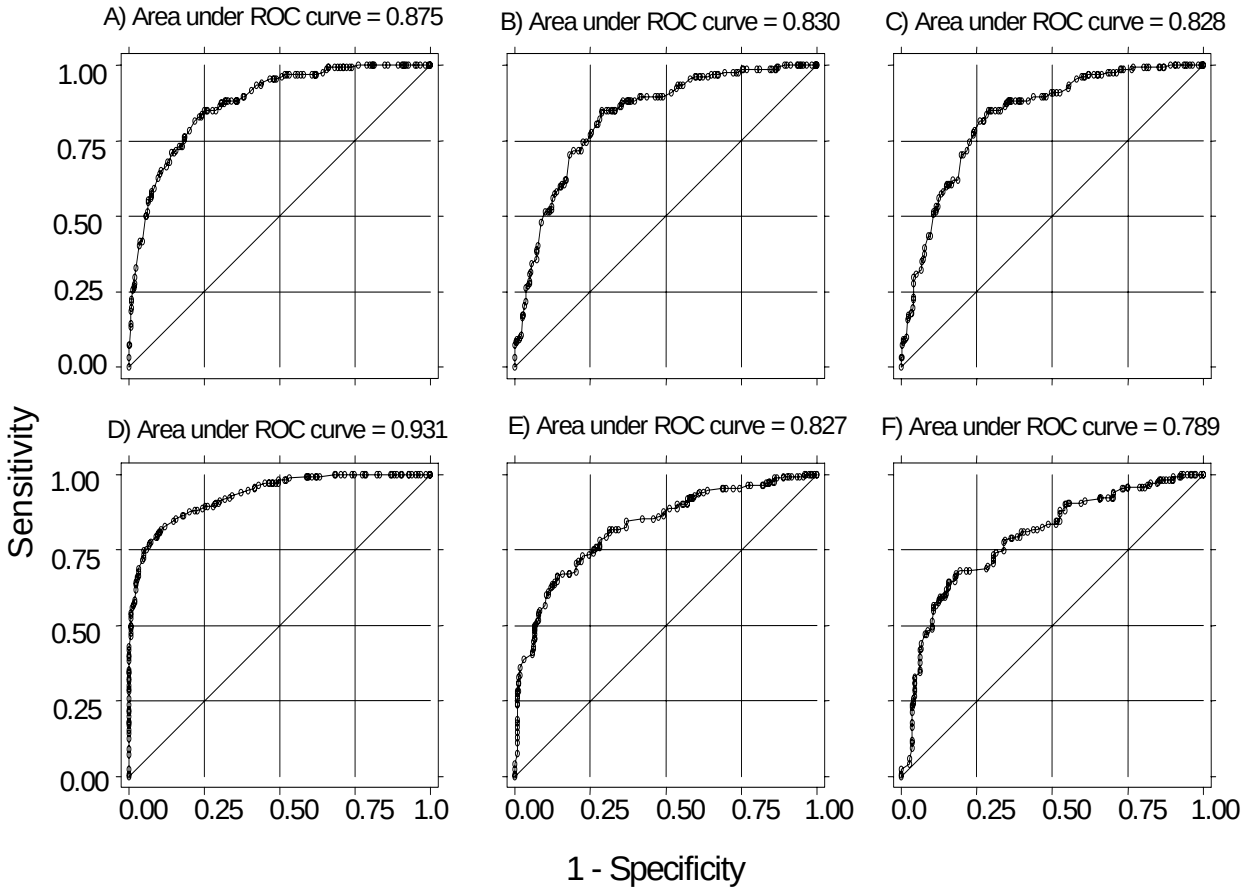

Figure 3. ROC analyses for Forest-Open Edge Type: Negative Edge Response with A) Species, B) Family and C) no Random Effect; Positive Edge Response with D) Species, E) Family, and F) no Random Effect.

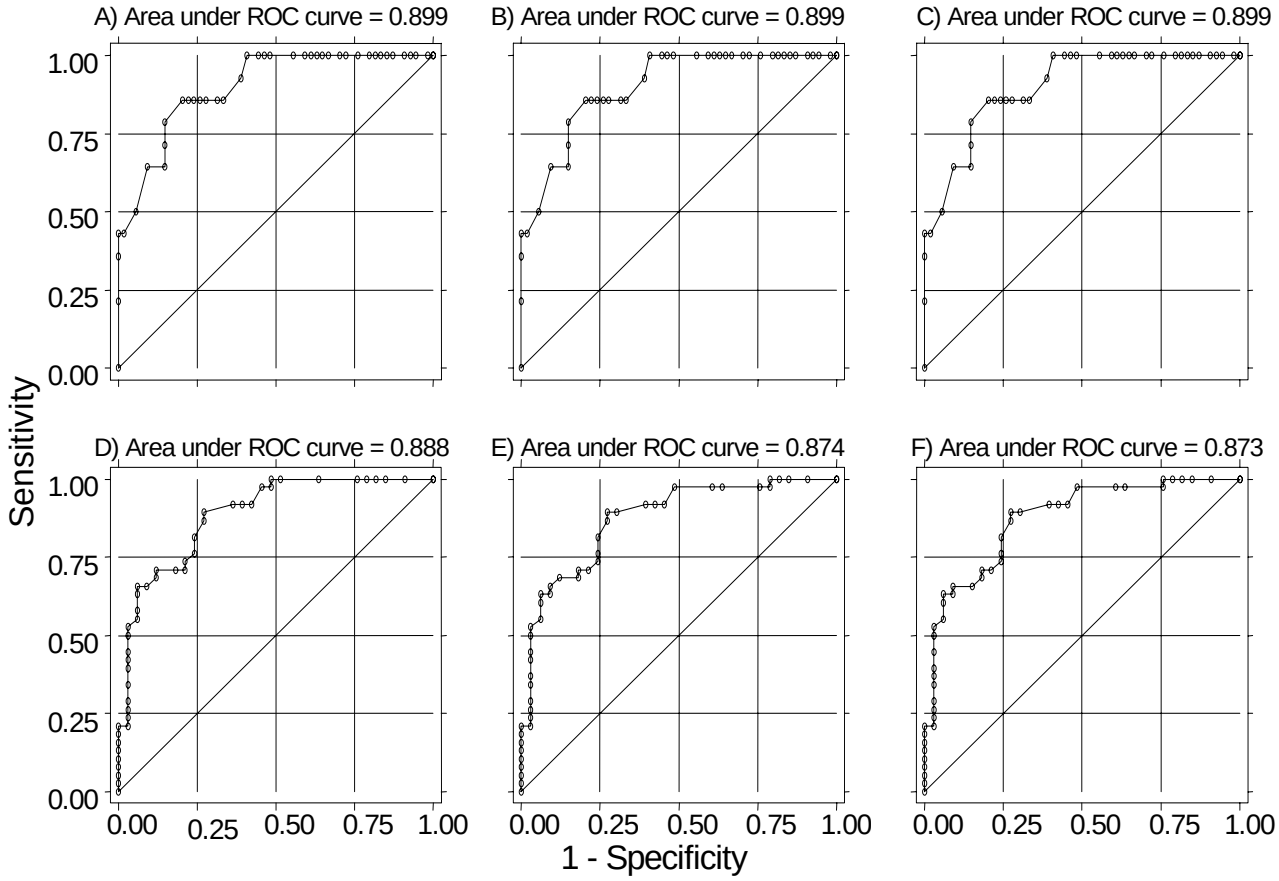

Figure 4. ROC analyses for Open-Forest Edge Type: Negative Edge Response with A) Species, B) Family, and C) no Random Effect; Positive Edge Response with D) Species, E) Family, and F) no Random Effect.

Table 1. Literature included in meta-analysis of avian response to edge.

Focal Habitat	Matrix Habitat	Location	Reference
deciduous forest	powerline corridor	Tennessee	Kroodsma 1984a
deciduous forest	clearcut	New Hampshire	King et al. 1997
coniferous forest	prairie, river, suburb powerline corridor	California	Brand and George 2001
mixed forest	clearcut	Texas	Lay 1938
deciduous forest	clearcut, agriculture	Wisconsin	Brittingham and Temple 1983
mixed forest	river	Maryland	Gates and Giffen 1991
deciduous forest	agriculture	Illinois	Johnston 1947
deciduous forest	agriculture	Michigan	Gates and Gysel 1978
deciduous forest	clearcut	Wisconsin	Flaspohler et al. 2001
deciduous forest	powerline corridor	Maryland	Chasko and Gates 1982
deciduous forest	agriculture, suburb	Maryland	Whitcomb et al. 1981
deciduous forest	road	Maine	Ferris 1979
deciduous forest	sapling	New Hampshire	DeGraaf 1992
deciduous forest	clearcut	Vermont	Germaine et al. 1997
deciduous forest	agriculture, marsh, powerline corridor	Florida	Noss 1991
deciduous forest	oldfield, crops, oldroad	Pennsylvania	Yahner 1995
deciduous forest	powerline corridor	Tennessee	Kroodsma 1982
deciduous forest	agriculture	Illinois	Marini et al. 1995
deciduous forest	road, powerline corridor	NewJersey	Rich et al. 1994
mixed forest	powerline corridor, river	Maine	Small and Hunter 1989
deciduous forest	river, road, clearcut, powerline corridor	Maryland	Evans and Gates 1997
oak woodlands	chaparral, grassland	California	Sisk et al. 1997
mixed forest, clearcut	clearcut, mixed forest	Texas	Strelke and Dickson 1980
coniferous forest	meadow, clearcut	Wyoming	Keller and Anderson 1992
pine barren	forest	Wisconsin	Niemuth and Boyce 1997
powerline corridor	deciduous forest	Tennessee	Kroodsma 1984a
powerline corridor	deciduous forest	Tennessee	Anderson et al. 1977
agriculture	deciduous forest	Illinois & Iowa	Best et al. 1990
powerline corridor	deciduous forest	Tennessee	Kroodsma 1987
grassland, chaparral	oak woodlands	California	Sisk and Margules 1993

Table 2. Selective agents occurring at edges with associated ecological / life-history traits

Selective Agents (mechanisms)	Ecological / Life-history Traits
Environmental Factors	Mesic habitat selection
	Foraging Substrate
	Diet
	Habitat Utilization
Biotic Interactions	Nest Type
	Incubation + Nesting period
	Cowbird host frequency
	Migratory Status
Environmental Factors and Biotic Interactions	Nest Substrate
	Nest Height
Stochastic Processes	Ecological Plasticity
	Body mass

Table 3. Ecological and life-history traits with predicted edge response in different edge types

Trait	Trait code	Level of trait (C vs. R)[1]	Edge type	Expected Odds Neg[2] (C vs. R)	Expected Odds Pos[3] (C vs. R)	Data Source [4]
Habitat Utilization	HU1	forest habitat (C) vs. open / both (R)	forest-open	greater	lesser	1, 2
	HU2	open habitat (C) vs. forest / both (R)	open-forest	greater	lesser	1, 2
Foraging Substrate	FS1	bark (C) vs. air / foliage / ground (R)	forest-open	lesser	NA	1
	FS2	ground (C) vs. air / foliage / bark (R)	forest-open	NA	greater	1
Diet	DI1	insectivore (C) vs. herb / omnivore (R)	forest-open	greater	NA	1
	DI2	omnivore (C) vs. herb / insectivore (R)	both	NA	greater	1
Mesic Habitat Selection	MH	obligate mesic (C) vs. non-obligate mesic (R)	forest-open	greater	NA	1, 2
Nest Height	NH	avg nest height: high (C) vs. low (R)	open-forest	lesser	greater	1
Nesting Substrate	NS	shrub (C) vs. tree /ground (R)	forest-open	NA	greater	1
Migratory Status	MS	long distance (C) vs. short dist or resident (R)	both	greater	NA	1, 2, 8
Nest Type	NT	open (C) vs. closed (R)	forest-open	NA	lesser	1
Time Inc + Nest	IN	days incubate + nest: long (C) vs. short (R)	both	greater	lesser	1, 9-20
Cowbird Host Frequenct	CH	common host (C) vs. rare host (R)	both	lesser	NA	1
Ecological Placticity	EP	index ranging from 4-13: high(C) vs. low (R)	forest-open	lesser	greater	1
Body mass	BM	body mass: high(C) vs. low (R)	forest-open	lesser	greater	3
Lifetime Reproduction	LR	clutch size x number of broods x longevity: high(C) vs. low (R)	both	lesser	greater	1, 4-7, 9-12, 21-33

[1] C = comparison category, R= reference category. For Binary variables, C vs. R categories indicated. For continuous variables, C is the higher level of the continuous variable, and R is the lower level of the continuous variable.

[2] Expected **Negative edge response:** the expected odds of being negative for the comparison category is (lesser or greater) than the odds of being negative for the reference category (or not used in candidate model set).

[3] Expected **Positive edge response**: the expected odds of being positive for the comparison categoriy is (less than or more than) the odds of being positive for the reference category.

[4] Data Source: 1. Ehrlich et al. 1988; 2. National Geographic Society 1992; 3. Dunning 1993; 4. Klimkiewicz and Futcher 1987; 5. Klimkiewicz et al. 1983; 6. Clapp et al. 1983; 7. Clapp et al. (1982); 8. Whitcomb et al. 1981.; 9. Conway 1999; 10. Robinson 1996; 11. Tenney 1997; 12. Rimmer and McFarland 1998; 13. Collins 1999; 14. Moldenhauer and Regelski 1996; 15. Greene et al. 1998; 16. Guinan et al. 2000 ; 17. George 2000; 18. Hopp et al. 1995; 19. Hall 1996; 20. Hamel 2000; 21. Davis 1995; 22. Rodewald and James 1996; 23. Williams 1996; 24. Morse 1994; 25. Morse 1993; 26. Richardson and Brauning 1995; 27. Pearson 1997, 28. Hall 1994; 29. Pitocchelli 1993; 30. Lowther 2000a; 31.Lowther 2000b; 32. Ingold and Wallace 1994; 33. Moskoff and Robinson 1996.

Table 4. Global models used in model selection to predict negative and positive edge response in two edge types

Edge type	Negative edge response		Positive edge response	
	Trait Description	**Code**	**Trait Description**	**Code**
Forest-open	Habitat Utilization 1	HU1	Habitat Utilization 1	HU1
	Time Incubate + Nest	IN	Time Incubate + Nest	IN
	Lifetime Reproduction	LR	Lifetime Reproduction	LR
	Migratory Status	MS	Body mass	BM
	Body mass	BM	Ecological Plasticity	EP
	Ecological Plasticity	EP	Nest Type	NT
	Diet 1	DI1	Diet 2	DI2
	Foraging Substrate 1	FS1	Nest Substrate	NS
	Cowbird Host Frequency	CH	Foraging Substrate 2	FS2
	Mesic Habitat Selection	MH		
Open-forest	Habitat Utilization 2	HU2	Habitat Utilization 2	HU2
	Time Incubate + Nest	IN	Time Incubate + Nest	IN
	Lifetime Reproduction	LR	Lifetime Reproduction	LR
	Migratory Status	MS	Nest Height	NH
	Cowbird Host Frequency	CH	Diet 2	DI2
	Nest Height	NH		

Table 5. Results of each trait included in the global models considered as a predictor of edge response by itself.

Trait	Coef.	S.E.	P-value	95% LCL	95% UCL	Reference [1]	Comparison [1]	Odds Ratio[1,2]
neg, f-o								
EP	-0.678	0.117	0.000	-0.907	-0.450	11	6	29.7
HU1	2.835	0.372	0.000	2.106	3.564	Open/Both	Forest	17.0
DI1	1.739	0.674	0.010	0.417	3.060	Herb/Omnivore	Insectivore	5.7
FS1	1.635	0.647	0.011	0.367	2.904	Air/Foliage/Ground	Bark	5.1
LR	-0.021	0.008	0.011	-0.037	-0.005	111.3	35.3	4.9
MH	1.306	0.536	0.015	0.255	2.357	Fac Mesic/Xeric	Oblig. Mesic	3.7
MS	1.147	0.431	0.008	0.303	1.992	Resident/Short dist	Long dist	3.2
BM	-0.013	0.005	0.014	-0.024	-0.003	80.2 grams	8.9 grams	2.5
IN	-0.025	0.034	0.466	-0.093	0.042	36 days	21 days	1.5
CH	0.249	0.426	0.559	-0.587	1.084	Rare	Common	1.3
pos, f-o								
EP	0.693	0.174	0.000	0.352	1.033	6	11	32.0
DI2	3.377	0.733	0.000	1.940	4.813	Herb/Insectivore	Omnivore	29.2
HU1	-3.204	0.607	0.000	-4.395	-2.014	Forest	Open/Both	24.6
NS	2.458	0.638	0.000	1.208	3.709	Ground/Tree	Shrub	11.7
LR	0.025	0.013	0.061	-0.001	0.051	35.3	111.3	6.7
NT	1.806	0.636	0.005	0.559	3.052	Closed	Open	6.1
FS2	1.455	0.713	0.041	0.057	2.852	Air/Bark/Foliage	Ground	4.3
BM	0.002	0.003	0.512	-0.004	0.007	8.9 grams	80.2 grams	1.2
IN	-0.016	0.037	0.672	-0.087	0.056	36 days	21 days	1.3
neg, o-f								
NH	-0.217	0.086	0.011	-0.385	-0.049	20 m	1.5 m	55.4
LR	-0.017	0.012	0.159	-0.040	0.006	133.3	41.5	4.8
HU2	1.499	0.736	0.042	0.056	2.941	Forest/Both	Open	4.5
IN	-0.316	0.145	0.029	-0.601	0.032	34 days	19.5 days	4.6
CH	1.481	0.880	0.093	-0.245	3.206	Rare	Common	4.4
MS	0.413	0.678	0.543	-0.916	1.742	Resident/Short dist	Long dist	1.5
pos, o-f								
NH	0.198	0.068	0.003	0.065	0.331	1.5 m	20 m	39.0
HU2	-1.870	1.119	0.095	-4.062	0.322	Open	Forest/Both	6.5
LR	0.019	0.011	0.097	-0.003	0.041	41.5	133.3	5.7
IN	0.115	0.062	0.064	-0.007	0.236	19.5 days	34 days	5.3
DI2	1.114	0.975	0.253	-0.797	3.026	Herb/Insect	Omnivore	3.1

[1] Odds ratio comparison vs. reference = $e^{\text{coef*unit difference between comparison and reference group}}$. The unit difference for a binary variable = ±1. The range used for continuous variables is 10th versus 90th percentile.

[2] Example interpretation of odds ratio: The odds of negative edge response for comparison group (Forest habitat utilization) = 17 times the odds of negative edge response for reference group (Open / both habitat utilization).

Table 6. Results of each trait included in the global models of the 4 candidate model sets considered individually.

Trait	Coef.	S.E.	P-value	95% LCL	95% UCL	Reference[1]	Comparison[1]	Odds Ratio[1]
neg, f-o								
AN	0.269	0.377	0.475	-0.469	1.008	Anthropogenic	Natural	1.31
AG	0.261	0.310	0.399	-0.346	0.868	Agricultural	Non-Agric	1.30
RE	0.227	0.424	0.593	-0.604	1.057	East	West	1.25
pos, f-o								
RE	-1.237	0.495	0.012	-2.208	-0.267	West	East	3.45
AG	-0.662	0.329	0.044	-1.307	-0.017	Non-Agric	Agricultural	1.94
AN	-0.070	0.402	0.861	-0.858	0.718	Natural	Anthropogenic	1.07
neg, o-f								
AG	2.736	1.320	0.038	0.148	5.324	Agricultural	Non-Agric	15.43
AN	-0.872	1.166	0.455	-3.158	1.414	Natural	Anthropogenic	2.39
RE	-0.276	1.233	0.823	-2.693	2.141	West	East	1.32
pos,o-f								
AG	-1.916	0.798	0.016	-3.480	-0.353	Non-Agric	Agricultural	6.79
AN	1.544	1.114	0.166	-0.639	3.727	Anthropogenic	Natural	4.68
RE	0.527	1.201	0.661	-1.828	2.882	East	West	1.69

[1] Odds ratio comparison vs. reference = $e^{\text{coef*unit difference between comparison and reference group}}$. The unit difference for a binary variable = ±1.

Table 7. Model selection results for forest-open edge type

model	num obs	num grps	log-lik	K	AICc	ΔAICc	w_i
Negative Edge Response							
HU1+MH+IN+EP+BM+LR	422	119	-192.14	8	400.63	0.00	0.182
HU1+CH+IN+EP+BM+LR	412	118	-192.93	8	402.22	1.59	0.082
HU1+MH+IN+LR+EP+BM+AN	422	119	-191.94	9	402.32	1.69	0.078
HU1+MH+IN+LR+EP+BM+RE	422	119	-192.01	9	402.45	1.82	0.073
HU1+MH+IN+LR+EP+BM+AG	422	119	-192.01	9	402.45	1.82	0.073
HU1+IN+EP+BM+LR	422	119	-194.23	7	402.72	2.09	0.064
HU1+MH+CH+IN+BM+LR	412	118	-193.27	8	402.90	2.27	0.059
HU1+MH+IN+BM+LR	422	119	-194.32	7	402.91	2.28	0.058
HU1+DI1+IN+EP+BM+LR	422	119	-193.59	8	403.53	2.90	0.043
HU1+MH+DI1+IN+BM+LR	422	119	-193.63	8	403.61	2.98	0.041
Positive Edge Response							
HU1+NS+DI2+IN+NT+LR+RE	412	118	-200.94	9	420.32	0.00	0.283
HU1+NS+DI2+IN+NT+LR	412	118	-202.61	8	421.57	1.25	0.151
HU1+NS+DI2+IN+NT+LR+AG	412	118	-201.91	9	422.27	1.95	0.107
HU1+DI2+IN+NT+LR	412	118	-204.10	7	422.48	2.16	0.096
HU1+DI2+IN+NT+BM+LR	412	118	-204.22	7	422.73	2.41	0.085
HU1+DI2+IN+NT+EP+LR	412	118	-203.54	8	423.43	3.11	0.060
HU1+NS+DI2+IN+NT+LR+AN	412	118	-202.53	9	423.50	3.18	0.058
HU1+DI2+FS2+IN+NT+LR	412	118	-204.06	8	424.48	4.16	0.035
HU1+NS+IN+NT+EP+LR	412	118	-204.79	8	425.94	5.62	0.017
HU1+NS+IN+NT+LR	412	118	-206.31	7	426.90	6.58	0.011
HU1+IN+NT+LR	412	118	-207.77	6	427.75	7.43	0.007

Table 8. Model selection results for open-forest edge type

model	num obs	num grps	log-lik	K	AIC_c	ΔAIC_c	w_i
			Negative Edge Response				
HU2+NH+CH+AG	68	35	-19.51	6	52.41	0.00	0.967
HU2+NH+CH	68	35	-25.86	5	62.68	10.27	0.006
HU2+NH+CH+LR	68	35	-24.68	6	62.74	10.33	0.006
HU2+NH+CH+IN	68	35	-25.04	6	63.46	11.05	0.004
HU2+NH+CH+IN+LR	68	35	-24.13	7	64.13	11.72	0.003
HU2+NH+CH+MS	68	35	-25.51	6	64.41	12.00	0.002
HU2+NH+CH+RE	68	35	-25.64	6	64.66	12.25	0.002
HU2+NH+CH+AN	68	35	-25.66	6	64.69	12.28	0.002
HU2+NH+CH+IN+MS	68	35	-24.47	7	64.80	12.39	0.002
HU2+NH+CH+MS+LR	68	35	-24.64	7	65.16	12.75	0.002
			Positive Edge Response				
HU2+NH+LR+AG	71	36	-32.13	6	77.56	0.00	0.953
HU2+LR+NH	71	36	-37.73	5	86.38	8.82	0.012
HU2+NH	71	36	-39.49	4	87.58	10.01	0.006
HU2+IN+LR+NH	71	36	-37.16	6	87.62	10.06	0.006
HU2+NH+LR+AN	71	36	-37.38	6	88.06	10.50	0.005
HU2+LR+NH+DI2	71	36	-37.56	6	88.42	10.86	0.004
HU2+NH+LR+RE	71	36	-37.60	6	88.52	10.96	0.004
HU2+IN+LR+NH+DI2	71	36	-36.65	7	89.08	11.52	0.003
HU2+IN+NH	71	36	-39.17	5	89.25	11.69	0.003
HU2+NH+DI2	71	36	-39.43	5	89.78	12.22	0.002

Table 9. Predictive Models for Positive and Negative Edge Response in Forest-Open edge type for both species and family random effects.

Trait	Coef.	S.E.	P-value	95% LCL	95% UCL	Reference[1]	Comparison[1]	Odds Ratio[3]
Negative Edge Response, Species Random Effect								
HU1	2.274	0.393	0.000	1.504	3.044	Open/Both	Forest	9.7
IN	0.106	0.036	0.003	0.035	0.177	21 days	36 days	4.9
EP	-0.211	0.103	0.041	-0.414	-0.008	11	6	2.9
MH	0.804	0.384	0.036	0.052	1.557	Xeric	Mesic	2.2
BM	-0.011	0.004	0.012	-0.020	-0.002	80.2 grams	8.9 grams	2.2
LR	0.006	0.006	0.361	-0.007	0.018	35.3	111.3	1.6
Negative Edge Response, Family Random Effect								
HU1	2.276	0.337	0.000	1.616	2.936	Open/Both	Forest	9.7
IN	0.101	0.032	0.001	0.038	0.163	21 days	36 days	4.5
EP	-0.175	0.083	0.035	-0.338	-0.013	11	6	2.4
MH	0.811	0.312	0.009	0.199	1.424	Xeric	Mesic	2.3
BM	-0.010	0.004	0.007	-0.018	-0.003	80.2 grams	8.9 grams	2.0
LR	0.008	0.005	0.166	-0.003	0.018	35.3	111.3	1.8
Positive Edge Response, Species Random Effect								
DI2	3.097	1.103	0.005	0.933	5.261	Insect/Herb	Omnivore	22.1
HU1	-2.690	0.594	0.000	-3.854	-1.525	Forest	Open/Both	14.7
IN	-0.095	0.054	0.078	-0.200	0.011	36 days	21 days	4.2
NS	1.296	0.738	0.079	-0.151	2.742	Tree/Ground	Shrub	3.7
NT	0.958	0.626	0.126	-0.268	2.184	Closed	Open	2.6
RE	-0.837	0.469	0.075	-1.757	0.831	West	East	2.3
LR	0.005	0.009	0.547	-0.012	0.023	35.3	111.3	1.5
Positive Edge Response, Family Random Effect								
HU1	-1.940	0.329	0.000	-2.584	-1.296	Forest	Open/Both	7.0
DI2	1.333	0.807	0.099	-0.249	2.914	Insect/Herb	Omnivore	3.8
NS	0.978	0.400	0.015	0.193	1.762	Tree/Ground	Shrub	2.7
NT	0.799	0.398	0.045	0.019	1.579	Closed	Open	2.2
IN	-0.035	0.037	0.338	-0.107	0.037	36 days	21 days	1.7
RE	-0.429	0.352	0.223	-1.119	0.261	West	East	1.5
LR	0.001	0.005	0.897	-0.010	0.011	35.3	111.3	1.1

[1] Odds ratio comparison vs. reference = $e^{\text{coef*unit difference between comparison and reference group}}$. The unit difference for a binary variable = ±1. The range used for continuous variables is 10th versus 90th percentile.

Table 10. Predictive Models for Positive and Negative Edge Response in Open-Forest edge type for both species and family random effects.

Trait	Coef.	S.E.	P-value	95% LCL	95% UCL	Reference[1]	Comparison[1]	Odds Ratio[1]
Negative Edge Response, Species Random Effect								
NH	-0.429	0.169	0.011	-0.760	-0.097	15 m	3 m	172.1
AG	-3.609	1.340	0.007	-6.236	-0.983	Agricultural	Non-Agric	36.9
HU2	1.536	0.937	0.101	-0.301	3.372	Forest/Both	Open	4.6
CH	0.831	1.058	0.432	-1.243	2.905	Rare	Common	2.3
Negative Edge Response, Family Random Effect								
NH	-0.429	0.169	0.011	-0.760	-0.097	15 m	3 m	172.1
AG	-3.609	1.340	0.007	-6.236	-0.983	Agricultural	Non-Agric	36.9
HU2	1.536	0.937	0.101	-0.301	3.372	Forest/Both	Open	4.6
CH	0.831	1.058	0.432	-1.243	2.905	Rare	Common	2.3
Positive Edge Response, Species Random Effect								
NH	0.199	0.074	0.007	0.054	0.344	3 m	15 m	10.9
AG	2.346	0.878	0.008	0.625	4.068	Non-Agric	Agricultural	10.4
LR	0.019	0.012	0.127	-0.005	0.043	41.5	133.3	5.5
HU2	-1.140	0.985	0.247	-3.070	0.789	Open	Forest/Both	3.1
Positive Edge Response, Family Random Effect								
NH	0.190	0.064	0.003	0.065	0.315	3 m	15 m	9.8
AG	2.227	0.741	0.003	0.775	3.679	Non-Agric	Agricultural	9.3
LR	0.018	0.011	0.107	-0.004	0.040	41.5	133.3	5.3
HU2	-1.028	0.839	0.221	-2.672	0.617	Open	Forest/Both	2.8

[1] Odds ratio comparison vs. reference = $e^{\text{coef*unit difference between comparison and reference group}}$. The unit difference for a binary variable = ±1. The range used for continuous variables is 10th versus 90th percentile for lifetime reproductive effort and 25th versus 75th percentile for nest height.

Table 11. ROC Analysis for 12 Predictive Models

	ROC Area	S.E.	95% LCL	95% UCL	Cut point	% Sensitivity	% Specificity	% Correctly Classified
				Forest-Open Edge Type				
Neg,Species	0.875	0.018	0.841	0.909	≥ 0.577	62.69	90.28	81.5
Neg, Family	0.830	0.021	0.790	0.871	≥ 0.461	70.15	81.94	78.2
Neg, Trait	0.828	0.021	0.787	0.869	≥ 0.461	57.46	86.81	77.5
Pos, Species	0.931	0.012	0.908	0.955	≥ 0.662	74.71	95.04	86.7
Pos,Family	0.827	0.021	0.786	0.868	≥ 0.698	66.47	85.95	77.9
Pos, Trait	0.789	0.023	0.744	0.834	≥ 0.646	64.12	84.30	76.0
				Open-Forest Edge Type				
Neg,Species	0.899	0.043	0.814	0.984	≥ 0.619	42.86	100.00	88.2
Neg, Family	0.899	0.043	0.815	0.982	≥ 0.619	42.86	100.00	88.2
Neg, Trait	0.899	0.043	0.814	0.984	≥ 0.619	42.86	100.00	88.2
Pos, Species	0.888	0.039	0.812	0.963	≥ 0.503	89.47	72.73	81.7
Pos,Family	0.874	0.042	0.792	0.956	≥ 0.394	89.47	72.73	81.7
Pos, Trait	0.873	0.042	0.791	0.955	≥ 0.378	89.47	72.73	81.7

EMPIRICAL VALIDATION OF A METHOD FOR PREDICTING SPECIES-SPECIFIC EDGE RESPONSE FOR BIRDS IN FORESTED LANDSCAPES

CHAPTER 2. Ph.D. Dissertation

DRAFT 1 (Submitted to Barry Noon)

by Arriana Brand

8/11/03

Abstract

In the face of rapid loss and fragmentation of habitat and limited research funding, there is not sufficient time and resources to study each species in each habitat for which conservation decisions need to be made. A predictive approach based on similarities in species' life-history and ecology is needed to predict the effects of habitat fragmentation on diverse communities. Côté and Reynolds (2002) suggest that in order for predictive models in conservation to be useful they need to be 1) easily parameterized and 2) generally applicable. Brand and Noon (in prep) have developed an easily parameterized set of models to predict edge response in a wide range of species in different landscapes utilizing ecological and life-history trait information obtained entirely from the literature. In order to assess the general applicability of these models, we have compared the predicted edge response of 25 species using models developed in a meta-analysis (Brand and Noon, in prep) with observed values obtained from field data collected for birds in the San Pedro River watershed. The observed edge responses were generated in a landscape different from that in which the models were developed, and thus serve to evaluate the robustness of the predictive models to novel locations/edge types. To estimate the predicted values, we classified the 25 most common San Pedro bird species as having a positive versus not-positive, and negative versus not-negative edge response using trait information from the literature, habitat variables from the study site, and fitted model coefficients of trait and environmental variables from a comprehensive meta-analysis. To obtain the observed edge response I used distance sampling (Buckland et al. 2002) to estimate density for each species in eight edge types, then used linear regression with site as a random effects to investigate species density as a function of distance from

habitat edge. The estimated slope coefficient of the regression equation, along with the p-value of the estimated slope parameter, was used to identify a species as positive, neutral, or negative edge response. Of 16 edge response / edge type combinations, the predictive models performed well in 7 cases (80-96% correct classification), adequate in 4 cases (64-76% correct classification), and poorly in 5 cases (29-55% correct classification). Generally the predictive models performed well for predicting negative edge response in both forest-open and open-forest edge types, adequately for positive edge response in the forest-open edge type, but poorly for positive edge response in the open-forest edge type. A logistic regression analysis was done to identify the environmental factors and trait variables associated with the correct classification of edge response. Results from these analyses provide guidance for the improvement of predictive edge models for application in novel landscapes / regions.

Introduction

Given the rapid loss, conversion, and fragmentation of habitat combined with limited resources available for research, it is not feasible to study each species in each habitat for which conservation decisions need to be made (Côté and Reynolds 2002, Mac Nally et al. 1997, 2000). While there are numerous studies that attempt to explain abundance or presense / absense of species based on patch size or distance from edge (Brand and George 2000, Germaine et al. 1997, King et al. 1997) there are very few studies that have attempted prediction beyond the sample in which the data were collected to novel species in novel landscapes (Kolar and Lodge 2002, Côté and Reynolds 2002). In order for the discipline of conservation biology to generate general principals for the protection of biological diversity, it must go beyond case-by-case studies of each species in each habitat (Mac Nally and Bennett 1997). The ability to reliably predict the impacts of habitat loss and fragmentation for many species in diverse environments is necessary to accelerate conservation planning and to identify conservation priorities (Côté and Reynolds 2002, MacNally and Bennett 1997).

Effectively irreversible decisions regarding land conversions are continually being made by land-management agencies and planning departments. For example, city and county planners decide the locations of roads and suburban developments, the U.S.D.A. Forest Service decides on the location of clear cuts or selective cutting stands, and The Nature Conservancy must decide which parcels of land to purchase and restore. Environmental consultants often have to write Environmental Impact Assessments (E.I.A.) that attempt to identify and report on the impacts of proposed developments. In these cases where decisions are made with short-term deadlines, it is seldom possible to

study all species that may be affected. Simple, straightforward guidelines are needed to predict the effects of, and discriminate among, alternative land use decisions to assist with the selection of the best size and spatial arrangement of remaining undeveloped land to maximize the benefits to biodiversity (Bright 1993).

Prediction of a species' response to induced or natural edges is a means to understand vulnerability to habitat loss and fragmentation that can be used pro-actively as a decision making tool for conservation planning. Anticipated edge response can help to decide the optimal size, shape and proximity of habitat types in order to minimize biodiversity loss for edge sensitive species. Given proposed changes in habitat configuration on the landscape, being able to predict the edge response of potentially affected species allows one to forecast whether one would expect that species to increase in abundance, remain the same, decline in abundance, or go locally extinct as a result of habitat change. Knowledge of a species' edge response can also be combined with GIS tools (e.g., Effective Area Model; Sisk et al. 1997) to forecast changes in species' abundance as a function of different habitat configurations.

For predictive models to be useful for conservation applications they need to be 1) easily parameterized and 2) generally applicable to novel locations (Côté and Reynolds 2002). Few attempts have been made to make species-specific predictions of the impacts of habitat fragmentation beyond the system in which the models were developed. For example, Lens et al. (2002) used fluctuating asymmetry to predict avian persistence in fragmented landscape which were highly predictive in the system in which the models were developed, but did not test more general predictions in novel locations and required 6 years of detailed field studies in order to parameterize. Mac Nally et al. (1997) used 3

relatively easily obtainable trait variables to parameterize their models, but found their models to have virtually no predictive power when applied to real systems (Mac Nally et al. 2000). Davies et al. (2000) identified traits of beetles that may predict local extinction in habitat fragments, but did not test their predictions in new locations. To date, there has been no means to predict vulnerability to habitat loss and fragmentation that meet the requirements for useful predictive models as set forth by Côté and Reynolds (2002).

In an effort to provide a tool to assist with conservation decisions, predictive models of edge response have been developed (Chapter 1). A set of *a priori* models pertaining to putative mechanisms occurring at edges was used to identify a relatively small number of ecological and life-history traits and environmental variables that may be predictive of avian edge response. A meta-analytic approach using a dataset in a wide set of species within different habitats and regions within the continental United States was then used to develop predictive models (Chapter 1). These models are parameterized utilizing readily-available ecological and life-history trait information obtained from published literature. My assumption is that ecological and life-history traits can be used in lieu of detailed studies of the edge response in each habitat to provide an efficient means to predict species-specific effects of habitat fragmentation for previously unstudied species in novel locations.

Empirical validation is needed to assess the general applicability of any predictive modeling approach. A robust validation should apply the predictive models to different environment / species set from that in which the predictive models were originally developed. The purpose of this paper is to 1) assess general applicability of the predictive models (described in Chapter 1) by comparing predicted edge response with

those observed by previously unstudied species in a desert riparian system fundamentally different from the temperate forests in which the predictive models were developed; 2) provide the quantitative tools needed for other researchers or managers to apply these models to other species / regions; and 3) identify environmental factors as well as species' traits that used as edge predictor variables to improve classification success.

Methods

Predicted Edge Response

A meta-analytic approach using data from 30 studies across North America (Chapter 1) was used to predict species-specific edge response for birds on the San Pedro River in southeastern Arizona. Four different models separately predict positive (versus not-positive) and negative (versus not-negative) edge response in forest-open and open-forest edge types. A forest-open edge is considered to occur from the edge into the forest interior, whereas an open-forest edge is considered to occur from the edge to the interior of "open" habitat such as grassland.

Ecological and Life-history Trait Database

Eleven life-history and ecological trait variables and two environmental variables selected with AICc model selection procedure (Burnham and Anderson 2002) were used to predict edge response in at least one of the predictive equations (Chapter 1, Table 1). A trait database containing these same variables was then developed for 25 bird species on the San Pedro River.

Three variables were derived from habitat descriptions in Ehrlich et al. (1988) and National Geographic (1992). First, habitat utilization was classified in two ways depending on edge type. For the forest-open edge type, habitat utilization was classified

as forest versus open or both forest and open habitat. For the open-forest edge type, habitat utilization was classified as open versus forest or both forest and open habitat. Second, bird species were classified according to their degree of mesic habitat selection. Bird species that use moist habitat exclusively were classified as obligate mesic in contrast to species that do not require exclusively mesic habitat. Third, an ecological plasticity index was based on a species' total number of common nest substrates, prey items, and foraging methods (Ehrlich et al. 1988) added to the number of habitat types used ranging from 1-5 (Ehrlich et al. 1988 and National Geographic 1992).

Diet, nest height, nest substrate, nest type, and cowbird host frequency were all classified as binary variables based on Ehrlich et al. (1988). Diet was classified as omnivore versus non-omnivore (herbivore or insectivore). Average nest height was taken as the average of minimum and maximum nest heights. Nesting substrate was classified as shrub versus non-shrub (tree or ground). Nest type was classified as open (cup or platform nests) or closed (cavity or pendant nests). Brown-headed cowbird host frequency was classified as common or rare based on Ehrlich et al. (1988). Where the information was lacking, cavity nesters were classified as rare cowbird hosts.

The length of the incubation and nestling period was obtained by adding the average number of incubation days to the average number of days for the nestling period. Information from Ehrich et al. (1988) was supplemented as needed for the Abert's Towhee, Lucy's Warbler, Lesser Goldfinch, Black-throated sparrow, and Gila Woodpecker (Watt and Willoughby 1999, Tweit and Finch 1994, Johnson et al. 1997). Because this information was not available in the above sources, the duration of the nestling period for the Gila Woodpecker, Lucy's Warbler, and Lesser Goldfinch was

obtained, respectively, by averaging the average nestling period for the six other *Melanerpes* woodpeckers, four other *Vermivora* warblers, and three other *Carduelis* goldfinches for which the nestling period was known from Ehrlich et al. (1988).

Body mass data were obtained for all 25 species from Dunning (1992). When separate means were presented for males and females, I took the average body mass. When body mass was reported from different geographic locations I used the value closest geographically to southeastern Arizona.

Lifetime reproductive effort was calculated as the product of average clutch size, number of broods per season, and longevity. Clutch size was estimated as the average of the range of clutch size for a given species (Ehrlich et al. 1988). The number of broods per season taken from Ehrlich et al. (1988) was supplemented for Abert's Towhee, Ash-throated Flycatcher, Brown-crested Flycatcher, Brown-headed Cowbird, Summer Tanager, and Yellow Warbler (Cardiff and Dittmann 2002, Lowther 1993, Robinson 1996, Tweit and Finch 1994, Cardiff and Dittmann 2000, Lowther et al. 1999). Longevity was obtained from published records (Klimkiewicz and Futcher 1987, Klimkiewicz et al. 1983, Clapp et al. 1983). Because the records were unavailable, longevity for Vermillion Flycatcher, Cassin's Kingbird, Lucy's Warbler, and Black-chinned Hummingbird was obtained, respectively, by averaging the longevity for the other species in the same genus: the 3 *Contopus* flycatchers, 2 *Tyrannus* kingbirds, 7 *Vermivora* warblers, and 1 *Archilochus* hummingbird for which the longevity was reported (Klimkiewicz and Futcher 1987, Klimkiewicz et al. 1983, Clapp et al. 1983).

In addition to the life-history and ecological trait variables, two environmental variables were classified for the study area based on predictive equations developed in

the meta-analysis (Chapter 1). The two environmental factors used in at least one of the predictive equations categorized habitat as agricultural versus non-agricultural, and the regions as east versus west. All habitat types on the San Pedro study area were classified as non-agricultural and western.

Predicting Probability of Edge Response

To calculate the probability of positive or negative edge response one needs first to determine the appropriate logistic regression equation. The appropriate prediction equation depends on the edge response (positive versus negative) and edge type (forest-open versus open-forest) being modeled. Each of the four prediction equations is written as a linear function of the relevant variables, coefficients, and random effects using the standard logit link function with the log odds as the outcome (McCullagh and Nelder 1989). The four prediction equations are provided in the Appendix. For example, the equation to predict negative edge response in forest-open edge type is:

$$\text{log odds} = \ln(p/(1-p)) \qquad \text{(eqn. 1)}$$

$$= B_0 + B_1 * HU1 + B_2 * IN + B_3 * EP + B_4 * MH + B_5 * BM + B_6 * LR + \text{random effect}$$

where,

p = probability of positive or negative edge response

B_0 , B_1 , B_2 , B_3 , B_4 , B_5 and B_6 are the coefficients, and

HU1, IN, EP, MH, BM, and LR are life-history and ecological traits variables (Table 1).

Given a prediction equation, numeric values are needed for the variables, coefficients, and random effects in order to calculate the log odds of positive or negative edge response. The coefficient for each variable, obtained in a meta-analysis, depends on the prediction equation and whether species or family was used as the random effect (Chapter 1) and is provided in the Appendix. The ecological and life-history trait variables were obtained from the literature, and the environmental variables from study site information. All life-history and ecological trait as well as environmental variables in the prediction equations were either continuous or binary. Continuous variables, such as body mass, took on the appropriate value from the literature depending on the species. Binary variables such as HU1 were coded either 0 or 1 (see Appendix for coding of binary variables). The random effect played the role of an offset, and depends on the species being modeled. If species or family was included in the meta-analysis (Chapter 1) then the numerical value for that random effect is available in the Appendix. However, if the species or family was not used in the meta-analysis, then the random effect information is not available and should be set to 0. Once all of the appropriate numeric values have been obtained, they are plugged into the above linear equation in order to calculate the log odds.

In order to estimate the probability of a positive or negative edge response, it is necessary to transform the log odds. Once the log of the odds has been calculated, it is a simple matter to transform that number to obtain the probability by the following:

$$p = (e^x / (e^x+1)) \qquad \text{(eqn. 2)}$$

where x = log odds.

The predicted probability of a negative or positive edge response is then compared with a cut point from the meta-analysis in order to predict a species' edge response (Chapter 1). Which cut point is appropriate depends on the edge type, edge response, and whether species, family or no random effect is used. These results are given in the Appendix. If the predicted probability of a negative edge response is greater than the cut point, then the prediction is negative. If the predicted probability of a negative edge response is less than the cut point, then the prediction is not-negative. The analogous process was used to predict positive versus not-positive edge response.

Observed Edge Response

In order to assess the general applicability of the predictive edge models on the San Pedro River, we estimated density as a function of distance from edge to identify the edge response of 25 species in 8 edge types. The desert riparian habitats contained within the San Pedro River were fundamentally different from the temperate forested regions in which the predictive models were developed, and thus serve as a robust validation of the predictive models.

Field Protocol

The upper and middle San Pedro River, including areas within the San Pedro Riparian National Conservation Area, provided an excellent opportunity to study natural edges between adjacent habitats and to test the predictive edge model. The San Pedro River has two primary associated zones of riparian vegetation extending perpendicular from the river to the surrounding desert scrub communities. First, a primary riparian zone consists of gallery forests dominated by Freemont cottonwood (*Populus fremontii*)

and Gooding willow (*Salix gooddingii*). A secondary riparian zone consists of mequite (*Prosopis* spp.) with sacaton grass (*Sporobolus wrightii*). In many areas along the river corridor distinct natural edges occur between the primary and secondary riparian and desert scrub communities.

Eight edge types are being investigated which represent both sides of a given edge. Forest-open edges represent the transition from the edge into the forest interior. Open-forest edges represent the transition from the edge into the adjacent "open" habitat. Four of the 8 edge types occur at the primary riparian to secondary riparian interface, including both sides of the edge where cottonwood is adjacent to mesquite, and both sides of the edge where cottonwood is adjacent to grassland. Two edge types occur between the secondary riparian habitats at both sides of the mesquite / grassland edge. Two edge types occur at the secondary riparian to non-riparian interface including both sides of the mesquite / desert scrub edge.

The edge types on the San Pedro River that most resemble those used to develop the predictive equations (Brand and Noon, in prep) were cottonwood adjacent to herbaceous, and herbaceous adjacent to cottonwood. In order to assess how robust the predictions are to edge types different from the meta-analysis, we also used novel edge types in this empirical validation of the predictive models. Mesquite is a unique habitat type limited to the southwest regions that does not fit nicely within the categorization of habitat as "forest" or "open" used in the meta-analysis. In this empirical validation, we classified mesquite as both forest and open, depending on what it was adjacent to. For example, when adjacent to cottonwood forest, mesquite is relatively shorter and was considered "open" habitat. When adjacent to grassland, mesquite is relatively taller, and

was considered to be forest habitat. Use of these novel edge types enables assessment of prediction robustness.

In order to estimate bird density across the different types of edges, a total 284 sampling locations were established on 23 sampling areas in the upper and middle reaches of the San Pedro River. Each sampling area consists of 11-14 point count locations on 2-3 transects. Points were located 100 m apart along the habitat gradient perpendicular from the river extending through primary riparian, to secondary riparian, to desert scrub vegetation communities. Points count locations occurring at varying distances from habitat edges are being used to construct edge response functions.

Each point represents the center of a variable circular plot of 60 m radius. Distance sampling was used at each variable circular plot. At each point, an observer mapped the location of each individual on field sheets representing a specific circular plot marked with cross-hairs at increments of 10 m. The distance and angle of each individual bird from the observer (i.e. point-center) was estimated by sight or sound with the aid of a Yardage Pro 400 Laser Rangefinder. Surveys were conducted from 10 minutes before sunrise until 3 hrs after sunrise.

Approximately 2,720 point count surveys were conducted during the 1998-2001 field seasons. Each point was visited between 6-14 times, and the survey effort was used to adjust density estimates in the analysis. A total of 10 observers conducted surveys during the 4 year study. In a given field season, two weeks training was done prior to beginning surveys on the survey techniques as well as the identification of birds by sight and sound. Within a given year, observers were rotated between sites so that each point count location was survey approximately the same number of times by each observer.

Distance Sampling Analysis

The distance from the observer to individual birds was used to estimate a detection function, which in turn, was used to estimate the density of birds for each point count location based on based on computational algorithms in program DISTANCE (Buckland et al. 1993). Since we wanted to obtain a per-point density estimate to use in modeling edge response functions, data were combined for a given species at a given point location for all visits within and between years. Differing number of visits to each point transect was accounted for by incorporating a survey effort multiplier in the Distance Sampling analysis. Between 5-15% of the data were truncated to eliminate heaping, depending on the pooled detection function observed for each species following the methods in Buckland et al. (1993).

Detection functions were allowed to vary by species and by habitat. In the most general case, detection functions for a given species may be allowed to vary by each of the 4 major habitat types: cottonwood, mesquite, grassland, and desert scrub. At the other extreme, all four habitats may be pooled to obtain a single detection function for a given species. Intermediate approaches to modeling the detection function included pooling two or more of the habitats. For example, when plant species composition differs but structure is similar, it may be more parsimonious to combine the detection functions from those two habitats. Candidate detection functions included 1) pooling desert with herbaceous and pooling cottonwood with mesquite, 2) pooling herbaceous, desert and mesquite separately from cottonwood, and 3) pooling desert and herbaceous with detection functions for mesquite and cottonwood modeled separately.

Another important aspect of modeling the detection function is rarity of a given species in a given habitat. Even common bird species such as the Yellow-breasted Chat that are abundant in primary riparian habitats may be rare in other habitat types such as desert scrub. When a particular species in a particular habitat type is rare, it may be necessary to pool the detection function across habitats. For example we might pool desert scrub with grassland for a given species that has low number of detections in one of those habitats. This procedure enables estimation of density for a given species / habitat combination with few detections by utilizing data from the same species but in other habitat types that are similar in terms of the detection function.

All candidate detection functions were run for each species. AIC model selection implemented within program DISTANCE 3.5 was used to select the best detection function for each species from which to estimate per point density for that species. This analysis was done for the 25 most common species across all habitats. The per-point density estimates was then used along with the distances from edges of point-transect locations to come up with the edge response functions.

Edge Response Functions

Edge response functions were implemented for 25 species in 8 edge types using linear regression with density as a function of distance from edge in Stata 7.0 (StataCorp 2002). Density of each species was estimated for each point transect location as described above. Distance of point count locations to the closest edge was based on differentially corrected UTM coordinates of points and edges obtained with a Trimble GSP unit accurate to 2-5 m, a classified image of the upper San Pedro (Watts et al. 1996), and field reconnaissance. The number of point count locations varied from 13 to 24

locations per edge type ranging from 0 m to 258 m into (check) interior habitat from the closest relevant edge. No overlapping "zero" points were used on either side of a given edge for the development of edge response functions (Ecology 86:3048-3059 find ref).

There were two complications with the linear regression analysis that were accounted for in the analysis methodology. First, there is a lack of independence in point count locations within sites which was addressed by using site as a random effect. Second, using standard error estimates associated with each density estimate obtained from Distance 3.5 increases the efficiency of the linear regression analysis (Greene 2000). However, it is not possible to use site as a random effect in the same analysis with the weighted least squares regression, since the statistical methods for this problem have not yet been developed (Greene 2000). As such, I used two different analysis methods, depending on the degree of site-to-site variability as indicated by the intra-class correlation coefficient (rho) obtained from the linear regression analysis with site as a random effect (Figure 1). When the estimated rho indicated that site-to-site variability was relatively important (rho > 0.15) I used site as a random effect and ignored the standard error estimates associated with each density estimate. When the estimated rho value indicated that site-to-site variability in density was unimportant (rho < 0.15) I used weighted least squares regression with standard error estimates associated with each density estimate as the weight ($1/SE^2$), and used site as a cluster to obtain robust standard error estimates and to account for the lack of dependence of point count locations within sites (StataCorp 2002). Because program Distance 3.5 provides a false 0 values for the standard error when the density is estimated to be 0, I obtained standard error estimates when density = 0 by doing a regression of standard error as a function of density,

excluding the zeros, for each species in each edge type, and used the y-intercept of the regression equation as the estimate of the standard error (R^2 ranged between 75-95%).

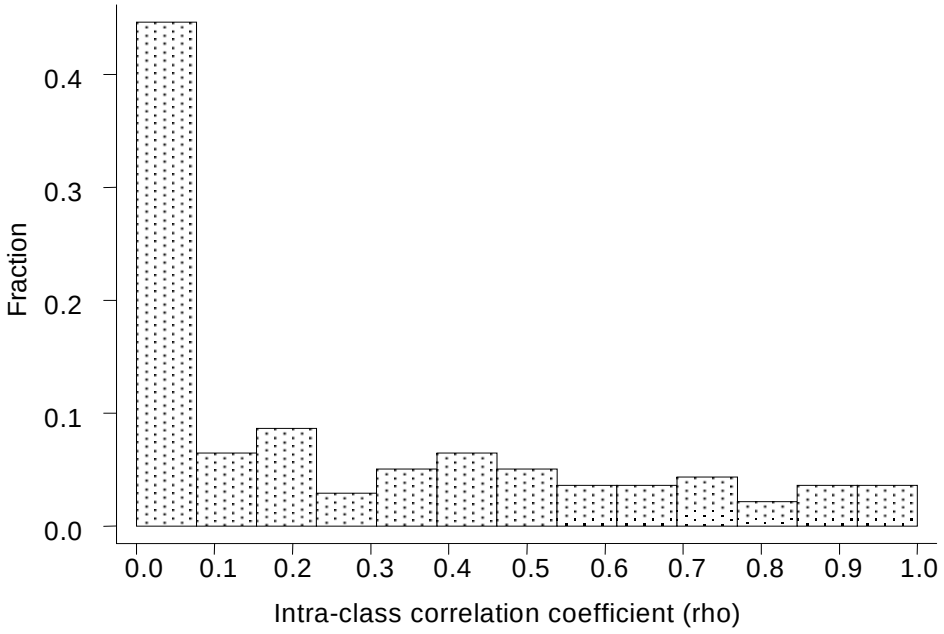

Figure 1. Intra-class correlation coefficient (rho) used in the determination of which analysis method to use.

Regardless of whether I used site as a random effect or weighted least squares regression to develop the edge response function, I used the slope coefficient of the regression equation along with the p-value of the estimated slope parameter in order to identify the edge response for each species. If the slope was positive and the p-value < 0.2, the edge response was categorized as negative (lower density at the edge than in the interior). If the slope was negative and the p-value was < 0.2, the edge response was categorized as positive (higher density at the edge than in the interior). If the p-value was

> 0.2, the edge response was categorized as neutral. Edge response was categorized for all species / edge type combination with > 3 non-zero density estimates at any distance from edge. For each species in each edge type, the positive, neutral, or negative edge response was then re-categorized as two binary variables: positive versus not-positive, and negative versus not-negative, in order to compare the observed with predicted edge response.

Comparison of Observed with Predicted

In order to empirically assess the validity of the predictive models, we compared the observed edge response of 25 species in 8 edge types on the San Pedro River with predicted edge response obtained from predictive equations and trait information obtained from the literature (Brand and Noon, in prep). I compared the observed with predicted edge response for each of the 4 sub-edge types in each of the forest-open and open-forest edge types. To compare with predicted edge response, I classified the observed edge response as negative vs. not-negative and positive versus not-positive. I then developed 2x2 tables for the 8 edge types for each of the predictive models (positive and negative) in order to calculate the % correctly classified as well as the number of observations (species) in each cell.

In order to better understand aspects of the predictive edge models that were successful, I then developed a binary variable to represent correct classification (correct vs. not-correct) and used logisitic regression to identify environmental and trait factors related with the probability of correct classification. I used both environmental factors (edge type, sub edge type, focal habitat, and matrix habitat) as well as the traits that were used in each of the predictive models. This analysis of the discrepancy between observed

and predicted is analogous to analysis of residuals in a linear regression context, and may be used to help identify the environmental factors and trait variables that were not as effective in applying the predictive models developed from datasets across North America to a novel dataset in a desert riparian system in southeastern Arizona.

Results

Observed Edge Response

Edge response was categorized as positive, neutral, or negative for 25 species in a total of 8 edge types using either weighted least squares linear regression or linear regression with site as a random effect (Tables 2-5). Of the 8 edge types, 4 represented forest-open edge type with cottonwood (Table 2) or mesquite as the focal habitat (Table 3), and 4 represented the open-forest edge type with cottonwood (Table 4) or mesquite as the matrix habitat (Table 5).

The edge responses observed for the open-forest edge type consisted primarily of neutral, with a fewer number of positive and negative responses. For the forest-open edge type with cottonwood as the focal habitat, 15% of the observed edge responses were negative, 20 % were positive, and 65% were neutral (Table 2).

Table 2. Observed Edge Response in Forest-Open Edge Type with Cottonwood focal habitat

	Cottonwood / Herbaceous					Cottonwood / Mesquite				
Species	Coef	S.E.	P-value	method	Edge Resp	Coef	S.E.	P-value	method	Edge Resp
ABTO	0.037	0.172	0.829	re	neutral	-0.046	0.268	0.863	re	neu
ATFL	0.147	0.138	0.311	wt	neu	-0.109	0.099	0.295	wt	neu
BEVI	*insufficient observations*					-0.286	0.295	0.332	re	neu
BEWR	0.075	0.162	0.645	re	neu	0.008	0.152	0.961	wt	neu
BCHU	0.087	0.167	0.613	wt	neu	-0.146	0.464	0.759	wt	neu
BTSP	*insufficient observations*					*insufficient observations*				
BLGR	-0.039	0.011	0.006	wt	pos	-0.148	0.075	0.049	re	pos

BCFL	-0.041	0.035	0.271	wt	neu	0.046	0.140	0.739	re	neu
BHCO	-0.159	0.090	0.109	wt	pos	-0.298	0.246	0.225	re	neu
BUOR	0.032	0.081	0.696	wt	neu	0.136	0.173	0.429	re	neu
CAKI	-0.017	0.020	0.426	wt	neu	0.115	0.170	0.496	re	neu
COYE	0.457	0.268	0.088	re	neg	0.348	0.391	0.373	re	neu
GIWO	-0.060	0.100	0.550	re	neu	0.249	0.161	0.123	re	neg
HOFI	0.015	0.090	0.879	re	neu	-0.111	0.129	0.392	re	neu
LEGO	-0.231	0.105	0.052	wt	pos	0.123	0.085	0.175	wt	neg
LUWA	0.084	0.256	0.742	re	neu	-0.569	0.238	0.038	wt	pos
MODO	-0.059	0.029	0.066	wt	pos	0.111	0.035	0.001	re	neg
NOCA	*insufficient observations*					-0.010	0.033	0.774	wt	neu
SOSP	-0.211	0.144	0.174	wt	pos	0.867	0.587	0.140	re	neg
SUTA	0.013	0.068	0.852	wt	neu	0.263	0.157	0.095	re	neg
VERD	0.013	0.032	0.678	re	neu	-0.034	0.019	0.102	wt	pos
VEFL	0.337	0.323	0.296	re	neu	0.638	0.226	0.018	wt	neg
WWDO	-0.012	0.080	0.883	re	neu	0.074	0.231	0.749	re	neu
YWAR	-0.330	0.493	0.503	re	neu	0.797	0.686	0.245	re	neu
YBCH	-0.144	0.266	0.588	re	neu	-0.760	0.275	0.006	re	pos

For the forest-open edge type with mesquite as the focal habitat, 13% of the observed edge responses were negative, 13 % were positive, and 74% were neutral (Table 3).

Table 3. Observed Edge Response in Forest-Open Edge Type with mesquite focal habitat

	Mesquite / Herbaceous					Mesquite / Desert Scrub				
Species	Coef	S.E.	P-value	method	Edge Resp	Coef	S.E.	P-value	method	Edge Resp
ABTO	0.094	0.084	0.313	wt	neu	0.253	0.079	0.008	wt	neg
ATFL	0.017	0.216	0.942	wt	neu	-0.001	0.194	0.994	wt	neu
BEVI	*insufficient observations*					0.239	0.240	0.319	re	neu
BEWR	0.232	0.190	0.223	re	neu	0.131	0.176	0.458	re	neu
BCHU	-0.476	0.282	0.092	re	pos	0.035	0.143	0.813	wt	neu
BTSP	-0.171	0.215	0.463	wt	neu	-0.662	0.170	0.002	wt	pos
BLGR	0.055	0.097	0.593	wt	neu	0.182	0.066	0.019	wt	neg
BCFL	-0.001	0.009	0.910	wt	neu	0.022	0.040	0.591	wt	neu
BHCO	-0.160	0.074	0.083	wt	pos	0.015	0.082	0.857	wt	neu
BUOR	*insufficient observations*					0.076	0.114	0.504	re	neu
CAKI	-0.016	0.006	0.062	wt	pos	0.025	0.023	0.288	wt	neu
COYE	0.027	0.027	0.320	re	neu	-0.011	0.061	0.861	re	neu
GIWO	0.001	0.052	0.982	re	neu	-0.041	0.047	0.382	re	neu
HOFI	-0.016	0.018	0.400	wt	neu	-0.187	0.090	0.037	re	pos

LEGO	0.004	0.004	0.299	wt	neu	0.062	0.074	0.400	re	neu
LUWA	-0.161	0.596	0.787	re	neu	0.970	0.520	0.089	wt	neg
MODO	-0.021	0.024	0.429	wt	neu	0.031	0.064	0.633	re	neu
NOCA	0.018	0.028	0.543	wt	neu	0.038	0.033	0.249	re	neu
SOSP	*insufficient observations*					0.046	0.043	0.281	re	neu
SUTA	0.078	0.058	0.235	wt	neu	0.045	0.077	0.567	wt	neu
VERD	0.089	0.070	0.259	wt	neu	0.042	0.051	0.426	wt	neu
VEFL	-0.045	0.026	0.140	wt	pos	0.008	0.007	0.303	wt	neu
WWDO	0.023	0.010	0.073	wt	neg	-0.011	0.008	0.202	wt	neu
YWAR	0.022	0.048	0.646	re	neu	0.011	0.015	0.477	wt	neu
YBCH	0.204	0.137	0.135	re	neg	0.386	0.182	0.034	re	neg

Compared with the forest-open edge type, the open-forest edge type with cottonwood matrix habitat had more positive edge responses but fewer negative and neutral edge responses. For the open-forest edge type with cottonwood as the matrix habitat, 8 % of the observed edge responses were negative, 35 % were positive, and 57 % were neutral (Table 4).

Table 4. Observed Edge Response in Open-Forest Edge Type with cottonwood matrix habitat

	Herbaceous / Cottonwood					Mesquite / Cottonwood				
Species	Coef	S.E.	P-value	method	Edge Resp	Coef	S.E.	P-value	method	Edge Resp
ABTO	-0.209	0.069	0.002	re	pos	-0.132	0.142	0.379	wt	neu
ATFL	-0.051	0.038	0.181	re	pos	0.047	0.030	0.151	wt	neg
BEVI	*insufficient observations*					0.042	0.158	0.789	re	neu
BEWR	-0.022	0.010	0.072	wt	pos	-0.165	0.137	0.260	wt	neu
BCHU	-0.123	0.051	0.053	wt	pos	0.032	0.169	0.853	wt	neu
BTSP	-0.016	0.008	0.067	re	pos	-0.046	0.074	0.540	re	neu
BLGR	-0.030	0.026	0.302	wt	neu	-0.057	0.073	0.435	re	neu
BCFL	-0.005	0.004	0.271	wt	neu	-0.053	0.072	0.462	re	neu
BHCO	-0.007	0.055	0.905	re	neu	-0.045	0.093	0.642	wt	neu
BUOR	-0.000	0.000	0.401	wt	neu	-0.111	0.025	0.002	wt	pos
CAKI	-0.017	0.027	0.563	wt	neu	-0.039	0.042	0.354	re	neu
COYE	-0.286	0.109	0.009	re	pos	-0.106	0.057	0.063	re	pos
GIWO	-0.028	0.013	0.070	wt	pos	-0.076	0.064	0.236	re	neu
HOFI	-0.016	0.012	0.219	wt	neu	-0.009	0.032	0.797	wt	neu
LEGO	0.012	0.013	0.383	wt	neu	-0.007	0.007	0.320	wt	neu
LUWA	-0.018	0.009	0.090	wt	pos	1.816	0.642	0.005	re	neg
MODO	-0.012	0.026	0.654	wt	neu	-0.002	0.024	0.925	wt	neu

NOCA	-0.004	0.011	0.702	re	neu	0.051	0.053	0.338	re	neu
SOSP	0.042	0.069	0.540	re	neu	-0.230	0.094	0.014	re	pos
SUTA	0.095	0.043	0.028	re	neg	0.042	0.039	0.300	wt	neu
VERD	0.017	0.011	0.164	wt	neg	-0.011	0.049	0.817	re	neu
VEFL	-0.160	0.069	0.021	re	pos	-0.028	0.036	0.468	wt	neu
WWDO	-0.042	0.012	0.015	wt	pos	-0.083	0.055	0.128	re	pos
YWAR	-0.032	0.020	0.162	wt	pos	-0.099	0.041	0.039	wt	pos
YBCH	-0.040	0.018	0.065	wt	pos	-0.192	0.228	0.398	re	neu

For the open-forest edge type with mesquite as the matrix habitat, 4 % of the observed edge responses were negative, 33 % were positive, and 63 % were neutral (Table 5).

Table 5. Observed Edge Response in Open-Forest Edge Type with mesquite matrix habitat

	Herbaceous / Mesquite					Desert Scrub / Mesquite				
Species	Coef	S.E.	P-value	method	Edge Resp	Coef	S.E.	P-value	method	Edge Resp
ABTO	-0.021	0.014	0.190	wt	pos	-0.011	0.005	0.054	wt	pos
ATFL	-0.091	0.038	0.017	re	pos	-0.125	0.056	0.026	re	pos
BEVI	-0.009	0.024	0.712	re	neu	-0.003	0.002	0.242	wt	neu
BEWR	-0.050	0.033	0.142	re	pos	-0.009	0.006	0.142	wt	pos
BCHU	*insufficient observations*					-0.110	0.209	0.599	re	neu
BTSP	-0.073	0.031	0.058	wt	pos	0.005	0.101	0.961	re	neu
BLGR	0.068	0.069	0.328	re	neu	-0.023	0.012	0.084	wt	pos
BCFL	*insufficient observations*					-0.023	0.022	0.296	re	neu
BHCO	-0.025	0.020	0.263	wt	neu	0.009	0.033	0.782	re	neu
BUOR	-0.017	0.034	0.619	re	neu	-0.034	0.015	0.048	wt	pos
CAKI	-0.029	0.042	0.488	re	neu	-0.017	0.013	0.184	re	pos
COYE	0.006	0.022	0.777	re	neu	0.001	0.028	0.976	wt	neu
GIWO	-0.014	0.007	0.085	wt	pos	-0.011	0.022	0.607	re	neu
HOFI	-0.061	0.029	0.081	wt	pos	0.039	0.023	0.106	wt	neg
LEGO	0.041	0.037	0.314	wt	neu	-0.005	0.006	0.401	wt	neu
LUWA	-0.069	0.050	0.218	wt	neu	-0.177	0.084	0.036	re	pos
MODO	0.016	0.036	0.674	wt	neu	-0.012	0.021	0.559	re	neu
NOCA	0.003	0.029	0.918	re	neu	0.040	0.013	0.003	re	neg
SOSP	*insufficient observations*					*insufficient observations*				
SUTA	0.028	0.035	0.464	wt	neu	-0.062	0.046	0.174	wt	pos
VERD	0.022	0.048	0.643	re	neu	0.026	0.034	0.434	re	neu
VEFL	-0.050	0.133	0.710	re	neu	-0.001	0.001	0.368	wt	neu
WWDO	-0.024	0.024	0.324	re	neu	-0.010	0.011	0.360	re	neu
YWAR	-0.002	0.007	0.809	wt	neu	-0.004	0.004	0.324	wt	neu
YBCH	-0.029	0.062	0.637	re	neu	-0.017	0.011	0.170	wt	pos

Predicted Edge Response

Using the logistic regression equation to predict a negative (versus not-negative) edge response in forest-open edge type, none of the 25 species were predicted to have a negative edge response.

Table 3. Negative Forest-Open Edge Response Predictions

Species	Random Effect	HU1[2]	IN	EP	MH[2]	BM	LR	Prob	Cutpoint	Edge Response
ABTO	family	O/B	26.5	8	**FM/X**	46	60.1	0.078	0.461	not-neg
ATFL	family	O/B	30	9	FM/X	27.2	22.1	0.084	0.461	not-neg
BEVI	family	O/B	25.5	6	FM/X	8.5	55.3	0.134	0.461	not-neg
BEWR	species	O/B	27	9	FM/X	9.9	45.5	0.076	0.577	not-neg
BCHU	family	O/B	35.5	9	FM/X	3.4	25.0	0.173	0.461	not-neg
BTSP	family	O/B	21.3	8	FM/X	13.5	42.0	0.058	0.461	not-neg
BLGR	species	O/B	21	9	FM/X	28.4	47.3	0.035	0.577	not-neg
BCFL	family	O/B	30.5	10	FM/X	43.8	36.0	0.071	0.461	not-neg
BHCO	species	O/B	22	10	FM/X	43.9	71.3	0.028	0.577	not-neg
BUOR	family	O/B	26	9	FM/X	33.8	29.6	0.057	0.461	not-neg
CAKI	family	O/B	35	8	FM/X	45.6	58.9	0.165	0.461	not-neg
COYE	species	O/B	22	9	FM/X	10.1	79.3	0.045	0.577	not-neg
GIWO	family	O/B	41.8	8	FM/X	64.9	67.8	0.256	0.461	not-neg
HOFI	family	O/B	28	11	FM/X	21.4	104.3	0.095	0.461	not-neg
LEGO	family	O/B	25.5	8	FM/X	9.5	51.0	0.095	0.461	not-neg
LUWA	family	O/B	21.6	7	FM/X	6.6	58.5	0.084	0.461	not-neg
MODO	species	O/B	26.5	11	FM/X	119	96.7	0.021	0.577	not-neg
NOCA	species	O/B	22	9	FM/X	44.7	137.8	0.049	0.577	not-neg
SOSP	species	O/B	23.5	8	OM	20.8	99.2	0.141	0.577	not-neg
SUTA	species	F	21	10	FM/X	28.2	48.0	0.183	0.577	not-neg
VERD	none	O/B	31	9	FM/X	6.8	50.3	0.135	0.532	not-neg
VEFL	family	O/B	29.5	6	FM/X	14.4	37.5	0.160	0.461	not-neg
WWDO	family	O/B	28	8	FM/X	153	108.8	0.045	0.461	not-neg
YWAR	family	O/B	22	9	OM	9.5	40.1	0.113	0.461	not-neg
YBCH	species	O/B	19	6	OM	25.3	62.4	0.112	0.577	not-neg

HU1 (Habitat Utilization) O/B = open/both, F=forest; MH (Mesic Habitat Selection) FM/X = facultative mesic/xeric; OM=obligate mesic.

Using the appropriate equation to predict a positive (versus not-positive) edge response in forest-open edge type, we predicted that 9 of 25 species had a positive edge response (36%).

Table 4. Positive Forest-Open Edge Response Predictions

Species	Random Effect	HU1	DI	IN	NS	NT	LR	RE	Prob	Cutpoint	Edge Response
ABTO	family	O/B	H/I	26.5	S	O	60.1	W	0.818	0.662	pos
ATFL	family	O/B	H/I	30	T/G	C	22.1	W	0.230	0.662	not-pos
BEVI	family	O/B	H/I	25.5	S	O	55.3	W	0.176	0.662	not-pos
BEWR	species	O/B	H/I	27	T/G	C	45.5	W	0.125	0.698	not-pos
BCHU	family	O/B	H/I	35.5	T/G	O	25.0	W	0.427	0.662	not-pos
BTSP	family	O/B	H/I	21.3	S	O	42.0	W	0.842	0.662	pos
BLGR	species	O/B	H/I	21	S	O	47.3	W	0.916	0.698	pos
BCFL	family	O/B	H/I	30.5	T/G	C	36.0	W	0.229	0.662	not-pos
BHCO	family	O/B	H/I	22	T/G	O	71.3	W	0.775	0.662	pos
BUOR	family	O/B	H/I	26	T/G	C	29.6	W	0.567	0.662	not-pos
CAKI	family	O/B	H/I	35	T/G	O	58.9	W	0.364	0.662	not-pos
COYE	species	O/B	H/I	22	S	O	79.3	W	0.951	0.698	pos
GIWO	family	O/B	O	41.8	T/G	C	67.8	W	0.590	0.662	not-pos
HOFI	family	O/B	H/I	28	T/G	O	104.3	W	0.655	0.662	not-pos
LEGO	family	O/B	H/I	25.5	T/G	O	51.0	W	0.666	0.662	pos
LUWA	family	O/B	H/I	21.6	T/G	C	58.5	W	0.380	0.662	not-pos
MODO	species	O/B	H/I	26.5	T/G	O	96.7	W	0.717	0.698	pos
NOCA	species	O/B	H/I	22	S	O	137.8	W	0.693	0.698	not-pos
SOSP	species	O/B	H/I	23.5	T/G	O	99.2	W	0.867	0.698	pos
SUTA	species	F	H/I	21	T/G	O	48.0	W	0.662	0.698	not-pos
VERD	none	O/B	H/I	31	S	C	50.3	W	0.516	0.646	not-pos
VEFL	family	O/B	H/I	29.5	T/G	O	37.5	W	0.406	0.662	not-pos
WWDO	family	O/B	H/I	28	T/G	O	108.8	W	0.608	0.662	not-pos
YWAR	family	O/B	H/I	22	t/g	O	40.1	W	0.570	0.662	not-pos
YBCH	species	O/B	H/I	19	S	O	62.4	W	0.938	0.698	pos

2 HU1 (Habitat Utilization) O/B = open/both, F=forest; DI (Diet) H/I=herbivore/insectivore, O=omnivore; NS (Nest Substrate) T/G=tree/ground, S =shrub; NT (Nest Type) C=closed, O=open; RE (Region) E=east, W= west.

Using the appropriate equation to predict a negative (versus not-negative) edge response in open-forest edge type, we predicted that 3 of 25 species had a negative edge response (12%).

Table 5. Negative Open-Forest Edge Response Predictions

Species	**Random Effect**	HU2	NH	CH	AG	prob	cutpoint	edgeresp
ABTO	family	F/B	5	C	NA	0.297	0.619	not-neg
ATFL	family	F/B	11.5	R	NA	0.011	0.619	not-neg
BEVI	family	F/B	3	C	NA	0.499	0.619	not-neg
BEWR	family	F/B	10	R	NA	0.021	0.619	not-neg
BCHU	none	F/B	6	R	**NA**	0.107	0.619	not-neg
BTSP	family	O	1	R	NA	0.826	0.619	neg
BLGR	species	F/B	7.5	C	NA	0.127	0.619	not-neg
BCFL	family	F/B	17.5	R	NA	0.001	0.619	not-neg
BHCO	family	F/B	7.5	C	NA	0.127	0.619	not-neg
BUOR	family	F/B	22.5	R	NA	0.000	0.619	not-neg
CAKI	family	F/B	37.5	R	**NA**	0.000	0.619	not-neg
COYE	species	O	1.5	C	NA	0.898	0.619	neg
GIWO	family	F/B	22.5	R	NA	0.000	0.619	not-neg
HOFI	family	F/B	20	C	NA	0.001	0.619	not-neg
LEGO	family	O	16	R	NA	0.008	0.619	not-neg
LUWA	family	F/B	7	R	NA	0.073	0.619	not-neg
MODO	none	F/B	20	R	**NA**	0.000	0.619	not-neg
NOCA	family	F/B	8	C	NA	0.105	0.619	not-neg
SOSP	species	F/B	1.5	C	NA	**0.655**	0.619	neg
SUTA	family	F/B	22.5	R	NA	0.000	0.619	not-neg
VERD	none	O	11	R	NA	0.061	0.619	not-neg
VEFL	family	F/B	14	R	NA	0.004	0.619	not-neg
WWDO	none	F/B	14.5	R	**NA**	0.003	0.619	not-neg
YWAR	family	F/B	7.5	C	NA	0.127	0.619	not-neg
YBCH	species	F/B	3	C	NA	0.499	0.619	not-neg

2 HU2 (Habitat Utilization) F/B= forest/both, O=open; CH (Cowbird Host Frequency) C=common, R=rare; AG (Agricultural) A=agricultural, NA=non-agricultural

Using the appropriate equation to predict a positive (versus not-positive) edge response in open-forest edge type, we predicted that 11 of 25 species had a positive edge response (44%).

Table 6. Positive Open-Forest Edge Response Predictions

Species	Random Effect	HU2	NH	LR	AG	Prob	Cutpoint	Edge Response
ABTO	family	F/B	5	60.1	NA	0.212	0.394	not-pos
ATFL	family	F/B	11.5	22.1	NA	0.318	0.394	not-pos
BEVI	family	F/B	3	55.3	NA	0.145	0.394	not-pos
BEWR	family	F/B	10	45.5	NA	0.349	0.394	not-pos
BCHU	none	F/B	6	25.0	NA	0.139	0.378	not-pos
BTSP	family	O	1	42.0	NA	0.032	0.394	not-pos
BLGR	species	F/B	7.5	47.3	NA	0.196	0.503	not-pos
BCFL	family	F/B	17.5	36.0	NA	0.653	0.394	pos
BHCO	species	F/B	7.5	71.3	NA	0.310	0.503	not-pos
BUOR	family	F/B	22.5	29.6	NA	0.812	0.394	pos
CAKI	family	F/B	37.5	58.9	NA	0.992	0.394	pos
COYE	species	O	1.5	79.3	NA	0.061	0.503	not-pos
GIWO	family	F/B	22.5	67.8	NA	0.896	0.394	pos
HOFI	family	F/B	20	104.3	NA	0.912	0.394	pos
LEGO	family	O	16	51.0	NA	0.398	0.394	pos
LUWA	family	F/B	7	58.5	NA	0.277	0.394	not-pos
MODO	none	F/B	20	96.7	NA	0.908	0.378	pos
NOCA	species	F/B	8	137.8	NA	0.712	0.503	pos
SOSP	species	F/B	1.5	99.2	NA	0.192	0.503	not-pos
SUTA	family	F/B	22.5	48.0	NA	0.858	0.394	pos
VERD	none	O	11	50.3	NA	0.183	0.378	not-pos
VEFL	family	F/B	14	37.5	NA	0.498	0.394	pos
WWDO	none	F/B	14.5	108.8	NA	0.806	0.378	pos
YWAR	family	F/B	7.5	40.1	NA	0.232	0.394	not-pos
YBCH	species	F/B	3	62.4	NA	0.132	0.503	not-pos

HU2 (Habitat Utilization) F/B= forest/both, O=open; AG (Agricultural) A=agricultural, NA=non-agricultural.

Comparison of Observed with Predicted Edge Response

To compare observed with predicted edge response, I tabulated the number of species within each of the 8 edge types that were correctly classified (observed as well as predicted negative, and observed as well as predicted not-negative) or incorrectly classified (observed negative but predicted not-negative, and observed not-negative but predicted negative; Table 7). The analogous table was done for the positive as well as the negative predictive model (Table 7). Of 16 edge response / edge type combinations, the predictive models did an excellent job in 7 cases (80-96% correct classification), a good job in 4 cases (64-76% correct classification), and a poor job in 5 cases (29-55% correct classification). Generally the predictive models did an excellent job for the negative edge response in both forest-open and open-forest edge types, a good job for the positive edge model in the forest-open edge type, but did a poor job in the positive open-forest (Table 7).

Table 7. Percent Correctly classified for negative and positive edge predictive models in forest-open and open-forest sub-edge types

edge type	obs not-neg / pred not-neg	obs not-neg/ pred neg	obs neg / pred not-neg	obs neg/ pred neg	% correctly classified
forest-open					
CH	21	0	1	0	95.5
CM	18	0	6	0	75.0
MH	20	0	2	0	90.9
MD	21	0	4	0	84.0
open-forest					
HC	19	3	2	0	76.0
MC	20	3	2	0	80.0
HM	20	2	0	0	90.9
DM	20	2	2	0	83.3
edge type	obs not-pos / pred not-pos	obs not-pos/ pred pos	obs pos / pred not-pos	obs pos/ pred pos	% correct classification
forest-open					
CH	14	3	0	5	86.4
CM	14	6	2	2	66.7
MH	11	7	3	1	54.6
MD	15	8	1	1	64.0

	open-forest				
HC	4	8	9	3	29.2
MC	11	9	3	2	52.0
HM	8	8	4	2	45.5
DM	7	8	6	3	41.7

Environmental Factors

I used logistic regression to identify the environmental factors associated with incorrect classification. Four environmental factors were each considered as predictors by themselves: edge type (forest-open vs open-forest), sub edge type (each of the 8 specific edge types), and focal or matrix habitat (cottonwood, herbaceous, mesquite or desert scrub).

There was no difference in the probability of correct classification for the negative predictive models between the forest-open and open-forest edge type ($p=0.578$). However for the positive models, the odds of incorrect classification was 2.9 times greater in the open-forest than in the forest-open edge type ($p<0.0001$).

Evaluating the predictive ability by the 8 sub-edge types on the San Pedro helps to evaluate how robust the predictive models were for edge types different from those in which the meta-analysis was developed. Of the forest-open edge type, cottonwood/herbaceous was the most similar to the dataset in which the predictive models were developed, and thus was used as a reference. For the negative predictive model, the cottonwood / mesquite edge type was 7.0 times more likely to incorrectly classify edge response than cottonwood / herbaceous ($p=0.084$), but there was no difference between the mesquite / desert scrub and mesquite / herbaceous edge types from the cottonwood / herbaceous. For the positive predictive model, the mesquite / desert scrub edge type and mesquite / herbaceous edge type were 3.6 and 5.3 times more

likely to incorrectly classify (p=0.089 and p=0.027 respectively) compared with the cottonwood/herbaceous edge type, but cottonwood/mesquite was not significantly different from cottonwood/herbaceous. In the open-forest edge type, none of the edge types were significantly different in terms of the probability of correct classification.

We next used focal habitat (cottonwood, herbaceous, mesquite or desert scrub) as a predictor for probability of correct classification. For the forest-open edge type, there was no difference in the probability of correct classification between mesquite and cottonwood focal habitat for the negative predictive model (p=0.733). However, for the positive predictive model the mesquite focal habitat was 2.2 times more likely to incorrectly classify edge response than cottonwood focal habitat (p=0.091). In the open-forest edge type, there was no difference in the probability of correct classification between mesquite or desert scrub focal habitat compared with herbaceous in either the negative or positive predictive models (p=0.874, p=0.609, p=0.701 and p=0.223, respectively).

Finally, we used matrix habitat as a predictor for probability of correct classification. For the forest-open edge type, mesquite was 4.6 times more likely to incorrectly classify than the herbaceous matrix habitat for the negative predictive model (p=0.046) but there was no difference between the desert and herbaceous matrix habitat for the positive predictive model (p=0.237). For the open-forest edge type, the matrix habitat was unrelated with correct classification of edge response (p>0.341).

Ecological and Life-history Traits

Relevant traits from each of the 4 predictive models were used as predictors of correct classification. This approach may help to understand the different mechanisms

that may be operating on birds on the San Pedro as compared with the kinds of habitats included that were used to develop the predictive models using multiple studies from across the U.S. (Brand and Noon in prep).

In the negative predictive model in forest-open edge type, each trait included in the predictive model was used as a predictor for correct classification. Of the 6 traits in the predictive model, only ecological plasticity had any predictive value for the probability of correct classification. A more ecological plastic bird species (index value of 10) was 5.2 times more likely to incorrectly classify edge response than a less ecologically plastic bird species (index value of 6; $p=0.072$).

Of the 3 traits included in the negative predictive model in the open-forest edge type, HU2 and NH were predictive of incorrect classification. For the HU2 trait, the probability of correct classification for an open habitat bird was 13.2 times more likely to be incorrectly classified than for a forest/both habitat bird ($p<0.0001$). For NH, an 11-m high nest was 6.4 times more likely to be incorrectly classified than a 1-m nest height ($p=0.002$).

Of the 6 traits included in the positive predictive model in the forest-open edge type, 3 traits had predictive value for probability of correct classification: IN, NS, and NT. For the duration of incubation + nestling period, the odds of correct classification for a long duration (35 days) was 5.8 times more likely to be incorrectly classified compared with a shorter duration (20 days; $p=0.021$). For nest substrate, shrub nests were 4.3 times more likely to be incorrectly classified than a ground/tree nests ($p=0.003$). For nest type, an open nest was 9.2 times more likely to be incorrectly classified than a closed nest ($p=0.004$).

Of the 3 traits included in the positive predictive model in the open-forest edge type, only NH had predictive value for the probability of correct classification. A 1-m nest height was 1.8 times more likely to be incorrectly classified compared with an 11-m height nest (p=0.033).

Discussion

The predictive models did an excellent job in 9 of 16 edge response / edge type combinations (75-96% correct classification). The negative predictive models correctly classified 75-96% of species' edge responses in 4 forest-open edge types, and 76-91% of species' edge responses in 4 open-forest edge types. The positive predictive models correctly classified 64-86% of species' edge responses in 3 forest-open edge types, but only correctly classified 29-55% for 1 forest-open and 4 open-forest edge types. In order to assess the aspects of these models that broke down in their ability to predict edge response for birds on the San Pedro River, I used logistic regression to evaluate environmental factors and traits related with probability of incorrect classification.

When considering environmental factors as predictors of probability of correct classification, we evaluated edge type, sub-edge type, matrix habitat and focal habitat. We found no evidence that edge types or other environmental factors were related with probability of incorrect classification for the open-forest edge type. However, there was evidence that probability of incorrect classification was related with environmental factors for the forest-open edge type with both the negative and positive predictive models. For the negative predictive model, incorrect classification was significantly more likely with the cottonwood / mesquite than the cottonwood / herbaceous edge type, and with mesquite compared to herbaceous matrix habitat. For the positive predictive

model, the mesquite / desert scrub and mesquite / herbaceous edge types were significantly more likely to incorrectly classify edge response compared with the cottonwood/herbaceous edge type, as well as with mesquite focal habitat compared with cottonwood focal habitat.

Based on these results, mesquite habitat appears to be the environmental factor most related with probability of incorrect classification. Mesquite in its shrub/tree form (*Prosopis velutina* and related species) occurs primarily in the desert southwest region of the U.S. No studies have previously investigated avian edge response in mesquite habitat, and it was not used in the development of the predictive models (Brand and Noon, *in prep*.). Higher probability of incorrect classification for negative edge response with mesquite as matrix habitat, and for positive edge response with mesquite as the focal habitat, implies that mesquite is used by birds more than would expect based on the predictive models. Mesquite provides an excellent nest substrate for many of the riparian birds species (*personal observation*), and may provide resources beyond what would expect based on the predictive models.

In addition to environmental factors, I considered each trait as a predictor for probability of correct classification for the relevant predictive model. For the forest-open edge type, traits were related with incorrect classification of edge response for both the positive and negative predictive models. Ecological plasticity was the only trait that was a significant predictor of incorrect classification for the negative predictive model. Brand and Noon (*in prep*) considered ecological plasticity to be related with increased disturbance and stochastic processes occurring at edges. Because of the linear nature and increased spatial heterogeneity of the riparian corridor (Saab 1999), stochastic processes

may differ less between edge and interior environments when compared with the more contiguous forests of the west, Midwest and eastern US in which these predictive models were developed (Brand and Noon in prep). In the positive predictive model, 3 traits were significant predictors of incorrect classification. The 3 traits: duration of the incubation plus nestling period, nest substrate, and nest type, are all related with nesting biology considered to vary between edge and interior environments due to increased predation and parasitism at edges (Brand and Noon *in prep*). A study in a riparian system in Montana has found that predation and parasitism is not related with edge and patch size (Tewksbury et al. 1998). If this is similar on the San Pedro, it may indicate that mechanisms of predation and parasitism are not predictive of edge response in riparian systems.

Two traits were significantly related with probability of incorrect classification of edge response in the open-forest edge type: habitat utilization and nest height. For habitat utilization, 4 species were classified as using 'open' habitat: Lesser Goldfinch, Black-throated Sparrow, Common Yellowthroat, and Verdin. Of the 16 species/sub-edge type combinations, only the Verdin in herbaceous/cottonwood showed a negative edge response, while counter to predictions, all other species/subedgetype combinations showed a neutral or positive edge response. Due to the narrowness of the riparian corridor, the majority of the species we examined seemed to be using more than one habitat type, rather than using the open habitat type exclusively, which in turn, affected the observed edge responses. In addition to habitat utilization, nest height was not successful in predicting edge response in either the positive or negative predictive models. Counter to predictions, birds with high nests were less likely to show a positive

edge response, and birds with low nests were less likely to show a negative edge response. Cross boundary subsidies again seem to explain this result. Birds with high nests appeared to utilize resources in the open habitat (personal observation) and low nesting species such as the Song Sparrow, Yellow-breasted Chat, and Common Yellowthroat used the forest habitat more than predicted due to their dependence on mesic habitat.

That particular environmental factors and traits fail to predict edge response for birds on the San Pedro River is not surprising due to inherent differences between this desert riparian system compared with the more contiguous forest landscapes of the west, Midwest, and eastern United States in which the models were developed (Brand and Noon in prep). Differences between the systems are apparent with the differences in edge response. Brand and Noon (in prep) tabulated species-specific edge responses from 30 different studies and found positive, neutral, and negative edge response of 42%, 26%, and 32% for forest-open, and 54%, 25%, and 21% for open-forest edge types. For birds on the San Pedro River, I found positive, neutral, and negative edge response of 20%, 65%, and 15% for forest-open with cottonwood as the focal habitat, 13%, 74%, and 13% for forest-open edge types with mesquite as the focal habitat, 35%, 57%, and 8% for open-forest with cottonwood as the matrix habitat, and 33%, 63%, and 4% for open-forest edge types with mesquite as the matrix habitat. While lack of statistical power is a potential problem in any edge study, I believe that the increased number of neutral edge responses, and relatively low number of negative edge responses, may result from characteristics of the landscape composition and structure of desert riparian system. Edges on the San Pedro River addressed in this paper result from the hydrologic drivers

such as depth to groundwater associated with topographic relief, rather than being artificially induced edges resulting from agriculture, forestry practices, or urbanization. Birds may be more adapted to naturally occurring edges and be able to benefit from edges and cross boundary subsidies. Additionally, the riparian strip is more narrow than the deciduous, coniferous and mixed forests used in the development of the predictive models, and may not be sufficiently wide to reach a maximum potential distance of edge influence. Finally, the riparian system on the San Pedro is spatially heterogeneous with relatively large gaps in the forest canopy and along the river channel, and thus the spatial scale at which edges were defined may not have been entirely appropriate for all of the species that we were investigating.

That the models did not predict perfectly does not diminish from the fact that they predicted edge response for previously unstudied species in novel edge types surprisingly well. The only other attempt to predict species' responses to habitat fragmentation based on easily parameterized models had virtually no predictive power (Mac Nally and Bennett 1997, Mac Nally et al. 2000). While 4 traits in the forest-open edge type and 2 traits in the open-forest edge type failed in their predictive ability, the majority of traits contained within the predictive models, and hypothesized to be related with different mechanisms operating on birds at edges, did a good job of predicting edge response for birds on the San Pedro River.

This work contributes to development of tools to predict species' responses to human perturbations using easily parameterized models that are widely applicable. Readily available ecological and / or life-history trait information has been successfully used to predict which fish species are probable invaders (Kolar and Lodge 2001, 2002),

population declines in beetles (Davies et al. 2000), corridor use based on movement behaviors of butterflies (Haddad 1999), and plant performance in ecological restoration (Pywell et al. 2003). Environmental variables have also been used to predict butterfly species richness (Nally et al. 2003). These diverse, successful attempts indicate that use of readily available information from the literature and public maps may provide predictive power to address environmental problems.

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USING THE EFFECTIVE AREA MODEL TO PREDICT ABUNDANCE AT THE LANDSCAPE SCALE

CHAPTER 3. Ph.D. Dissertation

DRAFT 1 IN PROGRESS (Not yet submitted to Barry Noon)

by Arriana Brand

Introduction

The Effective Area Model (EAM; Sisk et al. 1997) provides an important tool for land managers to predict relative impacts of landscape alteration on animal populations. The EAM utilizes edge response functions (e.g. density as a function of distance from edge) along with landscape maps to predict the relative abundance of species in novel landscapes or regions. Despite the large amount of effort given to the study of edges, this is the only tool currently available that projects information from edge response studies in a given focal/matrix habitat to population level responses at the landscape scale.

The EAM can be compared with a null model that provides a naïve prediction of abundance. Given an average density of a given species in a given habitat type, and knowledge of the area of that habitat type, the null model projects abundance at the landscape scale but ignores the effects of within-habitat heterogeneity resulting from proximity to adjacent habitat types. The null model provides a benchmark for comparison to assess whether use of edge responses within the EAM is an improvement to the naïve approach to projecting abundance at the landscape scale.

Previous approaches to comparing the relative performance of the EAM and null models ranked species abundances in validation sites similar to those in which the model was parameterized (Sisk et al. 1997). The approach presented here attempts to evaluate the extent to which the EAM is an improvement to the null model in terms of overall model bias in sites that are categorically different from those in which model predictions were made. We sampled in validation sites from different regions, degrees of isolation, presence of water, and focal habitats in order to evaluate whether these additional site-

level variables impact the relative predictive performance of the null and EAM models. While the parameterization of the EAM is currently limited to edge response functions that remain consistent regardless of other site-level variables, our goal here is to assess whether inclusion of an offset parameter may be an efficient way to refine and improve the EAM.

In addition to evaluating the relative performance of the EAM, part of the goal of this project was to develop methodology to estimate edge response functions. In previous annual reports we used model selection to evaluate whether linear versus non-linear (exponential, logistic, and gompertz functions) provided a better fit for the data. Using this approach, linear models were supported for most species in most edge types. However, since there is often a clear breakpoint representing the maximum distance of edge influence, our final approach utilizes a piecewise linear model where a distinct breakpoint occurs, an otherwise uses a linear model.

The overall objectives of this section of the annual report were to 1) present the final approach to developing edge response functions for San Pedro birds, 2) to predict abundance for 20 species in 50 validation sites using both the EAM and null models, 3) to compare the relative predictive performance of the EAM and null models in terms of overall model bias, and 4) to evaluate the importance of site-level variables in terms of the comparison of the EAM vs. null model performance, as well as in terms of overall EAM model bias, to suggest possible future refinements to the EAM.

Methods

Predicted Abundance

The predicted abundance for 25 species in 50 validation sites was estimated for both the EAM and null models by utilizing edge response functions developed in the model parameterization along with habitat maps developed for each of the validation sites. Appropriate parameter values for each validation site were implemented within both the EAM and null models to generate predicted abundance for each species in each validation site.

Field Protocol

The upper and middle San Pedro River, including areas within the San Pedro Riparian National Conservation Area, provided an excellent opportunity to study mostly natural edges between adjacent habitats and to develop edge response functions needed to parameterize the Effective Area Model.

The San Pedro River watershed has two primary associated zones of riparian vegetation extending perpendicular from the river to the surrounding desert scrub communities. First, a primary riparian zone consists of gallery forests dominated by Freemont cottonwood (*Populus fremontii*) and Gooding willow (*Salix gooddingii*). A secondary riparian zone consists of mesquite (*Prosopis* spp.) interspersed with patches of Sacaton grass (*Sporobolus wrightii*). In many areas along the river corridor distinct natural edges occur between the primary and secondary riparian and desert scrub communities.

Eight edge types were investigated representing both sides of a given edge. Four of the 8 edge types occur at the primary riparian to secondary riparian interface, including

both sides of the edge where cottonwood is adjacent to mesquite, and both sides of the edge where cottonwood is adjacent to grassland. Two edge types occur between the secondary riparian habitats at both sides of the mesquite / grassland edge. Two edge types occur at the secondary riparian to non-riparian interface including both sides of the mesquite / desert scrub edge.

In order to estimate bird density across the different types of edges, a total 284 sampling locations were established on 23 sampling areas in the upper and middle reaches of the San Pedro River. Each sampling area consists of 11-14 point count locations on 2-3 transects. Points were located 100 m apart along the habitat gradient perpendicular from the river extending through primary riparian, to secondary riparian, to desert scrub vegetation communities. Points count locations occurring at varying distances from habitat edges were used to construct edge response functions.

Each point represents the center of a variable circular plot of 60 m radius. Distance sampling was used at each variable circular plot. At each point, an observer mapped the location of each individual on field sheets representing a specific circular plot marked with cross-hairs at increments of 10 m. The distance and angle of each individual bird from the observer (i.e. point-center) was estimated by sight or sound with the aid of a Yardage Pro 400 Laser Rangefinder. Surveys were conducted from 10 minutes before sunrise until 3 hrs after sunrise.

Approximately 2,720 point count surveys were conducted during the 1998-2001 field seasons. Each point was visited between 6-14 times, and the survey effort was used to adjust density estimates in the analysis. A total of 10 observers conducted surveys during the 4 year study. In a given field season, a minimum of two weeks training was

done prior to beginning surveys on the survey techniques as well as the identification of birds by sight and sound. Within a given year, observers were rotated between sites so that each point count location was surveyed approximately the same number of times by each observer.

Distance Sampling Analysis

The distance from the observer to individual birds was used to estimate a detection function, which in turn, was used to estimate the density of birds for each point count location based on computational algorithms in program DISTANCE (Buckland et al. 2002). Since we wanted to obtain a per-point density estimate to use in modeling edge response functions, data were combined for a given species at a given point location for all visits within and between years. Differing number of visits to each point transect was accounted for by incorporating a survey effort multiplier in the Distance Sampling analysis. Between 5-15% of the data were truncated to eliminate heaping, depending on the pooled detection function observed for each species following the methods in Buckland et al. (2002).

AIC model selection (Burnham and Anderson 2002) was used to select the best detection function for each of the 25 species. Candidate detection functions were allowed to vary by habitat in the attempt to improve model parsimony. In the most general case, detection functions for a given species were allowed to vary by each of the 4 major habitat types: cottonwood, mesquite, grassland, and desert scrub. At the other extreme, all four habitats were pooled to obtain a single detection function for a given species. Intermediate approaches to modeling the detection function included pooling two or more of the habitats. It was considered appropriate to pool habitats for candidate detection

functions when plant species composition differed but structure was similar. Candidate detection functions included 1) pooling desert with herbaceous and pooling cottonwood with mesquite, 2) pooling herbaceous, desert and mesquite separately from cottonwood, and 3) pooling desert and herbaceous separately from pooling mesquite and cottonwood.

Another important aspect of modeling the detection function is rarity of a given species in a given habitat. Even common bird species such as the Yellow-breasted Chat that are abundant in primary riparian habitats may be rare in other habitat types such as desert scrub. When a particular species in a particular habitat type is rare, it may be necessary (rather than just parsimonious) to pool the detection function across habitats. For example we might pool desert scrub with grassland for a given species that has low number of detections in one of those habitats. This procedure enables estimation of density for a given species / habitat combination with few detections by utilizing data from the same species but in other habitat types that are structurally similar, and thus are expected to be similar in terms of the detection function.

All candidate detection functions were assessed for each species. AIC model selection was used to select the best detection function for each species from which to estimate per point density for that species. This analysis was done for the 25 most common species across all habitats.

Distance of point count locations to the closest edge was based on differentially corrected UTM coordinates of points and edges obtained with a Trimble GSP unit accurate to 2-5 m, a classified image of the upper San Pedro (Watts et al. 1996), and field reconnaissance. The number of point count locations varied from 13 to 24 locations per edge type ranging from 0 m to 258 m into interior habitat from the closest relevant edge.

No overlapping "zero" points were used on either side of a given edge for the development of edge response functions (Baker et al. 2002). The distance from edge information along with per-point density estimates were then used to estimate edge response functions.

Edge Response Functions

Edge response functions were implemented for 25 species in the 8 edge types using either linear or piecewise linear regression with density as a function of distance from edge in Stata 7.0 (StataCorp 2002; Figure 1).

A total of 200 edge response functions were implemented for 25 species in 8 edge types. Of the total, the piecewise linear regression model converged in 135 cases. In the remaining 65 species / edge type combinations where a clear breakpoint was not discernable, simple linear regression analysis was used to estimate the edge response function.

While there may be a lack of independence in point count locations within sites, a random effect was not used since the EAM is not currently parameterized to accept random effect analyses. Since analyses implemented without use of a random effect are unbiased, they don't greatly affect the parameterization of the EAM and null models.

The estimates of the regression analysis parameters were used as the inputs to the EAM as currently parameterized: the breakpoint (Dmax) representing the maximum distance of edge influence, as well as the edge density and basal (interior) density. The piecewise linear analyses provide these basic inputs for the EAM. When the piecewise linear regression model did not converge, simple linear regression was used, for which Dmax was taken as the maximum distance of the sampling effort (i.e. the maximum

distance from edge sampled). Using simple linear regression analyses the edge density was taken as the intercept parameter (density when distance = 0) and the basal density was calculated by using the linear regression equation = (edge density) + (slope parameter) x (maximum distance sampled). Examples of both the linear and piecewise linear approaches to modeling the edge response function are shown in Figure 1.

In order to parameterize the null model, the basal density obtained for each of the 200 species / edge type combination using either the piecewise linear or linear regression analyses was considered to be constant across and entire habitat patch regardless of distance from adjacent habitats.

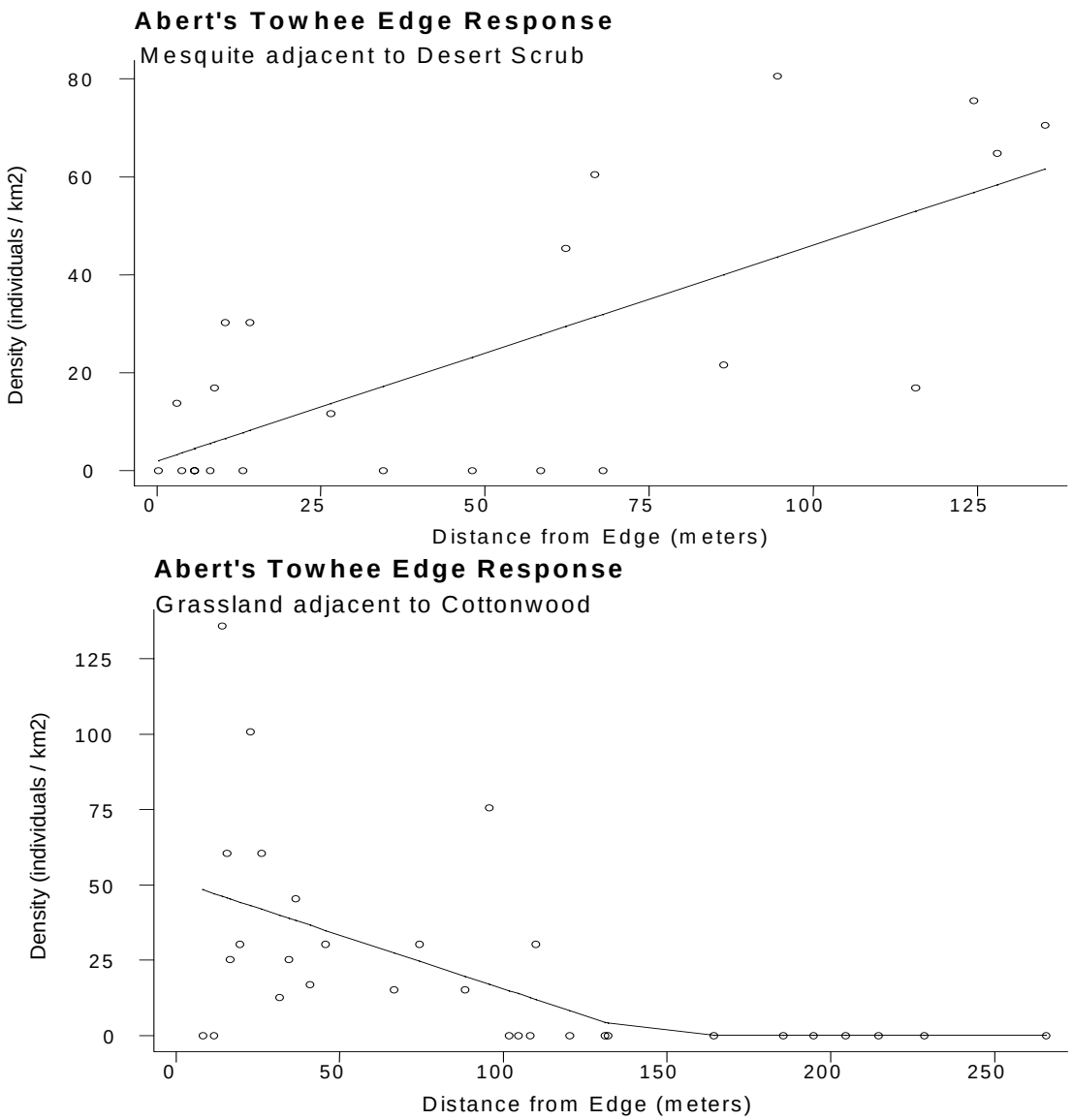

Figure 1. Edge response function for Abert's Towhee in mesquite adjacent to desert scrub using simple linear regression, and in grassland adjacent to cottonwood using piecewise linear regression.

Validation Study Sites

A total of 50 sites located from within 1 km of the San Pedro River to over 200 km away were used to evaluate the predictive performance of the EAM. Validation sites were established in 4 general areas: sites on the San Pedro River additional to those in which edge response functions were parameterized, on the east and west ranges of Fort

Huachuca, on Sonoita Creek managed by The Nature Conservancy, and on the newly created Empire Cienega National Riparian Conservation Area managed by the BLM. Seven of these sites had been set up in 2000 for the pilot validation work, and an additional 47 sites were newly set up in 2001. Four sites that had been used in 2000 were no longer accessible, and thus were dropped for the work in 2001.

Validation sites were allowed to vary by 3 additional factors in addition to region: focal habitat, degree of isolation, and presence / absence of surface water. Of the 50 validation sites, 34 sites were composed of cottonwood focal habitat, and 16 sites were composed of mesquite focal habitat. Cottonwood habitat was adjacent to mesquite, grassland or both. Mesquite focal habitat was adjacent to desert scrub, or both cottonwood and desert scrub. Cottonwood sites were classified as isolated if they were greater than 100 m from the primary riparian corridor on the River. Mesquite sites were classified as isolated if they were narrow strips vegetation occurring in washes vs. comprises of the secondary riparian corridor immediately adjacent to the primary riparian corridor. Sites were also classified based on surface water presence / absence. Almost all mesquite sites had water absent, so that there is a confounding between surface water and focal habitat. Almost all isolated sites had water absent so there is also confounding between surface water and isolation.

I used a Trimble GPS unit to record UTM coordinates along the edges of each habitat within validation sites in order to develop habitat maps for use in the EAM and null models. Classification of habitat types within sites was done by field reconnaissance. The perimeter of each validation site was grouped and differentially corrected in Pathfinder Office to obtain accuracy of 2-5 m. The location data was then

brought into ArcView 3.2 for the creation of habitat patch polygons. Adjacent habitat was also placed onto each polygon in ArcView GIS software.

At each validation site, from 1-3 point count locations were established and each point location within a validation site was buffered out to 60 m. The buffered polygon was used as the outer limit of predicted abundance using both the EAM and null models in order to standardize the area of estimation between the predicted and observed abundance.

Observed Abundance

At each validation site, from 1-3 point count locations were established depending on the size of the habitat patch. Of the 50 sites, 5 sites had 2 point count locations and 1 site had 1, while the remainder contained 3 point count locations. There were 95 plots in the 34 cottonwood sites, and 47 plots in the 16 mesquite sites, for a total of 142 plots. Each site was visited between 3-6 times for approximately 450 surveys conducted during the 2000-2001 field seasons.

Distance sampling was used to obtain an estimate of abundance for each species in each of the 50 sites. The distance sampling field effort was similar to that described above for the development of edge response functions. Since we wanted to obtain a per-site density estimate to compare with the predicted abundance for each site, data were combined for a given species at a given site for all visits within and between years. Differing number of visits to each site was accounted for by incorporating a survey effort multiplier in the Distance Sampling analysis. A total of 2 observers conducted surveys during the 2 years, with a single observer (L.A.B.) doing the majority of validation surveys in both years. Between 2-15% of the data were truncated to eliminate heaping,

depending on the pooled detection function observed for each species following the methods in Buckland et al. (2002). Sufficient detections were obtained to enable estimation of abundance of the 20 most common species by validation site. All data was analyzed in program Distance 3.5.

AIC model selection (Burnham and Anderson 2002) was used to select the best detection function from which to estimate per site density for each of the 20 species. Eight candidate detection functions were assessed for each species, including detection functions allowed to vary by habitat, riparian corridor width, adjacent habitat, and intermediates of the above. In addition, a global detection function was used that pooled across all sites. I used the recommended sample size of 50 detections per detection function strata, so that I used the best AIC with a minimum of 50 detections per strata. All candidate detection functions were assessed for each species (Buckland et al. 2002). Despite using 8 candidate detection functions, only 2 detection functions were used across the 20 species: focal habitat (separate detections for cottonwood vs mesquite) or global (pooling across all sites), probably due to relatively small sample sizes for the species-specific analyses.

Comparison of Observed and Predicted

I felt that the best way to assess the relative performance of the EAM and null models was to compare the relative bias between observed and predicted using both methods. First, the observed abundance for each species in each validation site was paired with abundances predicted using both the EAM and null models. I then regressed the predicted abundance on the observed abundance separately for each species to evaluate the relationship between observed and predicted separately for both the EAM

and the null models. I used simple linear regression to obtain the fitted observed line as a function of the predicted. This fitted observed line is the line that best represents the average observed abundance at different levels of the predicted (both EAM and null) abundances. The predicted line (predicted versus predicted) was also graphed, representing the benchmark for a 1:1 relationship that would indicate a "perfect" predictive relationship. Comparing the difference between the fitted observed versus predicted, for each level of the predicted, is analogous to comparing the bias of the EAM vs. the bias of the null model (Figure 2).

Comparing the mean absolute difference between fitted observed vs. predicted (EAM vs. null) for each validation site would be appropriate for a paired t-test analysis, except that the fitted observed line is dependent on all of the observations and thus the independence assumption of the t-test is not met. As such, this analysis was implemented using a bootstrap methodology using 10,000 replicates of the 50 sites with replacement to estimate the mean absolute bias of the EAM, the mean absolute bias of the null model, and the difference between the mean bias of the null and EAM models. The upper and lower 95% percentile confidence interval was calculated for each statistic, and two one sided p-value were calculated for the alternative hypotheses that mean absolute bias for the null is greater than the EAM (i.e. the EAM performs better) or that the mean absolute bias for the EAM is greater than the null (i.e. the null performs better). I reported the p-value that was appropriate depending on the sign of the difference between the mean absolute bias of the EAM and null models.

In addition to doing this analysis for all of the sites, I also subset the sites based on focal habitat, isolation, presence of water, and region. In comparing the performance

of the EAM and null model separately for each subset of the site-level variables, it was possible to ascertain whether these site-level variables may be affecting the ability of the EAM or null model to predict relative abundance in validation sites that are different from those in which the models were parameterized.

Because we are really interested in whether further refinement of the EAM may improve the ability to predict abundance, I also investigated the EAM bias by itself (not in reference to the null model) as a function of the four site-level variables. If the bias was higher in one focal habitat than another, for example, then an additional offset pertaining to levels of the site-level variables (such as isolated vs. not isolation) may improve predictions in future refinement of the EAM.

Results

Comparison of the mean absolute bias between the two approaches to predicting abundance is shown for the Black-throated Sparrow and the Yellow-breasted Chat (Figure 2). The Black-throated Sparrow is an example of a species for which the null model outperformed the EAM, as seen with the smaller mean absolute deviation between the fitted observed line and the predicted line for the null model (Figure 2). The Yellow-breasted Chat is an example of a species for which the EAM outperformed the null model, as seen with the smaller mean absolute deviation between the fitted observed line and the predicted line for the EAM (Figure 2).

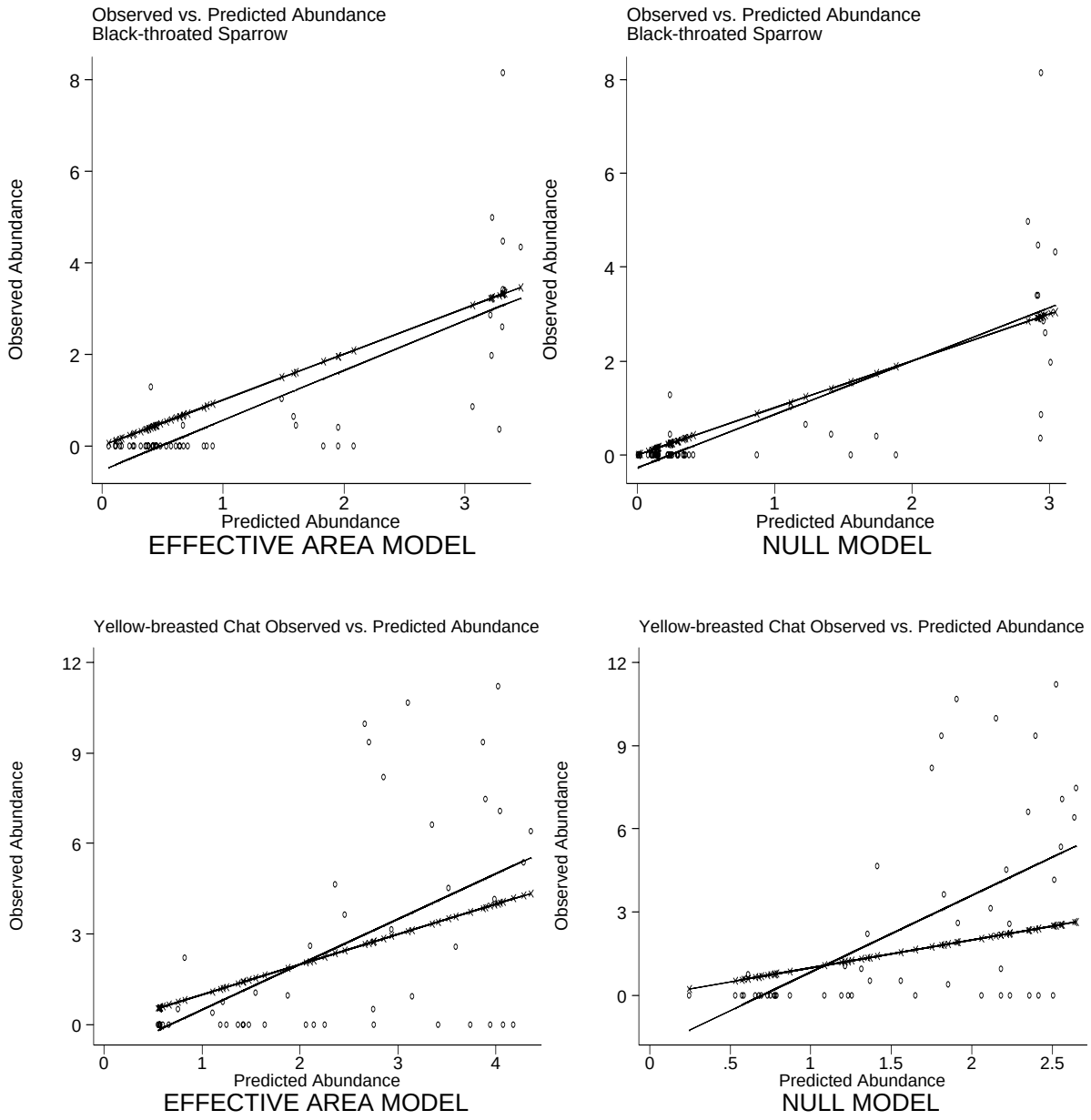

Figure 2. Black-throated Sparrow and Yellow-breasted Chat predicted line at 45 degree angle with x marks, fitted observed line without x marks.

When evaluating the relative performance of the EAM and null models utilizing all validation sites, it was possible to discern a significant difference (P-value < 0.05) in terms of mean absolute bias between the EAM and null models for 12 of 20 species. Of the 12 species, the EAM performed better than the null for 10 species, and the null

performed better than the EAM for 2 species. As an overall assessment, the EAM outperformed the null for 83.3 % of species for which it was possible to discern a difference when considering all validation sites (Table 1).

Table 1. Mean absolute bias for EAM, null and difference between EAM and null.

Species	Null Bias	EAM Bias	Δ Bias (Null-EAM)	Δ Bias 95% LCL	Δ Bias 95% UCL	P-value	Best Model
ABTO	0.457	0.463	-0.005	-0.466	0.266	0.456	neither
ATFL	0.404	0.462	-0.058	-0.214	0.086	0.187	neither
BCFL	1.776	1.646	0.130	0.105	0.151	0.001	**EAM**
BEWR	0.738	0.591	0.147	-0.103	0.224	0.103	neither
BHCO	1.021	0.852	0.169	0.079	0.257	0.005	**EAM**
BLGR	0.586	0.459	0.126	0.085	0.163	0.000	**EAM**
BTSP	0.197	0.425	-0.228	-0.321	-0.002	0.022	**NULL**
BUOR	0.757	0.529	0.228	0.072	0.272	0.007	**EAM**
CAKI	4.134	3.979	0.155	0.100	0.221	0.000	**EAM**
COYE	1.188	1.123	0.064	-0.029	0.164	0.089	neither
GIWO	0.759	0.743	0.016	-0.127	0.159	0.385	neither
HOFI	0.777	0.568	0.210	0.158	0.252	0.000	**EAM**
LEGO	1.127	1.146	-0.019	-0.098	0.059	0.309	neither
LUWA	3.490	2.152	1.339	1.013	1.693	0.000	**EAM**
MODO	0.622	0.614	0.008	-0.013	0.030	0.234	neither
SOSP	2.397	2.480	-0.083	-0.409	0.291	0.299	neither
SUTA	0.177	0.650	-0.473	-0.530	-0.134	0.005	**NULL**

WWDO	0.566	0.467	0.099	0.069	0.131	0.000	**EAM**
YBCH	1.312	0.568	0.743	-0.068	0.989	0.030	**EAM**
YWAR	1.752	1.601	0.151	-0.031	0.379	0.053	**EAM**

When comparing the performance of the EAM and null model separately for subsets of the site-level variables, the EAM still generally outperformed the null model across species and validation sites. However, 3 of the 4 site-level variables impacted the relative performance of the EAM vs. null models. The EAM showed better prediction relative to the null model in cottonwood focal habitat, isolated patches, and in sites where water was absent (Table 2). There was no difference based on regions in terms of the % of species for which the EAM outperformed the null (Table 2). The EAM did the best relative to the null model in isolated validation patches and in validation patches with water, for which the EAM outperformed the null for 91% of the species in which it was possible to discern a difference between the two approaches (Table 2).

Table 2. Comparison of EAM and null model relative performance by site-level variables

Subsetting Factors	Number of Sites	EAM better prediction	NULL better prediction	% EAM better prediction
Isolation				
Contiguous	36	6	4	60.0
Isolated	14	10	1	90.9
Water				
Present	13	6	4	60.0

Absent	37	10	1	90.9
Focal habitat				
Cottonwood/deciduous	34	11	3	78.6
Mesquite	16	4	2	66.7
Region				
San Pedro	18	4	1	80.0
Off -San Pedro	32	8	2	80.0
All Sites				
	50	10	2	83.3

Given the basic overall result that the EAM outperforms the null model for most species in terms of overall model bias, the next logical question pertains to whether it may be possible decrease the bias of the EAM by incorporating additional site-level variables. We found that 9 of the 20 species showed a significant difference in the EAM bias as a function of one or more of the four site-level variables (focal habitat, isolation, presence of water, and region).

Degree of isolation (isolated vs. contiguous) and presence of water (present vs. absent) were significant predictors of EAM bias for 5 of the 20 species. All 5 species showed higher bias in contiguous patches and in sites where water was present, which supports the idea that these variables are confounded. Three of the 5 species (Song Sparrow, Yellow-breasted Chat, and Yellow Warbler) are species that require mesic conditions (Ehrlich et al. 1988). Many of the validation sites on the Empire Cienega and Sonoita Creek were extremely moist, healthy perennial rivers, even compared to the San

Pedro River where the models were parameterized, which may explain the increased bias for these species.

Focal habitat (cottonwood vs. mesquite) was a significant predictor of EAM bias for 7 of the 20 species. Of these 7 species, 6 species (Brown-crested Flycatcher, Cassin's Kingbird, Lesser Goldfinch, Song Sparrow, Summer Tanager, and Yellow Warbler) showed a higher EAM bias for the cottonwood sites than for the mesquite sites. Only the Abert's Towhee showed a higher EAM bias for the mesquite than for the cottonwood sites. Of the 6 species that showed higher EAM bias in cottonwood sites, 3 of them also showed a higher EAM bias in contiguous sites with water present (Yellow Warbler, Song Sparrow, and Summer Tanager) and thus may have been responding to variation in Cottonwood between sites related to degree of isolation or presence of water. The 3 other species that showed higher bias in cottonwood focal habitat (BCFL, CAKI, and LEGO) may have been responding to other factors that varied between the cottonwood sites other than degree of isolation and presence of water, such as age structure or canopy height.

Region (San Pedro River vs. off- San Pedro River) was a significant predictor of EAM bias only for the Song Sparrow. This result indicates that the EAM predictions are robust across regions for the majority of species.

These results indicate that bias was higher for certain species based on one or more site-level variables, so that an additional offset pertaining to these site-level variables may improve predictions in future refinement of the EAM.

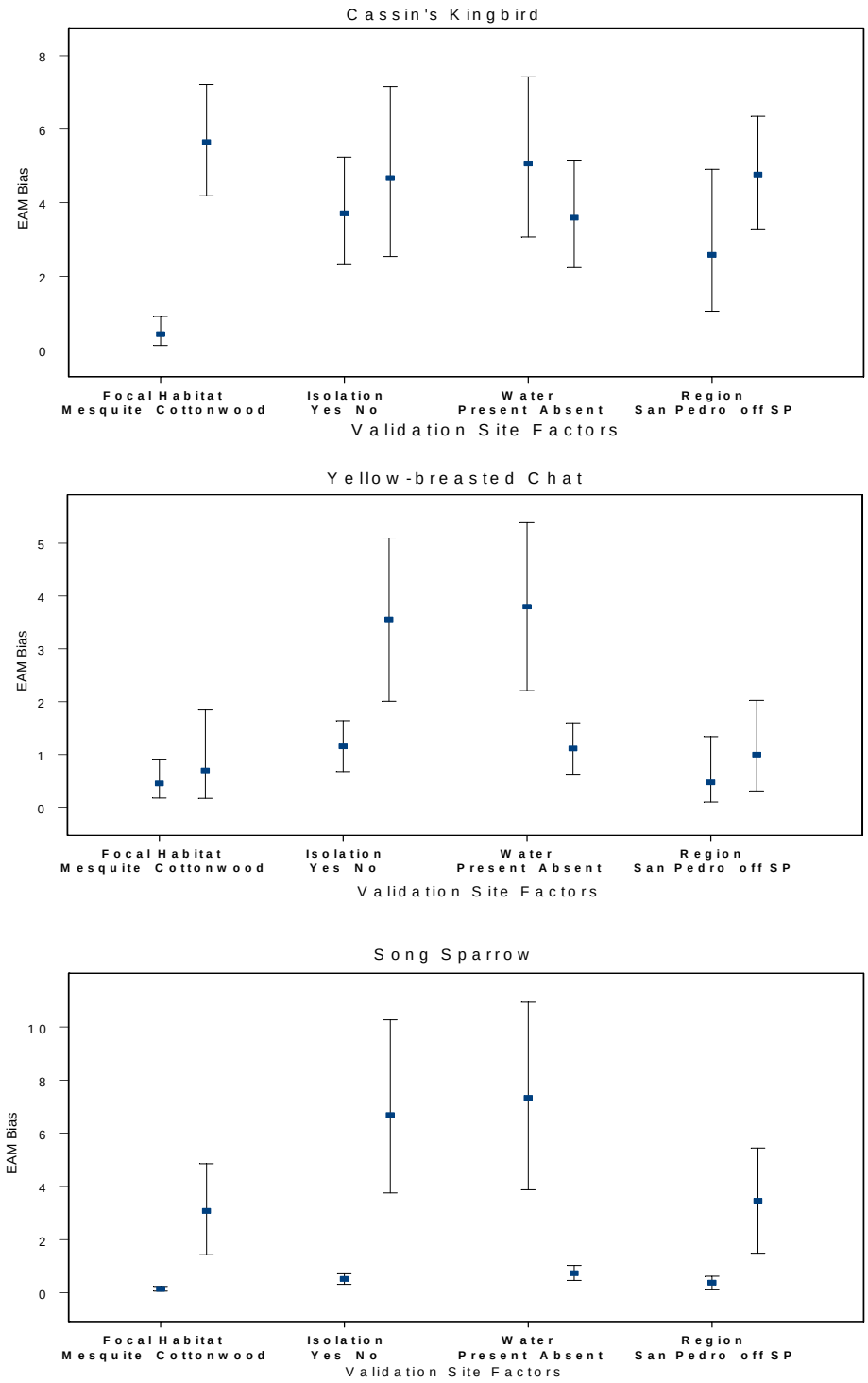

Figure 3. Mean absolute bias for Cassin's Kingbird, Yellow-breasted Chat, and Song Sparrow as a function of four site level variables: focal habitat, isolation, presence of water, and region.

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Table 1. Traits in the positive and negative predictive models for the forest-open and open-forest edge types.

Variable	Code	Level of variable	Predictive Model	
			Edge Response	Edge Type
Ecological and Life-history Traits				
Habitat	HU1	forest habitat vs. open / both	both	forest-open
Utilization	HU2	open habitat vs. forest / both	both	open-forest
Diet	DI	omnivore vs. herb / insectivore	positive	forest-open
Mesic Habitat Selection	MH	obligate mesic vs. facultative mesic / xeric	negative	forest-open
Nest Height	NH	avg nest height	both	open-forest
Nesting Substrate	NS	shrub vs. tree/ground	positive	forest-open
Nest Type	NT	open vs. closed	positive	forest-open
Time Inc + Nest	IN	days incubate + nest	both	forest-open
Cowbird Host Freq.	CH	common host vs. rare host	negative	open-forest
Ecological Placticity	EP	index ranging from 4-13	negative	forest-open
Body mass	BM	body mass	negative	forest-open
Lifetime	LR	clutch size x number of broods	both	forest-open
Reproduction		x longevity	positive	open-forest
Environmental Traits				
Region	RE	east vs. west	positive	forest-open
Agricultural Edge	AG	agriculture vs. non-agriculture	both	open-forest

Appendix A.

Predictive Equations:

Forest-Open negative Edge Response predictions

log odds = ln(p/(1-p))

$$= B_0 + B_1 * HU1 + B_2 * IN + B_3 * EP + B_4 * MH + B_5 * BM + B_6 * LR + RE$$

Forest-Open positive Edge Response predictions

log odds = ln(p/(1-p))

$$= B_0 + B_1 * HU1 + B_2 * DI1 + B_3 * IN + B_4 * NS + B_5 * NT + B_6 * LR + B_7 * RE + \text{random effect}$$

Open-Forest negative Edge Response predictions

log odds = ln(p/(1-p))

$$= B_0 + B_1 * HU2 + B_2 * NH + B_3 * CH + B_4 * AG + \text{random effect}$$

Open-Forest positive Edge Response predictions

log odds = ln(p/(1-p))

$$= B_0 + B_1 * HU2 + B_2 * NH + B_3 * LR + B_4 * AG + \text{random effect}$$

Coefficients

Forest-Open Edge Response Coefficients

Negative Edge Response				Positive Edge Response			
Species		Family		Species		Family	
Variable	Coef.	Variable	Coef.	Variable	Coef.	Variable	Coef.
HU1	2.273669	HU1	2.275723	HU1	-2.689564	HU1	-1.940262
IN	0.106033	IN	0.100532	DI2	3.097403	DI2	1.332838
EP	-0.2109502	EP	-0.17541	IN	-0.0946019	IN	-0.034967
MH	0.8043319	MH	0.811205	NS	1.295935	NS	0.977532
BM	-0.0111802	BM	-0.0104	NT	0.9577008	NT	0.799206
LR	0.0058196	LR	0.007619	LR	0.005355	LR	0.000682
YINT	-3.545817	YINT	-3.70894	RE	-0.8369763	RE	-0.429278

YINT	2.267461	YINT	0.692056

Open-Forest Edge Response Coefficients

Negative Edge Response				Positive Edge Response			
Species		Family		Species		Family	
Variable	Coef.	Variable	Coef.	Variable	Coef.	Variable	Coef.
HU2	1.535725	HU2	1.535725	HU2	-1.140179	HU2	-1.140179
NH	-0.4285529	NH	-0.428553	NH	0.1987352	NH	0.1987352
CH	0.8313024	CH	0.8313024	LR	0.0186318	LR	0.0186318
AG	3.60903	AG	3.60903	AG	-2.346469	AG	-2.346469
YINT	-3.157909	YINT	-3.157909	YINT	-1.135099	YINT	-1.135099

Codes for binary variables

All of the variables in the 4 predictive equations are either continuous or binary. Five continuous variables are Nest Height, Time Inc + Nest, Ecological Plasticity, Body Mass and Lifetime Reproduction. Continuous variables are used as is in the predictive equations, based on the numerical value appropriate for that trait for that species. Binary variables, however, need to be coded either 0 or 1 as follows:

Variable	**Code**	**Level of variable = 0**	**Level of variable =1**
Habitat Utilization	HU1	open / both	forest
	HU2	forest / both	open
Diet	DI	herb / insectivore	omnivore
Mesic Habitat Selection	MH	facultative mesic / xeric	obligate mesic
Nesting Substrate	NS	tree/ground	shrub
Nest Type	NT	closed	open
Cowbird Host Freq.	CH	rare host	common host
Region	RE	east	west
Agriculture	AG	agricultural	non-agricultural

Cutpoints

Edge Type	Edge Response	Random Effect	Cutpoint
Forest-Open	Negative	Species	0.577
		Family	0.461
		None	0.532
Forest-Open	Positive	Species	0.698
		Family	0.662
		None	0.646
Open-Forest	Negative	Species	0.619
		Family	0.619
		None	0.619
Forest-Open	Positive	Species	0.503
		Family	0.394
		None	0.378

Random Effects for species and families

Family and Species Random Effects for Negative and Positive Predictive Models in Forest-Open

Family	Species	Negative	Positive
Aegithalidae		9.66E-21	0.095155
	Common Bushtit	0.2976746	0.284812
Bombycillidae		-8.65E-22	0.146228
	Cedar Waxwing	-0.029638	0.740576
Cardinalidae		-2.72E-20	0.614902
	Blue Grosbeak	-0.068863	0.441872
	Indigo Bunting	-0.078381	0.838456
	Northern Cardinal	-0.151068	-1.52699
	Rose-breasted Grosbeak	-0.32989	2.471736
Certhiidae		1.55E-20	-0.15658
	Brown Creeper	0.3701205	-0.54826
Columbidae		-1.57E-21	0.281672
	Mourning Dove	-0.040401	0.531607
Corvidae		5.22E-21	-0.58151
	American Crow	-0.009839	0.831349
	Blue Jay	0.5713626	-3.77253
	Common Raven	-2.23E-06	-1.01511
	Fish Crow	-0.0183	0.231272
	Gray Jay	-0.282424	1.45676
	Scrub Jay	-0.080225	-1.32465
	Steller's Jay	-0.125162	0.960184
Cuculidae		8.71E-21	-0.49122
	Yellow-billed Cuckoo	0.2543628	-1.75397
Emberizidae		-1.18E-20	0.346071
	California Towhee	-0.027874	0.527918
	Chipping Sparrow	-0.037297	-0.78979
	Dark-eyed Junco	-0.116231	-0.09046
	Field Sparrow	-0.060109	1.098581
	Rufous-sided Towhee	0.2914248	-0.7166
	Song Sparrow	-0.211723	1.178462
	White-throated Sparrow	-0.029134	1.038148
Fringillidae		-1.66E-20	0.485338
	American Goldfinch	-0.08325	0.706097
	Cassin's Finch	0.0041753	1.285771
	Pine Siskin	-0.303306	1.300647
	Purple Finch	-0.044185	-0.06259
Hirundinidae		-2.70E-21	0.267477
	Violet-green Swallow	-0.092405	1.485993
Icteridae		-1.61E-20	0.897401
	Brown-headed Cowbird	-0.159287	.
	Common Grackle	-0.050969	0.322855

	Northern Bobwhite	-0.02696	1.069798
	Northern Oriole	-0.023262	0.925766
	Orchard Oriole	-0.050687	1.359452
	Red-winged Blackbird	-0.113003	0.999268
Laniidae		-2.58E-21	0.161679
	Loggerhead Shrike	-0.069487	0.776386
Mimidae		-5.60E-21	0.108581
	Brown Thrasher	-0.017411	0.025244
	California Thrasher	-0.01401	-1.4155
	Gray Catbird	-0.068528	0.575534
	Northern Mockingbird	-0.05706	0.670239
Odontophoridae		-7.57E-22	-0.00997
	California Quail	-0.020912	-0.01143
Paridae		-6.16E-21	-0.65535
	Black-capped Chickadee	-0.113394	-1.78006
	Carolina Chickadee	-0.143212	-0.4631
	Mountain Chickadee	-0.210288	-0.24689
	Mountain Chickadee	-0.210288	-0.24689
	Plain Titmouse	-0.079757	-0.20097
	Tufted Titmouse	0.3922079	-1.34676
Parulidae		-1.47E-21	-0.0371
	American Redstart	0.0882731	0.145774
	Black-and-white Warbler	-0.140291	-0.54093
	Black-throated Blue Warbler	-0.299342	-0.47407
	Black-throated Green Warbler	-0.035027	-1.28234
	Blue-winged Warbler	-0.03508	0.440538
	Canada Warbler	0.0592354	0.311252
	Cerulean Warbler	0.1147341	-0.56488
	Chestnut-sided Warbler	-0.595188	2.225569
	Common Yellowthroat	-0.286947	0.945092
	Hooded Warbler	0.245797	-2.18263
	Kentucky Warbler	0.5568311	-1.5861
	Louisiana Waterthrush	0.158669	-0.60789
	Magnolia Warbler	-0.394728	2.067092
	Mourning Warbler	-0.371419	2.018939
	Northern Parula	-0.005619	0.866119
	Orange-crowned Warbler	0.3443873	-1.65505
	Ovenbird	0.3772237	-1.33611
	Pine Warbler	0.3790835	-0.3211
	Prairie Warbler	-0.014824	0.288011
	Prothonotary Warbler	-0.145598	-0.54926
	Tennessee Warbler	-0.066199	0.600436
	Wilson's Warbler	-0.182505	-0.39924
	Worm-eating Warbler	0.38898	-1.23887
	Yellow-breasted Chat	-0.158139	0.495011
	Yellow-rumped Warbler	0.2117436	-0.89463
Passeridae		-1.24E-21	0.205254
	House Sparrow	-0.033234	0.828808
Phasianidae		-1.06E-22	0.214651

	Ruffed Grouse	-0.002477	0.720743
Picidae		-1.39E-20	0.182272
	Downy Woodpecker	0.2016654	-0.82197
	Hairy Woodpecker	0.1900769	-0.56145
	Northern Flicker	-0.240961	2.293035
	Pileated Woodpecker	0.2350155	-0.33494
	Red-bellied Woodpecker	0.1379592	-0.56871
	Red-cockaded Woodpecker	-0.316524	2.195931
	Red-headed Woodpecker	-0.098495	0.679444
	Yellow-bellied Sapsucker	-0.512691	-0.22467
Regulidae		-5.78E-21	-0.09613
	Golden-crowned Kinglet	-0.250726	-0.1543
	Ruby-crowned Kinglet	0.1009315	-0.34038
Sittidae		-1.42E-20	0.2739
	Brown-headed Nuthatch	0.1257482	-0.19399
	Red-breasted Nuthatch	0.3305428	-0.32635
	White-breasted Nuthatch	-0.589857	1.312954
Sturnidae		-3.58E-21	0.270788
	European Starling	-0.084438	0.70752
Sylviidae		6.61E-21	-0.8547
	Blue-gray Gnatcatcher	0.1872619	-2.32151
Thraupidae		-4.77E-21	0.186414
	Scarlet Tanager	0.1953388	-1.73161
	Summer Tanager	-0.302956	2.701919
Timaliidae		-8.58E-21	-0.05591
	Wrentit	-0.231266	-0.26172
Trochilidae		1.07E-20	-0.13246
	Allen's Hummingbird	0.2370601	-0.51174
	Anna's Hummingbird	0.2073978	-1.02423
	Ruby-throated Hummingbird	-0.157783	1.27083
Troglodytidae		9.24E-21	-0.2628
	Bewick's Wren	-0.070567	-1.06503
	Carolina Wren	0.2552459	-1.22516
	House Wren	-0.082802	1.372001
	Winter Wren	0.1724186	-0.49838
Turdidae		2.81E-20	-0.22235
	American Robin	-0.169577	0.005348
	Hermit Thrush	0.4445808	-0.15273
	Swainson's Thrush	-0.085794	0.635126
	Varied Thrush	0.1640337	-0.27036
	Veery	-0.166469	-1.1833
	Western Bluebird	-0.079827	-0.46579
	Wood Thrush	0.4613903	-0.94224
Tyrannidae		2.88E-20	-0.43522
	Acadian Flycatcher	0.3272718	-1.37378
	Eastern Kingbird	-0.052999	0.857283
	Eastern Phoebe	0.2231384	-1.79284
	Eastern phoebe	0.2231384	-1.79284
	Eastern Wood-pewee	-0.063458	0.432629

	Great Crested Flycatcher	0.3538775	-0.8448
	Least Flycatcher	0.2335511	-0.5394
	Pacific-slope Flycatcher	0.0929138	-0.13328
	Western Wood-pewee	-0.156899	-0.42485
	Willow Flycatcher	-0.0673	0.381575
Vireo		2.31E-20	-0.78923
	Hutton's Vireo	-0.386565	1.399006
	Philadelphia Vireo	-0.164816	1.580504
	Red-eyed Vireo	0.8981067	-2.27991
	Solitary Vireo	0.1674142	-0.43079
	White-eyed Vireo	-0.181475	-1.25886
	Yellow-throated Vireo	-0.330598	-0.92182

Family and Species Random Effects for Negative and Positive Predictive Models in Open-Forest

Family	Species	Negative	Positive
Alaudidae		-3.38E-18	-1.31E-26
	Horned Lark	-1.94E-21	-0.0437901
Cardinalidae		-2.26E-17	-3.25E-26
	Blue Grosbeak	-4.31E-21	-0.30436496
	Indigo Bunting	9.78E-21	-0.03306598
	Northern Cardinal	-1.85E-20	0.23014474
Charadriidae		-4.08E-18	-2.78E-26
	Killdeer	-2.34E-21	-0.09051192
Corvidae		-3.03E-19	-3.21E-27
	American Crow	-4.55E-27	0.00228793
	Blue Jay	-1.28E-22	-0.13545621
	Scrub Jay	-4.52E-23	0.12060789
Emberizidae		-2.29E-17	6.13E-26
	Dark-eyed Junco	-7.20E-22	-0.01170936
	Field Sparrow	1.16E-21	-0.10253811
	Rufous-sided Towhee	-1.17E-20	0.35946087
	Song Sparrow	-1.66E-21	-0.10403852
	White-crowned Sparrow	-1.98E-22	0.03364898
Fringillidae		-1.43E-19	-3.84E-26
	American Goldfinch	-8.17E-23	-0.12718885
Icteridae		9.35E-18	2.82E-27
	Brown-headed Cowbird	.	-0.13857964
	Common Grackle	-3.59E-23	0.03191027
	Northern Bobwhite	-9.51E-21	0.20676477
	Red-winged Blackbird	1.49E-20	-0.07128571
Mimidae		3.19E-17	-8.21E-27
	Brown Thrasher	6.47E-21	-0.03863819
	California Thrasher	1.19E-20	-0.02929845
	Gray Catbird	-5.51E-23	0.0414743
Paridae		-1.26E-18	8.16E-26

	Carolina Chickadee	-7.20E-22	0.25820873
Parulidae		-1.28E-18	-3.25E-26
	Chestnut-sided Warbler	-6.77E-22	0.11881357
	Common Yellowthroat	1.95E-22	0.1166193
	Prairie Warbler	-3.08E-22	-0.15757644
	Yellow-breasted Chat	5.51E-23	-0.16386413
Passeridae		-2.38E-22	5.12E-28
	House Sparrow	-1.09E-25	0.00140774
Picidae		0	0
	Red-headed Woodpecker	0	0.00002738
Thraupidae		-2.38E-21	5.86E-27
	Scarlet Tanager	-1.30E-24	0.01986534
Troglodytidae		-4.61E-18	-1.66E-26
	Carolina Wren	-2.65E-21	-0.05696374
Turdidae		-4.07E-21	3.38E-27
	American Robin	-2.34E-24	0.01109827
Tyrannidae		-3.51E-21	1.06E-26
	Eastern Kingbird	-1.42E-24	0.01033897
	Eastern Wood-pewee	-6.06E-25	0.02472705
	Great Crested Flycatcher	-4.55E-27	0.00098194
Vireo		1.94E-17	6.24E-27
	Red-eyed Vireo	-2.33E-23	0.05671437
	White-eyed Vireo	1.12E-20	-0.03623209

A PREDICTIVE MODEL OF EDGE EFFECTS

By Leslie Ries

Abstract

Edge effects are among the most thoroughly studied ecological phenomena, yet we lack a general, predictive framework to understand the patterns and variability observed. We present a conceptual model, based on resource distribution and habitat associations that predicts whether abundances near edges are expected to increase, decrease or remain unchanged for any species at any edge type. Predictions are based on whether resources are divided between habitats (predicts an increase near edges), spread equally among habitats (predicts a neutral edge response), found only in one habitat (decreased abundance in preferred habitat, increase in non-preferred), or concentrated along the edge (increase). There are several implications of our model that can explain much of the variability reported in the edge literature. For instance, our model predicts that a species might show positive, neutral *and* negative responses, depending on the edge type encountered, which explains some observed intra-specific variability in the literature. In addition, any predictable changes in resource use (for example, by region or season) may explain why some species show temporal or spatial variability in responses even at the same edge type. Finally, we offer a preliminary test of our model by making predictions for 52 species from three published studies of bird responses near forest edges. Predictions are based solely on general information about each species' habitat associations and resource use. Despite the fact that information on resource use was general and not site-specific, our model correctly predicted the direction of 25 out of 29 observed edge responses, although it tended to under-predict increases and over-predict decreases. This model is important because it helps make sense of a largely descriptive literature and allows future studies to be carried out under a predictive framework,

providing an important step forward in our understanding of how species respond to habitat edges and associated fragmentation.

Introduction

Changes in the distribution and abundance of organisms near habitat edges (sometimes called ecological boundaries or ecotones) are among the most extensively studied phenomena in ecology. Increases in avian richness and abundance at forest edges have been noted for several decades (Lay 1938, Johnston 1947) and led to early claims that edge habitat was beneficial for wildlife. However, the discovery that many songbirds experience higher predation and parasitism rates near forest edges (Gates and Gysel 1978, Chasko and Gates 1982, Wilcove 1985) led to a fundamental shift from a positive to negative view of edge effects and brought critical attention to the issue of habitat fragmentation (Brittingham and Temple 1983). Since these seminal reports, there has been an avalanche of studies describing edge responses for a number of taxa, with much of the focus remaining on forest edges (for reviews, see Paton 1994, Murcia 1995, Risser 1995, McCollin 1998, Lidiker 1999, Lahti 2001, Tscharntke 2002, Chalfoun et al. 2002, Sisk and Battin 2002).

Despite this explosion of interest, the field has remained largely descriptive, with no underlying framework to make sense of the patterns and variability described, giving the impression that general patterns of edge responses are elusive (Murcia 1995). However, the importance of this topic to ecology and its applications to conservation call for a synthesis of proposed mechanisms into a conceptual model that can make sense of previously reported patterns and allow future studies to be conducted within a more theoretical framework. This will lead to a greater understanding of the factors that influence edge responses and allow for predictions even for poorly studied species in a variety of landscapes. Therefore, our objectives are to 1) summarize the major patterns and proposed mechanisms reported in the literature; 2) present a conceptual model, based

on those mechanisms, that predicts edge responses for any species at any edge type; 3) explore the variability in the edge literature and its potential underlying causes within the framework of our model; and 4) offer a preliminary test of our model by determining how well it predicts the nature of edge responses for over 50 bird species, as reported in three published studies.

Edge response patterns and mechanisms

Results from dozens of field studies confirm that many species respond to habitat edges in a variety of ways. Species may show increases, decreases or no change in abundance, depending on the specific edge type. These changes may be due to abiotic or biotic changes in the environment (Murcia 1995), changes in interspecific interactions (Fagan et al. 1999), or a combination of these and other factors. In the avian literature, increased abundances near edges (also called positive edge responses) are generally more common than decreases or negative edge responses (Villard 1998, Sisk and Battin 2002). There currently is insufficient evidence to determine whether this pattern extends to other taxa. Neutral edge responses (no change in abundance near the edge) are probably under-reported due to publishing bias and have received little attention, despite their potential importance in understanding general underlying mechanisms.

Three mechanisms have been cited most commonly to explain increased abundances near edges: 1) spillover, 2) complementary resource distribution, and 3) edges as enhanced habitat. Increased abundances near edges have often been attributed simply to spillover, which occurs when individuals are found in non-habitat near the boundary with their preferred habitat. This increase in abundance may be due simply to proximity, but individuals may also be responding to changes in environmental conditions that make the edge a more hospitable environment, even when the adjacent patch is not considered suitable habitat. For instance, forest habitat near edges tends to be more similar to bordering open habitat (hotter, drier and with more light) compared to

the forest interior (Chen et al. 1999), while open habitat near the same edge experiences increased shading. Thus, organisms may "spill over" the edge because of its moderating influence on the relative qualities of adjacent patches. The second mechanism, complementary resource distribution (also called cross-boundary subsidies), occurs when two bordering patches contain different resources, and being at the edge allows the most convenient access to both (Dunning et al. 1992, McCollin 1998, Fagan et al. 1999). One classic example of this phenomenon is the brown-headed cowbird (*Moluthrus ater*), which forages in open pastures but parasitizes forest-dwelling songbirds (Brittingham and Temple 1983, Lowther 1993). Many other taxa that are associated with forest edges are assumed to be foraging in the open, yet obtaining other resources from the forest, including deer (Alverson et al. 1988) and numerous bird species (Gates and Gysel 1978, McCollin 1998).

The final mechanism explaining positive edge responses is that edges may contain resources absent or rare in both adjoining patches. This concentration of resources near edges may support increased abundances of species that rely on those resources (MacArthur and MacArthur 1961). One common example is shrub-dependent birds being attracted to forest edges that have developed a shrub layer rare or absent in either bordering habitat (Mills et al. 1991, Berg and Part 1994). In this case, if habitat were mapped finely enough, the edge might be identified as a unique habitat type and the observed response would not be considered a true "edge effect". However, most vegetation maps cannot capture such fine distinctions in habitat, and in many cases the increase in resource availability near edges may not constitute a unique vegetation class. This may be especially true when an organism that is responding to the presence of an edge provides the resource base for another organism, which may then also show an edge effect. A good example of this may be seen in the spotted owl (*Strix occidentalis*), which shows increased densities near edges when its prey base is dominated by wood rats

(*Neotoma spp*.), a species that shows an increased abundance near edges, while the owl shows no edge effect when its main prey base is dominated by flying squirrels (*Glaucomys sabrinus*), a species that shows no edge effect (Zabel et al. 1995). Another example is the butterfly *Lopinga achine,* an edge-associated species whose host plant is found in highest concentrations near forest edges, while shading from shrubs at these edges provides the most suitable microclimatic conditions for larval growth (Bergman 1999). These types of cascading edge effects may be very common.

Edge avoidance (decreased abundance near edges) is most commonly reported for habitat-specific species, usually forest "interior" species. Examples include the ovenbird, *Seiurus aurocapillus* (Burke and Nol 1998), the red-eyed vireo, *Vireo olivaceus* (King et al. 1997), the red-backed vole, *Clethrionomys gapperi* (Mills 1995) and the plant *Trillium ovatum* (Jules 1998). These species are generally assumed to be avoiding changes in the environment near edges that may be hostile to species adapted to interior conditions. This has been well documented for the ovenbird where the hotter, drier conditions near forest edges are associated with lower densities of their prey items (Burke and Nol 1998). Species associated with open habitat have also shown decreased abundances near forest edges, including butterflies (Haddad and Baum 1999) and grassland birds (O'Leary and Nyberg 2000, Fletcher and Koford, *in press*). Although these species may avoid less-preferred habitat, they still may spill over into bordering patches (as described above). Therefore, when a patch of suitable habitat borders a patch of non-habitat, a gradual transition from the highest densities in the interior of the preferred habitat to the lowest densities in the interior of adjoining non-habitat may be expected (Sisk and Margules 1993, Lidiker 1999). This transition in abundance is assumed to reflect a gradient in habitat quality, which may ultimately be based on resource availability and abiotic factors such as microclimatic shifts across the edge zone (Murcia 1995). All of the mechanisms presented above relate either to the availability or proximity of resources, and led us to

develop a conceptual model that uses resource distribution as a basis for predicting general edge responses.

A Resource-based Model of Edge Responses

For this model, we assume a simple landscape composed of two adjacent patches, each of which can be classified discretely as habitat or non-habitat, although we later relax this assumption and discuss the impacts of differing habitat quality on predicted edge responses. Here, habitat is defined as any patch that contains at least one utilized resource for the organism of interest. Resources may include provisions such as food or nest sites, as well as elements such as safe sites from predators, service-providers such as pollinators and seed dispersers, or abiotic resources such as light. If both of the adjacent patches contain resources, they are both identified as habitat, but of two different kinds (Habitat 1 and Habitat 2). Non-habitat is any patch that contains no utilized resources, and interior density levels are therefore assumed to be low or zero. This model is therefore a patch-based model with edges defined as the boundaries between patches. While patch definition may vary among researchers, the fact that patch *quality* is defined here as the presence or absence of resources means that our model should be broadly applicable even when landscapes are classified under different schemes. Our model predicts the expected change in abundance near edges between patches, based on patterns of resource distribution between those two patches, as illustrated in Figure 2.1.

When habitat borders non-habitat, then individuals are predicted to show a transitional response across the edge, as density gradually declines from a maximum in the interior of the habitat patch to a minimum in the interior of the non-habitat patch (Fig. 2.1a). This prediction is based on the assumption that conditions across the edge zone show a gradual transition from highest to lowest habitat quality. It is important to note that most empirical studies report responses within only one patch type (on one side of the edge), so a transitional response will appear to be either positive or negative,

depending upon the reference point of the observer (see responses on either side of the edge in Fig. 2.1a). For situations where both patches provide resources, edge responses are expected to vary depending on how those resources are distributed. When the two patches contain complementary (different) resources, the species in question is predicted to increase in abundance near edges (Fig. 2.1b), because being located near the edge offers the most convenient access to both sets of resources (Dunning et al. 1992, McCollin 1998, Fagan et al. 1999). However, when resources are supplementary (so there are no resources in one patch that can not be found in the other), there is no *a priori* reason to suspect that edges convey any advantage or disadvantage in accessing resources, so a neutral response is predicted (Fig. 2.1c). When resources are concentrated along the edge, then a positive edge response is again predicted (Fig. 2.1d).

Although this model is presented as if the distinction between habitat and non-habitat is discrete, in reality the relative difference in habitat quality between adjoining patches can vary continuously from the extreme differences between high quality habitat and non-habitat (Fig. 2.1a) to different patches of nearly equal quality (Fig. 2.1b). This should impact the nature and the strength of the edge response in predictable ways. For example, where both of the adjoining patches provide suitable habitat (Fig. 2.2a), then the nature of the edge response is predicted based on whether resource distributions are complementary or supplementary. When habitat quality is equal on either side of the edge and resources are complementary, responses are predicted to be positive on both sides of the edge (top panel of Fig. 2.2b). However, if one of the adjoining patches is of lower quality, the nature of the edge response will change (top panel of Fig. 2.2c), eventually becoming a transitional response when further degradation reduces the adjoining patch to non-habitat (Fig. 2.2d). A similar continuum exists from a neutral to a transitional response across an edge where resource distribution is supplementary, as illustrated in the lower panels of Fig. 2.2.

Variability explained by the model

By synthesizing many of the mechanisms that have been proposed in the edge literature into a single conceptual framework (Fig. 2.1), we suggest that many of the patterns and much of the variability reported in the edge literature may be explained. For instance, this model predicts that all species may show positive, negative and neutral edge responses, depending on the specific edge type encountered. This may explain many reports of variable edge responses for particular species at different edge types (Murcia 1995, Lidiker 1999). Thus, the claim that certain species or groups are intrinsically edge-avoiding (such as forest "interior" species) or edge-exploiting (such as predators), may be an artifact of a focus on a single edge type (edges between forest and open patches). As future field studies target different taxa and more edge types, we expect that most species will show a variety of edge responses, although there may be groups of species that are particularly insensitive to edges (explored below).

Another implication of this model is that changes in the use or distribution of resources may lead to changes in edge responses, even for the same species at the same edge type. When these changes are predictable, more refined edge response predictions are possible. For example, avian edge responses have been shown to vary between seasons (Noss 1991, Hansson 1994), and this may be due to predictable changes in resource use throughout the year. Many birds are known to show different habitat associations during winter and breeding seasons (which is intuitive based on the fact that nesting resources are not needed during the non-breeding season) and in those cases, our model will predict different edge responses during summer and winter, even at the same edge type. Likewise, regional variation in edge responses has been suggested for birds in the eastern vs. western U.S. (Sisk and Battin 2002). While this is difficult to test due to a paucity of studies in the west (Sisk and Battin 2002), such differences would be predicted by our model for any species showing regional differences in resource use.

One consequence of conducting research under this model framework is that characterization and comparison of edge responses requires investigators to account for habitat quality on both sides of the edge in their study design. Our model assumes that any patch containing resources can be considered "habitat", while any patch not containing resources constitutes "non-habitat". While a general classification of habitat, such as "forest" or "open", may often be a good proxy for resource availability (Dennis et al. 2003), that need not be the case. Many published studies include different habitat types under a single, broad classification such as "open", pooling, for example, grassland, crops, roads or development, all of which may present very different resource availability for different species. When using general vegetation classifications to represent habitats (a common practice that may be the only sensible option in many studies), it is necessary to know to what extent resource availability is associated with each habitat class. Unfortunately, this information is not often provided in the literature, hindering attempts to understand variability in edge responses reported in many studies. We suggest that future edge studies should include information on relative habitat quality and resource distribution on *both sides of the edge*. Even qualitative assessments would be helpful in evaluating the mechanisms underlying variability in edge responses.

Variability currently unexplained by the model

Despite the potential for our model to explain much of the inter- and intra-specific variability that has been reported in the literature, it is clear that even when factors such as habitat quality, resource distribution, and seasonal or regional variation in resource use are controlled for, some variability will remain. However, we suggest that this remaining variability will generally be restricted to finding both a consistent unidirectional edge response (either positive *or* negative) and neutral responses. For instance, Sisk and Battin (2002) review edge responses for 12 bird species whose results were reported in multiple studies, all at forest edges and all located in the eastern U.S. No species showed

both positive *and* negative responses, but most were reported to show neutral responses in some studies, as well as significant, unidirectional responses in others. For instance, the ovenbird (*Seiurus aurocapillus*) showed negative responses in two studies, with two additional studies reporting neutral responses. Similarly, the red-eyed vireo (*Vireo olivaceus*) had negative responses reported in three studies and a neutral response reported once.

One reason for this type of intra-specific variability is that there are several ecological factors that are known to influence the pattern of resource distribution relative to edges, as well as a species' response to that pattern. As these different ecological factors interact, realized edge responses will range along a continuum from strong to weak, and in some cases the effects may disappear altogether. Although there are likely several ecological factors that interact to change the strength of a species' edge response, those that have received the most attention are edge orientation and edge contrast (Murcia 1995). Edge orientation has been most rigorously explored within the plant literature. Several studies have shown how the directional orientation of the edge within the landscape may influence both the strength and depth of penetration of edge effects, but not the direction of the response (Wales 1972, Ranney et al. 1981, Palik and Murphy 1990, Fraver 1994). Edge contrast describes the degree to which bordering patches differ structurally from each other. Unfortunately, most studies have not controlled for habitat quality on both sides of the edge while varying edge contrast, making it difficult to separate the influence of edge contrast from habitat quality. However, Fletcher and Koford (*in press*) showed that the magnitude of negative edge responses for a grassland bird was stronger at forest (high-contrast) compared to agricultural (low-contrast) edges, even though both constituted equally poor habitat. Despite the paucity of studies that rigorously explore this issue, it is reasonable to suspect that edge contrast will influence the strength of edge responses when other factors are held constant. This is based on the

assumption that changes in habitat quality across edges are likely to be less pronounced when bordering patches are structurally more similar. Another factor suggested to impact the magnitude of edge responses is internal patch heterogeneity (Noss 1991, Restrepo and Vargas 1999) and there are likely other factors that underlie the variable strength of some edge responses. Identifying these factors and determining how they predictably interact with resource distribution will allow for important refinements to our model.

Another factor that may explain some unpredicted neutral edge responses is that certain species may intrinsically be less sensitive to the presence of habitat edges. Several authors have suggested that specific life-history or ecological traits should be associated with an intrinsic sensitivity to edges, including body size, mobility and defenses against predation (Wiens et al. 1985, Lidiker 1999). Based on our model, all species are expected to show positive, neutral and negative edge responses depending on the edge type encountered. Therefore, to truly gauge "intrinsic" edge sensitivity, it would be necessary to determine whether there are certain species or groups of species that either consistently show edge responses where they are predicted (edge-sensitive species) or *never* show edge responses, regardless of predictions (edge-insensitive species). This is currently difficult, because most studies have taken place at a single edge type (forest edges), and information on resource distribution is often lacking. However, there are several biological reasons to suspect that certain species or groups may be particularly sensitive or insensitive to edges (based, for instance, on the scale at which they perceive the landscape or the cues they use to asses habitat quality). By using our model to separate neutral responses into those that are predicted and those that are not, it may be possible to determine if there are life-history or ecological traits that are consistently associated with intrinsic sensitivity to edges. Once again, the identification of those characteristics, if they exist, would allow for important refinements to our model.

Ultimately, one of the difficulties of grappling with the underlying causes of variation in the nature and strength of edge responses is the limitation of many field studies. Most empirical studies of edge effects have low site replication and limited statistical power (Murcia 1995) and are unlikely to detect any but the strongest patterns. Therefore, it is difficult to determine if reported neutral edge responses are actually describing situations where a species is distributed evenly across an edge gradient (a truly neutral response) or if it is due to a lack of power to detect responses which may, in fact, be operative. Nevertheless, it is clear that there are many potential causes of the neutral responses that underlie much of the variability reported in the edge literature. Therefore, observing a *neutral* response when a positive or negative one is predicted may not indicate problems with the underlying framework of our model. Instead, the separation of predicted from unpredicted neutral responses should assist in future model refinement through the identification of factors (explored above) that underlie this variability (assuming a study had sufficient power to detect edge responses). In contrast, we consider the observation of a significant response that was *not* predicted (for example, observing a positive response when a negative one was predicted or observing a positive or negative response when a neutral one was predicted) to be indicative of either a flaw in the model framework or an incomplete knowledge of the distribution of critical resources for the focal organism, which may have led to a spurious prediction.

A Preliminary Test of the Model

Rigorous testing of this model will involve determining the distribution of critical resources throughout the landscape for each species of interest, predicting edge responses based on that information, and collecting independent verification data to test predictions. Such detailed data on habitat quality are not usually reported in the edge literature, and obtaining them will require directed field efforts, which we suggest should become standard information reported in future edge studies. However, habitat associations and

general resource use are well described for some taxa, particularly birds, and it is possible to apply the model absent local information on resource use and distribution, although predictions are likely to be affected by the relative coarseness of this information. In order to perform a preliminary test of our model, we made predictions of edge responses for bird species whose empirical responses had been reported in the recent literature. We then compared model predictions with observed responses to determine how well our model performed. We focused on North American birds because habitat associations are well described for most species. We limited our search to studies of multiple species at abrupt edges between forest and open habitats (because habitat associations are well described relative to both of those habitat types). In order to allow the most robust comparisons of predicted and actual responses, we selected studies where quantitative data on edge responses were presented, with statistics, for a minimum of ten species. In addition, we required at least three replicate sets of sampling points to increase the likelihood that edge responses, if present, were detected.

Three edge response studies met our criteria. Germaine et al. (1997) studied edge effects at small openings (0.4 ha) created by timber cuts in a hardwood forest in Vermont. Five independent study areas were established, with surveys being conducted within patch cuts, and inside the forest at three distance classes (50, 100, and 200 m) from forest edges. June surveys were conducted in 1991 and 1992 and data on the edge responses of 25 species were presented. Sisk et al. (1997) reported edge responses for 26 birds at oak woodland-grassland edges in central, coastal California (detailed statistics were reported in Sisk 1992). Four transects were surveyed during the 1988 and 1989 breeding season, with plots placed at the edge, 100 and 200 m into the oak woodland and grassland habitats. Brand and George (2001) studied edge effects of 14 species within redwood forest patches bordered by open habitat, including fields, roads or powerline corridors. They established 12 rectangular plots extending 400 m into the forest (no surveys were

conducted in open habitat) and performed surveys during the 1996 and 1997 breeding seasons. For all three studies, we examined edge responses within the forest patches.

Because all three of our focal studies took place within forest patches bordered by openings of various sizes and types, we needed to classify each species relative to their associations with forest and open habitat. For this coarse test of the model, we assumed that habitat association, as reported independently in the bird literature, relative to patch type (forest vs. open) was a suitable proxy for resource distribution. However, this assumption did not seem appropriate for shrub-dependent species because shrubs are often associated with both forest and open habitat. Therefore, shrub-dependent species were excluded from this test. We used detailed accounts from the Birds of North America series (individual references given in Table 2.1) to classify each species. When these accounts were unavailable, we used less-detailed information found in Ehrlich et al. (1988). All information on edge associations was ignored when making predictions. Each of the 59 species represented in the three studies was placed into one of the four following categories:

- FOREST: Species was associated solely with forest.
- OPEN: Species was associated solely with open habitat, which included any habitat with no overstory (including scrub).
- BOTH: Species was associated with both FOREST and OPEN habitats. This included any species that was identified as being associated with openings in forests or solely with open woodlands (thus, habitat associations were defined at a finer scale than the patch). Species that were classified as BOTH were further classified as to whether resource distribution was complementary or supplementary. When resource distribution was described as divided between habitats (always in reference to nesting and foraging), resource distribution was listed as COMPLEMENTARY. Absent this information, species accounts simply did not give any information on resource use,

and rather than assume it was supplementary, we classified resource distribution as UNKNOWN.

- SHRUB-DEPENDENT: Associated with shrub habitat. These species were excluded from the analysis.

Of the 59 species classified, seven were shrub-dependent and so were excluded from the model test. Table 2.1 summarizes habitat associations for the remaining 52 species and, for species associated with both forest and open habitat, whether or not resource distribution was determined to be complementary. Predictions were generated for these 52 species, with five of those species represented in two studies, resulting in a total of 57 separate tests of the model. Figure 2.3 illustrates how predictions were generated for each species and how well observations in the three studies matched each prediction. Of those 52 species, 29 were classified as forest-associated and therefore predicted to show a negative response at forest edges. No species was identified as being solely associated with open habitat. The remaining 23 species were classified as being associated with both forest and open habitat and, of those, five were shown to have complementary resource distribution and therefore predicted to show a positive edge response. For the remaining 18 species, we lacked the information to determine if resource use was complementary (Fig. 2.1b) or supplementary (Fig. 2.1c), so we predicted either a positive or neutral response, but excluded the possibility of a negative one.

Our model did well in predicting edge responses for the 57 cases tested from these three empirical studies (Table 2.2). With only the most basic information on habitat associations and resource use, we were able to correctly predict 25 out of 29 cases (86%) where positive or negative edge responses were reported, a significantly better result than would be expected if predictions were made at random (χ^2=15.21, df = 1, $p < 0.0001$). Our model did best when predicting positive responses. In four of the six cases when a positive response was predicted, it was observed with neutral responses occurring in the

remaining two cases. When we lacked information to differentiate between neutral and positive responses, but were able to exclude the possibility of predicting a negative response (18 cases), only neutral or positive responses were observed. Finally, our model was least successful in predicting negative edge responses. Of the 33 cases where negative responses were predicted, they occurred only 11 times, with 18 neutral and four positive responses observed. As explained above, the observed neutral responses may be due to lack of statistical power, insufficient detail regarding habitat quality, or intrinsic edge insensitivity, a possibility that is not currently addressed by our model. However, the four positive responses directly contradict the predictions of the model. One species (the dark-eyed junco, *Junco hyemalis*) is known to be associated with open-canopy forests and was listed as an edge-exploiter in its species accounts, information that we ignored when generating predictions. However, we have no explanation for the responses of the other three species (wood thrush, *Hylocichlla mestelina*, Swainson's thrush, *Cathaurs ustulatus*, and black-throated blue warbler, *Dendroica caerulescens*) all of which have strong forest associations. As better site-specific information on resource use and distribution becomes routinely reported within the literature, cases such as these, where observed edge responses are in direct contradiction of predictions, can be more rigorously explored.

Conclusions

Our predictive model presents a framework for understanding the broad patterns and much of the variability in edge responses reported in a large, mostly descriptive literature. This literature reports variable positive, neutral and negative edge responses for many species, suggesting complex mechanisms and few general patterns. However, when viewed in the light of this relatively simple model, it is clear that variability in edge responses should be expected, and that these responses are predictable based on the patterns of resource distribution and use by each species. We also present a framework

for investigating variation in edge responses that is not explained by our model, through the exploration of ecological factors that may underlie the variable strength of edge responses and the search for life-history or ecological traits associated with intrinsic edge sensitivity. By examining previous studies under the umbrella of this predictive framework, and incorporating modest habitat characterizations into future edge studies, a more mechanistic understanding of edge effects will emerge. As habitats become increasingly fragmented, conservation decisions will necessarily rely on predictive models of how multiple species are expected to respond to complex and continuously changing landscapes. This model of edge effects fills a gap in a larger conceptual framework that attempts to explain how habitat heterogeneity and the spatial patterning of landscapes impact the abundance and distribution of a broad range of organisms.

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Table 2.2. Tally of outcomes based on predicted edge responses and observed results for three studies published in the avian literature. Species by species predictions are shown in Table 2.1 and results in Figure 2.3.

	Result		
Prediction	**Neg**	**Neutral**	**Pos**
Neg	**11**	**18**	**4**
Neutral	**0**	**0**	**0**
***Neutral/Pos**	**0**	**8**	**10**
Pos	**0**	**2**	**4**

Neutral/Pos: Not enough information on resource use to differentiate between positive and neutral edge responses.

Figure Legends

Figure 2.1. A general model of edge responses that predicts changes in population abundance near habitat edges based on resource distribution. When resources are concentrated in one patch (a), then a transitional edge response (negative in one patch, positive in the other), is predicted. When different (complementary) resources are separated between the two patches (b) then a positive edge response is predicted. However, if patches contain supplementary resources (i.e. no essential resources are available in one patch that are not also available in the other,) then a neutral response is predicted (c). When resources are concentrated along the edge, then a positive response is once again predicted (d). In reality, all of these situations may exist along a continuous gradient of habitat quality in the adjoining patches (see Fig. 2.2).

Figure 2.2. The continuous nature of edge responses as bordering patch quality varies. For the case when two adjacent patches are of similar quality (a), the predicted edge response (change in abundance across the edge) is based on whether the distribution of resources (b) is complementary or supplementary (see figure 2.1). As habitat quality in the adjacent patch degrades (c; solid, then dashed lines show increasing degradation of Habitat II), then edge responses gradually begin to resemble the transitional response between habitat and non-habitat (d). Within this framework, edge responses are expected to be strongest when the adjacent patches are most different (either due to resource distribution or habitat quality).

Figure 2.3. Flowchart that demonstrates how edge response predictions were generated for 52 bird species, and how predictions compare with observed edge responses, as reported in three published studies. Model predictions were based on the habitat associations of each species, and the distribution of resources on both sides of the habitat edges (see Table 2.1 for species-by-species details). From this information, a positive, neutral or negative edge response was predicted based on our model (see Fig. 2.1 and text for details). In some cases, resource distribution was not known, so we predicted *either* a positive or neutral response, while excluding the possibility of a negative response (see Figs. 2.1b, c). Results are shown for each species (identified with standard four letter codes; latin and common names are given in Table 2.1) reported in three studies (Germaine et al. 1997, Sisk et al. 1997, Brand and George 2002). The superscript indicates the study reporting the observed responses. The type of edge response observed (positive, neutral, or negative) is indicated in parentheses after each species code.

Figure 2.1

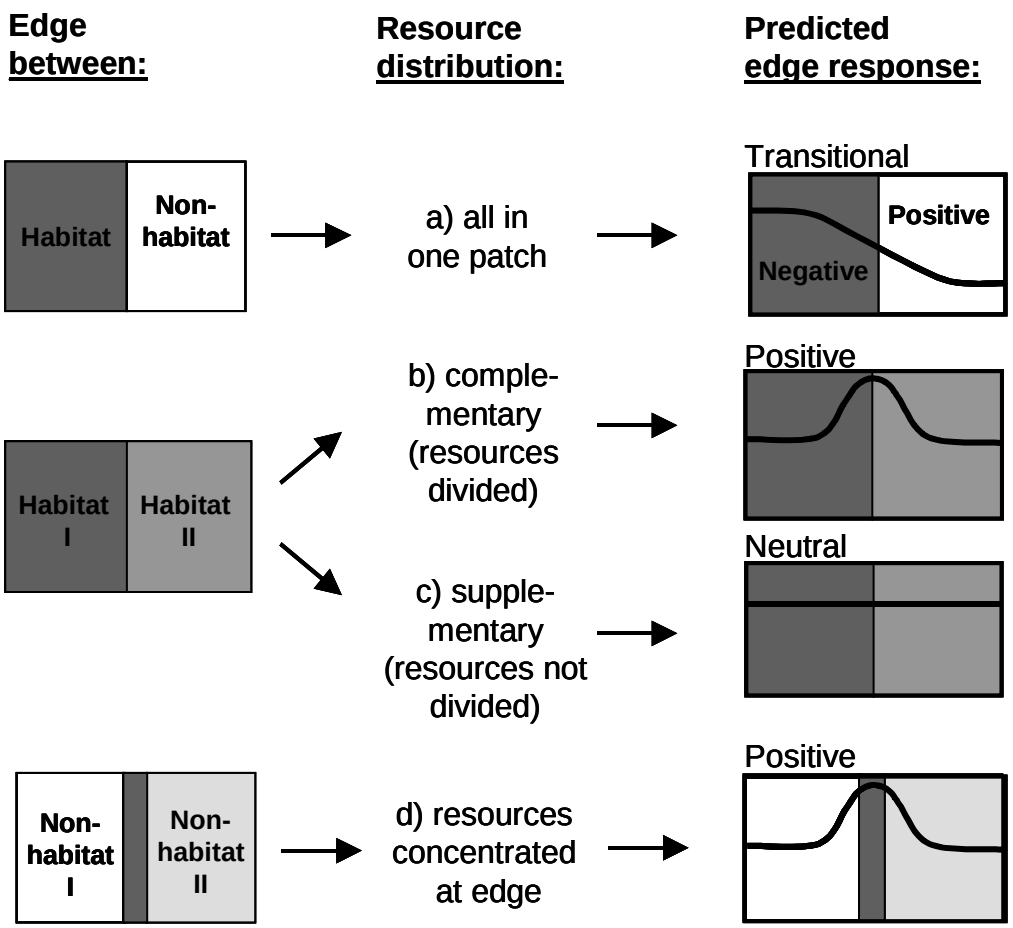

Edge between:
Resource distribution:
Predicted edge response:
Habitat
Non-habitat
a) all in one patch
Transitional
Positive
Negative
Habitat I
Habitat II
b) comple-mentary (resources divided)
Positive
c) supple-mentary (resources not divided)
Neutral
Non-habitat I
Non-habitat II
d) resources concentrated at edge
Positive

Figure 2.2

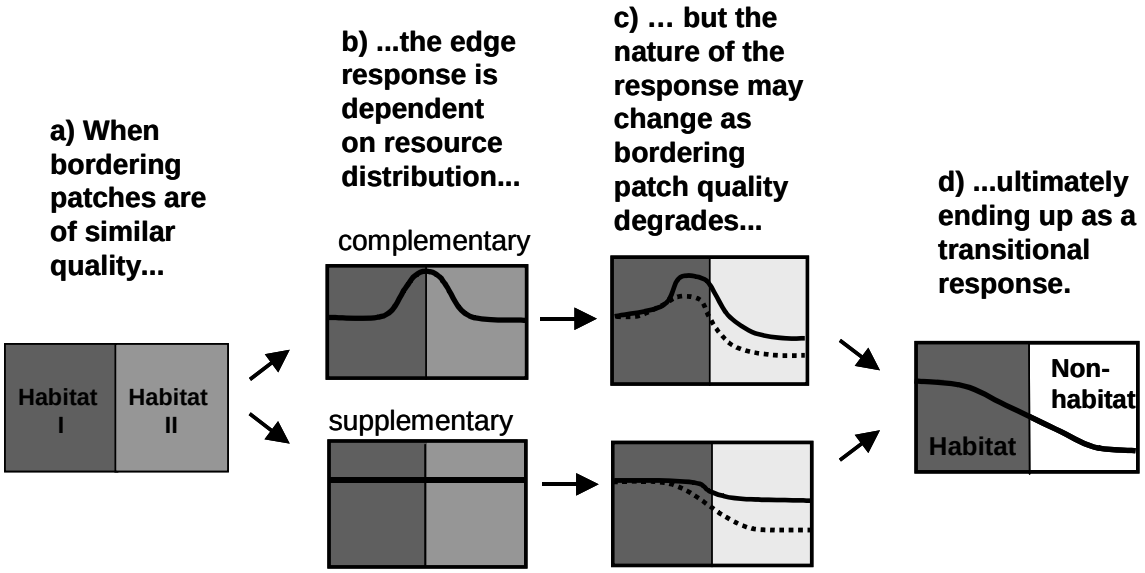
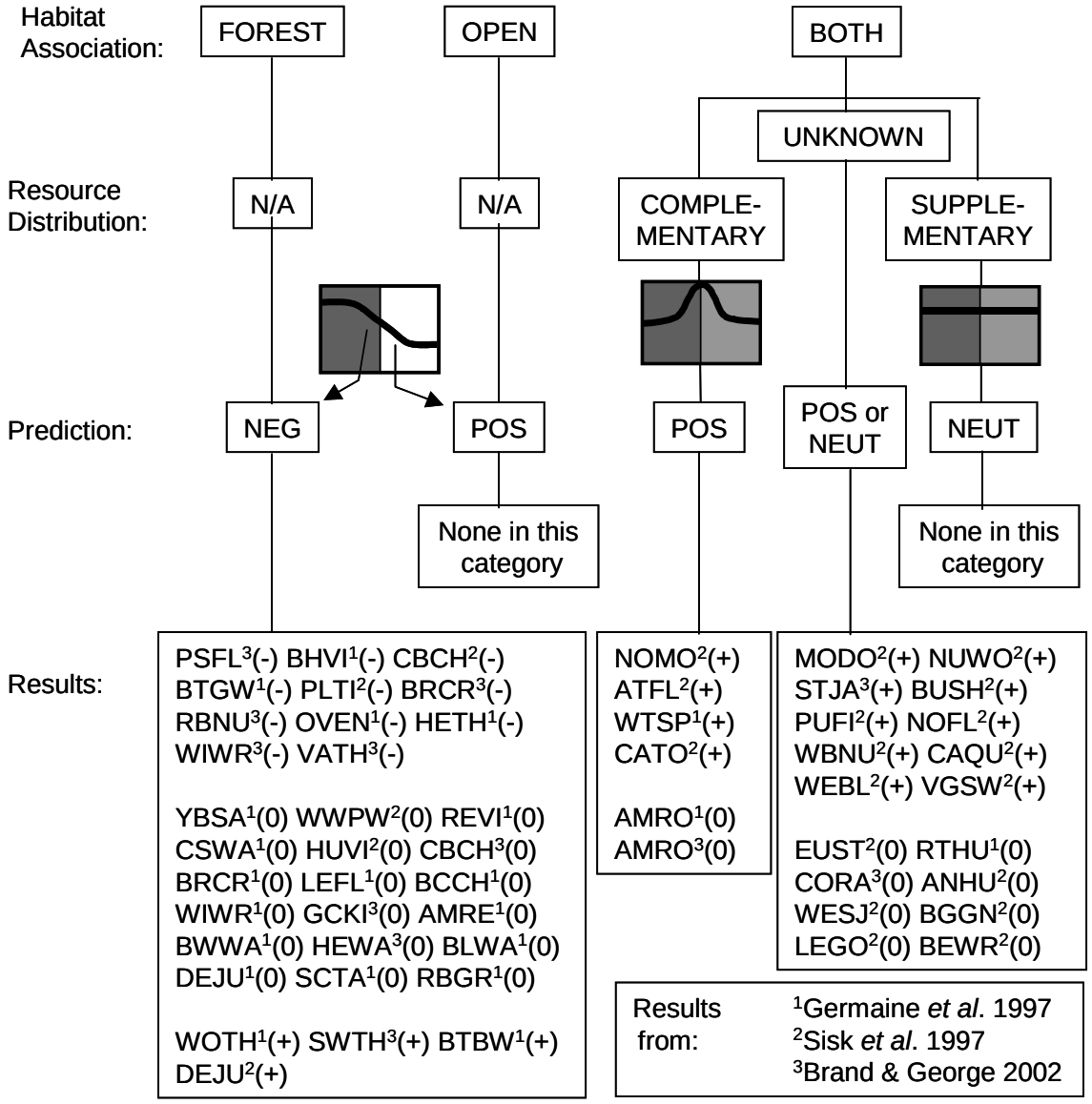

a) When bordering patches are of similar quality...
Habitat I
Habitat II
b) ...the edge response is dependent on resource distribution...
complementary
supplementary
c) … but the nature of the response may change as bordering patch quality degrades...
d) ...ultimately ending up as a transitional response.
Non-habitat
Habitat

Figure 2.3


Habitat Association:
FOREST
OPEN
BOTH
UNKNOWN
Resource Distribution:
N/A
N/A
COMPLE-MENTARY
SUPPLE-MENTARY
Prediction:
NEG
POS
POS
POS or NEUT
NEUT
None in this category
None in this category
Results:
PSFL3(-) BHVI1(-) CBCH2(-) BTGW1(-) PLTI2(-) BRCR3(-) RBNU3(-) OVEN1(-) HETH1(-) WIWR3(-) VATH3(-)
YBSA1(0) WWPW2(0) REVI1(0) CSWA1(0) HUVI2(0) CBCH3(0) BRCR1(0) LEFL1(0) BCCH1(0) WIWR1(0) GCKI3(0) AMRE1(0) BWWA1(0) HEWA3(0) BLWA1(0) DEJU1(0) SCTA1(0) RBGR1(0)
WOTH1(+) SWTH3(+) BTBW1(+) DEJU2(+)
NOMO2(+) ATFL2(+) WTSP1(+) CATO2(+)
AMRO1(0) AMRO3(0)
MODO2(+) NUWO2(+) STJA3(+) BUSH2(+) PUFI2(+) NOFL2(+) WBNU2(+) CAQU2(+) WEBL2(+) VGSW2(+)
EUST2(0) RTHU1(0) CORA3(0) ANHU2(0) WESJ2(0) BGGN2(0) LEGO2(0) BEWR2(0)
Results from:
1Germaine et al. 1997
2Sisk et al. 1997
3Brand & George 2002

BUTTERFLY EDGE EFFECTS ARE PREDICTED BY A SIMPLE MODEL IN A COMPLEX LANDSCAPE

By Leslie Ries

Abstract

Edge responses have been widely studied for decades and they form a critical component of our understanding of how organisms respond to different landscape structures. However, the lack of a general, conceptual framework has made it difficult to understand the patterns and variability reported within the edge literature. We present results on the edge responses of 15 butterfly species at 12 edge types within a complex, desert riparian landscape and show how those results can be more easily understood within the framework of a predictive model. This model proposes that organisms should avoid edges of less-preferred habitat, but show increased abundance near preferred habitat or habitat that contains additional resources. Observations matched model predictions more than would be expected by chance ($p = 0.01$) for the 176 species/edge combinations tested. In cases where positive or negative edge responses were predicted, observed edge responses matched those predictions 70% of the time, significantly more ($p < 0.001$) than would be expected by chance. When multiple edge responses were observed for the same species at the same edge type over the three-year study, in 13 of 14 cases those responses were in the same direction (positive *or* negative). The majority of unexplained variation came from observing unpredicted neutral results, which were over four times more likely compared to unpredicted positive or negative responses. The relative difference in the strength of habitat preferences was the main factor determining whether predicted edge responses were observed. The model did not perform equally well for all species and all habitat types, and we explore factors, such as internal habitat heterogeneity, gaps in knowledge on resource distribution, and species-specific

characteristics, that may have contributed to the observed variation. Overall, we suggest that edge responses may be predicted with relatively basic information (habitat preferences and resource distribution). Finally, when edge responses are observed, they are largely consistent and often predictable. Therefore, the key to better understanding their variable expression is to determine which ecological factors predictably weaken responses and lead to neutral results.

Introduction

Understanding ecological responses to the presence of habitat edges is critical to understanding landscape-scale phenomena such as the interaction of patches within a landscape mosaic (Wiens et al. 1985, Dunning et al. 1992, Cadenasso et al. 2003) or the impacts of habitat fragmentation (Laurence and Yensen 1991, Sisk and Margules 1993, Sisk et al. 1997). Edge effects have been studied for decades (e.g., Lay 1938, Johnston 1947), with a tremendous number of published studies emerging in the last twenty years, confirming that a variety of taxa do indeed respond to the presence of habitat edges (for reviews, see Paton 1994, Murcia 1995, Risser 1995, McCollin 1998, Lidiker 1999, Lahti 2001, Chalfoun et al. 2002, Sisk and Battin 2002). Despite the attention this topic has received, including an increasing focus on underlying mechanisms (Fagan et al. 1999, Cadenasso et al. 2003), there has been no overarching theoretical framework (Murcia 1995) or general model available to predict the responses of organisms to edges in a variety of landscapes (Chapt. 2).

The few, general edge-related patterns that have been noted, such as increases in predation and parasitism (Paton 1994, Lahti 2001) or the identity of certain species as "edge" or "interior" species (Temple 1986, Hansen and Urban 1992) not only comes largely from studies of birds at forest edges, but the consistency of even these patterns

has recently been challenged (Villard 1998, Chalfoun et al. 2001, Sisk and Battin 2002, Baker et al. 2003, Imbeau et al. 2003). As the scope and subject of the edge literature has expanded recently to include a wide variety of taxa, including insects (Didham et al.1998, Foggo 2001, Ries and Fagan 2003), nematodes (Imaz 2002), bats (Grindal 1999, O'Donnell 2000), microbes (Belnap et al. 2003), and many others, the lack of a conceptual framework has made it increasingly difficult to make any sense of the flood of reported patterns. A specific example of this can be found in an emerging literature on butterfly responses to habitat edges. While most of the studies on butterfly responses to edges have been in relation to the role edges play in directing movement or mediating dispersal (Schultz 1998, Haddad 1999, Meyer and Sisk 2001, Pryke and Samways 2001, Ries and Debinski 2001, Schultz and Crone 2001), several recent studies have shown that certain butterfly species either avoid (Shultz 1998, Haddad and Baum 1999) or are attracted (Ravenscroft 1994, Bergmann 1999, Wahlberg 2001, Ide 2002) to edges. Although some of these studies include data to show how changes in microclimate or host plant distribution were driving these patterns, there is no overarching framework to understand when specific butterfly species should be expected to avoid, be attracted to, or ignore edges. Therefore, it is difficult to extrapolate the results to other species or landscapes or gain a general understanding of which factors are most important in driving butterfly responses to habitat edges.

A recent focus on the variability of edge responses may leave the impression that edge responses are so species- and context-specific that it is largely an idiosyncratic phenomenon. However, much of this variation comes from comparing species' responses at different edge types (Murcia 1995). In addition, it is important to note that

when individual species do show different responses at the same edge type, this variability generally consists of observing uni-directional edge responses (positive *or* negative) in addition to neutral results rather than observing both positive and negative responses (Chalfoun et al. 2001, Sisk and Battin 2002, Chapt. 2). This suggests that we need edge response models that not only predict the direction of responses expected for a specific organism at a specific edge type, but that we also need to determine which factors may lead to failing to observe a response when one is expected. We recently proposed a model that suggests that the availability and distribution of resources throughout the landscape drive many of the edge responses reported in the literature (Chapt. 2). The objectives of this study were to: 1) describe the edge responses of several butterfly species at a variety of edge types in a complex landscape, 2) determine if the application of our predictive model of edge effects (described in detail below) can help make sense of those patterns, and 3) for variability that is not explained by our model, determine if there are ecological or species-specific factors that explains additional variation and can be used to refine our model for future applications.

A resource-based model of edge effects

This model (illustrated in figure 3.1) is a synthesis of many of the patterns and mechanisms that have been reported in the literature and is described fully in Chapter 2. The goal of the model is to predict where on a heterogeneous landscape edge-related gradients in density will occur. It is a patch-based model with edges defined as the boundary between two adjacent patches. Predictions are based on two factors: habitat preferences and the distribution of resources between those two patches. When a species shows a higher overall density in one of the adjacent patches, then that patch is defined as

the “preferred” habitat, and the other patch is defined as “less-preferred”. When there is no difference in density between the two patches, they are defined as “equally preferred”. Edge response predictions are made separately in each patch based on whether resources in the adjacent patch are complementary or supplementary to the patch where the prediction is being made (the focal patch). Complementary distribution is defined as the adjacent patch containing resources that are not also available in the focal patch (Dunning et al. 1992, McCollin 1998, Fagan et al. 1999), while supplementary distribution is defined as the adjacent patch containing no resources that are not also available in the focal patch. A positive edge response is always predicted when a patch is less preferred or resource distribution is complementary. When resource distribution is supplementary, a negative response is predicted when habitat is preferred and no response is predicted when there is no preference (Fig. 3.1). I used these general rules to make predictions for 15 butterfly species within desert riparian habitat, where I identified six different pairs of adjacent patch types. Surveys were done on both sides of the edge, resulting in patterns described at 12 different edge types.

By applying this model to numerous butterfly species at multiple edge types, we had the opportunity not only to test the general predictive power of the model but to determine if there are consistent ecological or species-specific factors associated with cases where the model did not accurately predict the observed outcome. As described above, much of the reported variation in the literature comes from species showing both uni-directional responses and no response at the same edge type, so identifying the factors that lead to unpredicted neutral results will be a key component in understanding the variability unexplained by our model. Ries and Sisk (Chapt. 2) reviewed three

factors that were likely to lead to observing no edge response, even when a positive or negative response is expected. Landscape characteristics, such as variation in the structural contrast of edges, edge orientation within the landscape, and internal heterogeneity of patches, may be associated with variation in edge response strength and subsequent detectability. In addition, although our model will always predict edge responses when there is a significant habitat preference (see Fig. 3.1), the resulting edge responses are predicted to be weak when habitat preferences are weak (Chapt. 2). The second factor, intrinsic insensitivity to edges, suggests the possibility that some species will generally be less likely to show edge responses, regardless of their habitat preferences, resource distributions, or any other factors that may be associated with edge responses. Several life-history or ecological characteristics have been suggested to be associated with decreased sensitivity to edges, including mobility, susceptibility to predation, and relative body size (Wiens et al. 1985, Lidicker 1999). Other factors are possible, some of which may vary depending on the taxon of study. Finally, it was noted that many studies lack sufficient replication to detect any but the strongest edge responses, so observed neutral results may, in some cases, be due to a lack of statistical power. In evaluating the performance of our model, we separate observed neutral results into those that were predicted by the model and those that were not in an attempt to identify landscape factors or species-specific traits that may correlate with a decreased likelihood of observing predicted responses. However, based on the reasons given above, observing unpredicted neutral results does not necessarily conflict with the underlying structure of our model. In contrast, situations where unpredicted positive or negative edge responses are observed (i.e. observing a positive response when a negative one was

predicted or observing a positive or negative response when a neutral one was predicted) will be considered indicative of a flaw either in the structure or application of the model and will be examined separately.

Test system: butterflies in desert riparian habitat

Butterflies in desert riparian habitat present an ideal system for conducting an empirical test of this model's predictions. Southeastern Arizona is a center of butterfly diversity, with approximately one-third of all North American species occurring there (Bailowitz and Brock 1991). Thus, butterfly responses to habitat edges can be examined for many species with a wide range of ecological traits. The area's high diversity has cultivated an active group of butterfly enthusiasts, thus many of the local host and nectar resources are described (Bailowitz and Brock 1991), facilitating the use of our resource-based model. The complex structure of desert riparian habitat leads to a multitude of edge types that vary from "classic" forest-open edges, to more subtle edges, such as those between riparian grasslands and desert scrub (Fig. 3.2). In addition, the narrow width of desert riparian habitat results in high edge to interior ratios, and edges tend to be clearly defined because riparian habitat has a strikingly different vegetation composition relative to the surrounding desert. Finally, although most riparian areas have been severely degraded due to water diversions, agriculture and development, they nevertheless provide crucial habitat for most of the regional wildlife (Naiman et al. 1993) so they are areas of critical conservation concern. This study took place on the Upper San Pedro River in southeastern Arizona, the last remaining free-flowing river in the region. Data were collected within the boundaries of the San Pedro Riparian National Conservation Area (SPRNCA) where grazing and agriculture have been excluded since 1987 (Krueper et al.

2003).

The Upper San Pedro River's riparian corridor exists as a two-tiered system with a primary floodplain and upland riparian zone surrounded by desert scrub (Fig. 3.3). The primary floodplain is dominated by Fremont cottonwood (*Populus fremontii*) with some willow (*Salix goodingii*) and, rarely, exotic salt cedar (*Tamarix chinensis*) which is common in many other systems. Because of its recruitment dynamics, there tend to be long narrow strips of *P. fremontii* interspersed with large canopy openings dominated by herbaceous vegetation or shrubs, including *Chysothamnus nauseosus*, *Bacharris salicifolia*, *Celtis sp.*, and *Ziziphus obtusifolia*, leading to a highly heterogeneous structure in the primary floodplain. The dominant woody vegetation in the upland riparian zone is mesquite (*Prosopis velutina*), although other shrubs, including *Atriplex sp.*, *Ziziphus obtusifolia*, *Acacia sp.*, *Flourensia cernua*, *Rhus microphylla*, *Celtis sp.*, and *Lyceum andersonii* are also common. This zone also demonstrates a high degree of heterogeneity in canopy structure, ranging from open grasslands to dense forests (called bosques) where the mesquite forms a closed canopy that reaches heights of 10 m. Intermediate between these two extremes are areas akin to open woodlands, where tall mesquite are abundant, yet sufficiently spaced to allow for the development of a thick herbaceous layer. These intermediate areas represent a mixed structure of open grassland with mesquite forests. To reduce the effects of internal heterogeneity in the upland riparian zone, we classified this zone into three habitat types: grassland (GRASS); mesquite-dominated bosques (MES); and grassland-mesquite mix (MIX) (Fig. 3.3). The surrounding desert scrub is characterized by widely-spaced, low shrubs, dominated by *Larrea tridentata*, *Acacia sp.*, *Prosopis velutina*, *Ephedra sp.*, and *Fouquieria splendens*.

The ground is rocky and often supports only a sparse herbaceous layer.

The juxtaposition of the cottonwood-dominated floodplain (CW), the three categories of upland riparian habitat (GRASS, MIX, and MES), and the surrounding desert scrub (DS) results in six combinations of adjacent habitat pairs of varying structural contrast. We considered edge responses separately on either side of the edges formed by those six habitat pairs, resulting in twelve edge types that were the focus of this study (Fig. 3.3). Structural contrast was defined as low, medium or high based on differences in vegetation height (Fig. 3.2). The category assigned to each of the twelve edge types is detailed in Figure 3.3.

Materials and Methods

Eighteen study areas were established during a three-year period (1999-2001) throughout the 70 km extent of the National Conservation Area (Fig. 3.4). One additional study area was established north of the boundary on land also owned by the Bureau of Land Management. Although we intended to survey the same areas over the three-year study period, some areas had to be abandoned due to fire and other areas located to replace them. Most study areas were at least 1 km from the next closest area with the same edge type, although in one case study areas were only 300 m apart (in one year only) and in two other cases, 500 m. Study areas were selected from aerial photographs by identifying focal edge types that were reasonably accessible, and where habitat was sufficiently wide to accommodate at least a 50 m transect. For purposes of analysis, each study area was considered to be one independent sample site within the boundaries of the SPRNCA. There were from two to six independent areas established for each edge type in each year, with most edge types represented in four to five independent study areas. Mesquite edge types were not surveyed in 2001.

In each study area, all focal edge types were identified, with each area containing up to eight different edge types (the average area contained four). For each edge type within a study area, the point along the edge where transects were established was chosen using a random number generator, subject to the restriction that the edge was well-defined at that point. Transects, placed perpendicular to the edge, consisted of contiguous 10 x 10 m plots that generally spanned both sides of the edge, extending up to 100 m into the interior of each habitat (Fig. 3.3). Because of the general configuration of the riparian landscape, some edge types could usually accommodate 100 m transects, while others were generally restricted to 50 m transects (Fig. 3.3). Desert scrub transects were always 50 m. There were one to three transects established for each edge type within each area, with all transects for the same edge type located within 50 to 100 m of each other. Multiple transects for one edge type within a single area were not considered independent and were pooled later for analysis. Transects were placed so that they were never closer to any another edge type (including roads and railways) than the identified edge. Each edge type in each year was represented by between 3 and 13 transects, with a mean of 8 transects per edge type.

Butterfly surveys were conducted from mid-August through early October in 1999, 2000, and 2001. Three (in 2000,2001) or four (in 1999) complete rounds of surveys were conducted during each year depending on the length of the butterfly flight season, with a survey round lasting three to four weeks. Surveys were begun in the morning after the dew had dried in unshaded areas and ended when the afternoon became overcast due to the seasonal monsoon weather pattern. Surveys began at one end of the transect, with an observer surveying alternate plots to the end of the transect, then

reversing direction and surveying the remaining plots on the way back. This ensured that patterns of abundance along the transect were not associated with time of day. The starting point of the transect was alternated between rounds. Surveys were only begun when the sun was not obscured by clouds. Each 10 x 10 m plot was searched for 3 minutes and all butterflies seen were recorded and, if necessary, caught for identification. Care was taken not to count the same butterfly twice, although double-counting may have occurred, particularly when butterflies were abundant. Nectaring and oviposition activity was recorded, including the species on which a butterfly was nectaring or ovipositing. At the end of each survey, an order-of-magnitude estimate (10s,100s,1000s) was made within each plot of the number of inflorescences of each species that was a potential source of nectar.

In order to identify the distribution of host plants, separate surveys on herbaceous plants were conducted once, during the middle part of each field season, when growth in most species was evident but biomass was not so great as to make detection of smaller plants impossible. A 10 x 2 m portion of the edge of each plot was searched to determine the presence or absence of ten herbaceous species identified as important local host plants, including *Aristilochia watsoni*, *Viguiera dentata*, *Helianthus annus*, *Matalea sp.*, *Sarcostemma sp.*, *Cassia leptocarpa*, *Cassia roemeria*, *Lepidium thurberi*, *Sphaeralcae sp.*, and *Sida sp.* Surveys of perennial, woody plant species were conducted once, in 2001, since woody plant distribution would experience little change over the three year course of the study. Presence or absence of the woody host plants *Atriplex sp.* and *Celtis sp.* was determined for each plot. In addition, percent cover of each major shrub species was estimated. Within the cottonwood habitat, diameter at breast height was recorded

for all trees over 7 cm in diameter, and spherical densiometer readings were taken to estimate canopy openness.

Data Analysis

Of the eighty species observed over the course of the study, 15 butterfly species were sufficiently abundant to be included in the analysis of edge responses. Densities of surveys during peak flight periods, identified separately for each species, were pooled to arrive at a single density measurement for each plot in each year. Edge responses were determined to be positive, negative or neutral using linear regression. Identification of positive and negative edge responses was based on finding a slope parameter significantly different from zero in the model. Because this study used plots within transects, which represent repeated measures along a non-independent sampling unit (Diggle et al. 1994), a mixed model was used with distance to edge as the fixed effect, study area included as a random effect, and plots within transects specified as repeated measures (Littel et al. 1996). Examination of the residuals at varying distances indicated decay in correlation strength as distance increased, so an autoregressive correlational structure was specified in the model (Diggle et al. 1994). The regressions were run with the number of transects in each area (1-3) used as a weighting factor.

In order to generate predictions from our model, we needed to describe habitat preferences of each butterfly species between adjacent patches at each of the six habitat pairs forming the twelve edge types (Fig. 3.3). Then, where habitat was equally or more preferred, it was necessary to determine whether resource distribution was complementary or supplementary. Finally, for the subset of species/edge type combinations where we were able to make predictions, we compared our predictions to

our observed edge responses. We preset our alpha level to 0.10 to identify habitat preferences and edge responses because our statistical power was fairly low and we wanted to identify situations where trends indicated that habitat preferences or edge responses may be operative. This also allowed us to minimize making type II errors, which is an important consideration in this study where we are interested not only in situations where differences are significant, but where there is no pattern. However, all of the comparisons that were used to generate predictions and the edge responses used to test those predictions were subjected to two all-inclusive goodness-of-fit tests (described below). These two tests will allow us to determine how well the responses we observed matched our predictions, or if those observed patterns were likely due to chance and the magnitude of those two p-values can be considered individually. All analyses were done in SAS (v 8.2) or SAS-JMP (v 4.0.4).

For this application of our model, habitat preferences were assigned separately for each of the six habitat pairs based on a species having a significantly higher density in one of the adjacent patches. To compare densities in each habitat pair, all plots were classified according to the five habitat types used in the study, cottonwood (CW), open grassland (GRASS), grassland-mesquite mix (MIX), mesquite-dominated bosques (MES) and desert scrub (DS). The plots situated 0-10 m from the edge were excluded from the analysis to avoid transition zones between habitat types. Density values from each plot within an area were pooled to arrive at one mean density for each habitat type within each independent area. Density data were not normal, but were consistent with having an underlying Poisson distribution. Therefore, a square root transformation was used in order to allow a parametric analysis (Zar 1996). ANOVA was then performed to

determine if habitat type, year, or habitat-by-year interactions were a significant source of variation for each species' density. If there was a significant habitat-by-year interaction, habitat associations were described separately for each year, otherwise data were pooled among years. When habitat was a significant source of variation (either in the pooled or by-year analysis) a pair-wise comparisons was performed between CW and the adjacent GRASS, MIX, and MES patches. A similar pair-wise comparison was also made for GRASS, MIX, and MES patches compared to DS (Fig. 3.3). When there was a significant difference between habitat pairs, then the one with a higher density was identified as the "preferred" habitat, and the one with a lower density as "less preferred". Habitat pairs were identified as being equally preferred when differences in density were insignificant. For this determination, we used a p-value of 0.30 to avoid Type II errors. When p-values fell between 0.10 and 0.30, no predictions were generated because habitat preferences could not be clearly determined.

Local nectar and host plants were identified through a combination of efforts, including: 1) associations published in a local field guide (Bailowitz and Brock 1991); 2) conversations with James Brock, an area butterfly expert who is currently writing a field guide to the caterpillars of North America; 3) our own nectaring and oviposition observations; and 4) observations of eggs and caterpillars on candidate host plants made throughout our three year study. Three butterfly species were identified as nectar and host plant generalists. The remaining twelve species were identified as having either specific host and/or nectar plant requirements. For each plot, the presence or absence of each resource was recorded and the overall probability of occurrence of those key resources was calculated for each habitat type within an area (again, excluding the 0-10m

plots). Proportions were arcsine transformed to permit appropriate use of parametric tests (Zar 1996). Analyses were once again either pooled between years or presented separately for each year when there was a significant habitat-by-year interaction.

In order to identify resource use as complementary or supplementary, it was necessary to determine if either host or nectar plant resources were concentrated in one of the adjacent habitats. For species identified as nectar and host generalists, resource use was listed as supplementary. For the species that we identified as having specific host and/or nectar plant resources, we considered resource distribution to be complimentary if either nectar or host plant resources were twice as likely to be encountered in the adjacent habitat. Otherwise, resources were listed as supplementary. For five species we had only limited data on their host plant usage and distribution, so, in those cases, our determination of resource distribution was partially based on observations we made throughout the three year study. In cases where data on resource use and distribution were limited, we identified confidence in resource distribution designations as low, otherwise they were identified as high. Predictions were not restricted to the cases where confidence was high because that would reduce the number of predictions that could be made. However, the level of confidence in the data on resource distribution will later be used to determine if that was a factor influencing how well the model performed.

Edge response predictions were compared to observations by building a 3 x 3 contingency table that tallied the number of times observations did or did not match predictions (Fig. 3.5). Each cell of the contingency table was classified as to cases where the model was "correct" (the predicted edge response was observed), "neutral" (a neutral result was observed where a positive or negative edge response had been predicted) or

"wrong" (an unpredicted positive or negative edge response was observed) as illustrated in Figure 3.5. To determine if model performance was better than expected by chance, the observed distribution was compared to a null model that assumed independent distribution among rows (predictions) and columns (observations). Fisher's exact test was used to determine if there were more "correct" observations than would be expected by chance, based on the value of the residuals, adjusted to totals in those cells (Agresti 1996). We also looked specifically at the subset of cases where positive or negative edge responses were predicted, and a Chi-square test was used to determine if observed responses were in the predicted direction more than 50% of the time. We also stratified these comparisons to determine if the model performed particularly well or poorly in specific habitats or for certain species.

Logistic regression was used to identify factors associated with model performance. The regressions were run separately to model the probability of three different outcomes: 1) observing neutral responses when a negative prediction was made, 2) observing neutral responses when a positive prediction was made, and 3) observing a "wrong" outcome (i.e. a positive response when a negative one was predicted or vice-versa, or a positive or negative response when a neutral one was predicted, see Figure 3.5). A mixed model was once again used for the logistic regression, but in this case species was used as the random component in the model. There were three candidate factors considered for all three models. The first was edge contrast, ranked as low, medium and high (1,2,3) as described in Figure 3.3. The second was the relative difference in habitat preferences (a continuous variable calculated from actual differences in density between each habitat pair). The third was our confidence in resource

distribution (0 when confidence was low, 1 when confidence was high and 2 when the information was not necessary to make predictions). A fourth factor was considered only for the case of modeling "wrong" outcomes, and that was the type of prediction made (0 if a neutral prediction was made and 1 if a positive or negative prediction was made).

Finally, in order to determine if there were any life-history or ecological traits associated with edge sensitivity, species were ranked according to their sensitivity to edges. Species were ranked from most to least sensitive based on the magnitude of the sum of the adjusted residuals indicating the relative occurrence of "neutral" results (Fig. 3.5). When that number was positive, it indicates more neutral results than expected by chance and, when negative, indicates fewer. Using information in Scott (1986), each species was identified as to several ecological traits that have been suggested to influence edge sensitivity (size, movement, degree of specialization, and vulnerability to predation) and we looked for any association between edge sensitivity and these species-specific traits.

Results

All of the fifteen species showed at least one edge response near at least one of the twelve edge types over the three years of study (Table 3.1). However, there was a great deal of variation in responses across species and among edge types. Twelve of the fifteen species showed positive, neutral, and negative edge responses to different edges, while the remaining three species showed only positive or negative responses, in addition to neutral results. Most observed results were neutral, with positive or negative responses observed 24% of the time. While there was substantial inter annual variability for each species in how they responded to the same edge type, this variability was mostly restricted to showing both neutral and uni-directional responses (either positive *or*

negative, but not both). In 13 out of 14 cases where a species showed significant edge responses at the same edge type for more than one year, the responses were in the same direction (highlighted in Table 3.1).

Model Predictions

In order to generate predictions from our model, we needed to consider both habitat preferences and resource distribution (Fig. 3.1). An example of how we used data to generate, then test, predictions is illustrated for one species (*Phoebis sennae*) at one of the six habitat pairs (cottonwood adjacent to grassland) in 1999 (Fig. 3.6). The first step in generating predictions was considering the habitat preference relative to both adjacent patches. *P. sennae* was shown to prefer grassland habitat (Fig. 3.6a). This was done for all 15 species at all six habitat pairs and a significant habitat preference was found in 53 cases ($p < 0.10$), no habitat preference was found in 44 cases ($p > 0.30$), and no predictions were made in the 25 remaining cases where p-values fell between 0.10 and 0.30 (Table 3.2). This resulted in a combined total of 294 separate opportunities (over three years) to test the predictions of the proposed model. For cases where habitat was either equally or more preferred, information on resource distribution was necessary to make predictions (see Fig. 3.1). No information on resource distribution was necessary when habitat was less preferred (in those cases, edge response predictions were always positive). Fig. 3.6b shows that host plants represented a complementary resource for *P. sennae* within grassland habitat near cottonwood edges (host plants were only found in less preferred habitat). For all 15 species at the twelve edge types, designations of resource distribution (complementary or supplementary) as well as our confidence in those designations (high or low) is shown in Table 3.3. These designations were made

based on the rules described earlier, using data and observations on host and nectar plant resources detailed in Appendix 1. Three species were identified as nectar and host generalists (in one case, host resources were not found within the study area), so resource use was listed as supplementary. For seven of the twelve butterfly species that we identified as having specific host and/or nectar plant resources, we had data on the probability of occurrence of their preferred host or nectar plants. For the remaining five species, we combined data and personal observations of resource distribution (detailed in Appendix 1).

Comparing Model Predictions and Observations

Predictions and observations for each habitat and each species are detailed in Table 3.4. For all habitats and species combined, the model was able to predict the observed edge response more than expected by chance ($p = 0.01$) as indicated by the positive value for the adjusted residuals in the "correct" category (Fig. 3.7). When the model was incorrect, it was 4.3 times more likely that no response was observed when a positive or negative response was predicted, rather than observing an unpredicted positive or negative ("wrong") response. This is also reflected by the fact that the adjusted residuals for the "neutral" category were higher than for the "wrong" category (Fig. 3.7). For cases where a significant edge response (positive or negative) was predicted, 70% of the observed significant edge responses were in the predicted direction, significantly more than would be expected if predictions were made at random, ($p < 0.001$, Table 3.4). The model was correct more often than expected by chance in all habitats except cottonwood (Fig. 3.7) with model performance highest in the upland riparian zone (grassland, grassland-mesquite mix, mesquite). Cottonwood habitat also performed

poorly in the direction test (Table 3.4), with observed responses in the predicted direction only 16.7% of the time. The poor model performance in the cottonwood zone is likely due to the internal heterogeneity of that habitat, which is discussed below. However, due to its overall poor performance, further evaluation of factors influencing model performance omit results from the cottonwood habitat.

The only factor that showed a consistent association with the observation of unpredicted neutral results was the relative density between the two adjacent habitats at each edge type. With greater differences in relative density, it was significantly more likely that the predicted edge response was observed when a positive prediction was made ($t = 2.54$, $df = 65$, $p < 0.05$). The same trend was present for negative predictions, but only approached significance ($t = 1.63$, $df = 59$, $p = 0.108$). Surprisingly, the model was more likely to correctly predict negative responses when edge contrast was low ($t = -2.04$, $df = 59$, $p < 0.05$), although this result was not observed for positive predictions ($p = 0.20$). Higher confidence in resource data either showed no effect (for positive predictions, $p = 0.67$) or was associated with a reduced probability of observing the predicted outcome ($t = -1.73$, $df = 59$, $p < 0.10$). The only factor that was significantly associated with the observation of unpredicted positive or negative edge responses ("wrong" outcomes) was the type of prediction made (positive or negative vs. a neutral prediction), with unpredicted edge responses observed more often when a neutral prediction was made ($t = -1.89$, $df = 204$, $p < 0.10$). The likelihood of observing an unpredicted positive or negative edge response was not influenced by edge contrast ($p = 0.37$), relative density ($p = 0.41$) or confidence in resource distribution data ($p = 0.53$).

Model performance also varied by species (Fig. 3.8) with the model performing

better than expected for nine of fourteen species (*Pieris protodice* was excluded because there were only two opportunities to test the model for this species). Ten of the 14 species showed observed responses in the predicted direction more than 50% of the time (Table 3.4). Ranking species according to their sensitivity to edges revealed increased vulnerability to predation as the only factor that was associated with increased edge sensitivity (Table 3.5). Size, movement, and hostplant specificity seemed unrelated to edge sensitivity for the fourteen species examined In general, members of the family Pieridae were the most sensitive to edges.

Discussion

The results of this study suggest that the highly variable edge responses of a diverse community, when viewed within the framework of our resource-based model, are fairly consistent and predictable, even in a complex landscape with a variety of edge types. The model performed significantly better than a null model (Fig. 3.7) and was able to predict the correct direction of edge responses about 70% of the time (Table 3.4). This suggests that many edge responses can be understood by considering the habitat preferences and resource distribution relative to adjoining habitats. This result contrasts with the conclusions that edge effects are idiosyncratic and difficult to understand or predict (Murcia 1995, Villard 1998, Chalfoun et al. 2001, Sisk and Battin 2002). In this study, the majority of negative edge responses can be attributed to species avoiding the edges of less-preferred habitat. In contrast, positive edge responses can be largely explained by increased densities near preferred habitat or organisms gaining access to resources restricted to adjacent patches. In addition, when multiple, significant edge responses were observed for the same species at the same edge type in more than one year of this three year study, in 13 of 14 cases, the responses were in the same direction.

This suggests that, for the same species at the same edge type, observed edge responses are largely consistent, with the majority of unexplained variation coming from unpredicted neutral results. When the model did not make the correct prediction, it was more than 4 times as likely that no response was observed where a positive or negative response was predicted, compared to cases of observing an unexpected "wrong" (positive or negative) edge response. This is an important distinction because there are several factors, such as edge orientation or structure, that are known to affect edge response strength, therefore making them less likely to be detected when weakened, especially when statistical power is low. Thus, failing to observe a predicted edge response, and instead observing a neutral result does not necessarily conflict with the underlying framework of this model. It does, however, suggest that certain factors interact with habitat preferences and resource distribution, potentially weakening edge responses to the point where they are no longer operative or become effectively undetectable.

There were strong differences in model performance based on habitat type, with the model performing best in the upland riparian habitat (grassland, grassland-mesquite mix, and mesquite) compared to the cottonwood and desert scrub habitat types (Fig. 3.7). One factor that clearly separated the cottonwood from the upland habitat was internal heterogeneity, which has been suggested as a factor that influences edge responses (Noss 1991). Heterogeneity was addressed in the upland habitat by separating it into three habitat types based on canopy structure (grassland, grassland-mesquite mix, and mesquite). In contrast, the cottonwood habitat was spatially heterogeneous with stands of closed-canopy cottonwoods interspersed with large openings. Cottonwoods tended to be concentrated along the edges, with openings more common in the interior of these

patches (data not presented). Most of our study species were more common in open canopy vs. closed canopy areas of cottonwood (data not presented). There were 11 unpredicted negative edge responses in the cottonwood habitat (33% of all unpredicted edge responses in the entire study), which we suggest may have been a response to the presence of closed-canopy cottonwood stands being close to the edge. In retrospect, it may have been more appropriate to separate the cottonwood habitat in a similar fashion to that done in the upland area, or even separate cottonwood stands and open areas into separate habitat types. This result suggests that the initial way that patches are defined within a landscape can have a strong influence on our ability to predict edge effects. There is no obvious reason for the relatively poor performance in the desert scrub habitat, which has a rather homogenous structure of widely dispersed low shrubs. One possible factor is that, considering the expansive nature of the desert scrub habitat, 50 m transects may have been too short to effectively detect edge responses.

The only factor that was consistently associated with observing a predicted edge response (positive or negative) was the difference in preference between the adjacent habitat pairs. This is consistent with our model, which predicts that stronger edge responses should occur when there are greater differences in habitat quality (Chapt. 2). Surprisingly, edge contrast showed no consistent pattern in relation to model performance. It was not associated with our ability to detect predicted positive responses, and it was negatively associated with predictive power for negative edge responses ($p < 0.05$). Even when these data were reexamined to control for habitat type, relative density, and year, low-contrast edges were still more likely to show predicted negative edge responses than were high-contrast edges. Because there were few cases in this study

where the effects of edge contrast could be rigorously compared, this result should be treated with some skepticism. Nevertheless, we found no evidence that edge structure played an important role in influencing realized edge responses.

Although edge structure has often been shown to be associated with observed edge effects (Cadenasso et al. 2003), to truly gauge the effects of edge contrast, habitat quality on either side of the edge needs to be controlled for. There have been few studies that have been able to examine structural contrast while controlling for habitat quality, but they show, contrary to our results, that increasing contrast is associated with stronger edge responses. Fletcher and Koford (2003) found that a grassland bird showed a stronger negative edge response at forest vs. crop boundaries even though both adjacent patch types constituted equally poor habitat. Ries and Debinski (2001) found that edge avoidance behavior for a prairie butterfly was stronger at high contrast edges. In order to rigorously explore the issue of edge contrast, more studies are needed that control for habitat quality while independently examining the role of structural contrast.

Butterfly species differed substantially with respect to model performance (Table 3.4 and Figure 3.8). Predicted responses for nine of the 14 species were correct more than expected by chance (Fig. 3.8). For the remaining five species where model performance was poor, it is possible that there was a gap in our knowledge relative to their primary local host or nectar plants. Alternatively, there may have been resources that were driving those species' distribution patterns that were not considered here, such as the availability of roosting sites, minerals or water (Dennis et al. 2003). However, where the model was incorrect, in most cases it was due to more neutral results than expected, the prevalence of which may indicate a species' relative sensitivity to edges in

general.

Only species that fail to show edge responses where they are predicted should be considered edge insensitive. General classifications of "edge", "interior", and "edge neutral" in birds, for instance, refer to their response to one edge type, forest edges. For example, birds that have been classified as "edge neutral" may be predicted by our model to not show any response to forest edges, but they may be predicted to show positive or negative responses at other edge types and, if they did, would not be truly edge insensitive. A species' level of edge sensitivity should be determined by how often they fail to show responses at edge types where significant responses are predicted (indicated by the two "neutral" cells in Figure 3.5, but not the center cell, where a neutral result is observed but also predicted). It is difficult to currently identify any species that meets this definition of edge insensitivity, because studies have previously not separated neutral results that were expected from ones that were not. However, if there are varying levels of edge sensitivity, it would be useful to identify factors that are associated with this variation. The only factor examined here that seemed to be related to edge sensitivity was vulnerability to predation, which was associated with increased sensitivity to edges (Table 3.5). Edges have long been associated with increased predation and parasitism (Chalfoun et al. 2001, Lahti 2001), and vulnerability to predation has been suggested as a factor that may cause species to be more sensitive to their presence (Wiens et al. 1985). Vulnerability to predation may have been driving some of the patterns observed in our study (Table 3.5), although the results are preliminary. It is also worth noting that most of these edge-sensitive, vulnerable species were in the sub-family Coliadinae within the family Pieridae (Table 3.5), which generally have fewer defenses against predation (Scott

1986). It is therefore possible that other factors common to this sub-family may explain their increased sensitivity to edges. For instance, lighter colored butterflies absorb radiation more slowly than darker butterflies (Scoble 1992). Members of Coliadinae (commonly called sulphurs) are generally yellow and orange, so may be relatively inefficient at capturing radiant heat. Conversely, the five least edge-sensitive butterflies in this study are all predominately brown or black. Therefore, relative sensitivity to microclimate may be a more important determinant of edge sensitivity in butterflies. If this pattern proves to be consistent, whether edge sensitivity is driven by vulnerability to predation, the interaction between microclimate and coloration, or some other factor is worthy of further investigation.

Conclusions

The results of this study suggest that edge responses are more predictable and consistent than is commonly believed. At first glance, the 364 edge responses we report for 15 butterfly species at 12 edge types over three years may seem like an intractable list of conflicting results that are not readily interpretable; however, when viewed within the conceptual framework of our model, many of the results begin to make ecological sense. Negative edge responses can be largely attributed to avoiding non-preferred habitat and positive responses to gaining access to resources in the adjacent patch. Although we detected many more neutral results than predicted, when multiple edge responses were seen for the same species at the same edge type, they were remarkably consistent. Our results highlight the need for better understanding of when neutral results are most likely to occur, and we have identified several factors, including landscape and species-specific variables that may weaken edge responses or make them inoperative, leading to the observation of neutral results. By separating responses into those that were predicted

from those that were not, it was possible to determine to what extent resources were driving edge responses. Furthermore, it made more tractable the exploration of factors, both extrinsic and intrinsic to the study species, that were associated with the likelihood of observing a predicted edge response, thus gaining further insight into the mechanisms driving edge dynamics.

Our model did well in making predictions for several butterfly species at a wide variety of edge types, suggesting that with relatively simple information (habitat preferences and general information on resource distribution), it is possible to make general predictions of when edge responses are most likely to occur. Although the application of our model in this context involved looking at host and nectar plant resources for butterflies, the model could be applied to a wide variety of situations where habitat preferences and general resource distributions are known. A previous, simpler test of the model showed that it was successful in predicting bird responses at forest edges (Chapt. 2), suggesting that this model may have general applicability. Despite decades of study and hundreds of published reports, a coherent, general framework for understanding edge responses has remained elusive because most studies were largely descriptive, with no underlying conceptual model to put variable observations into a larger context (Murcia 1995, Cadenasso et al. 2003, Chapt. 1). This study represents an important step forward in placing edge responses into a more conceptual framework, and develops a blueprint for future studies by suggesting which factors should be taken into account when examining edge responses. Further, the continued development of predictive models of edge responses is critical as we continue to explore the ecological consequences of land-use and management decisions that impact the structure and

function of heterogeneous, dynamic landscapes.

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Table 3.4. Comparison of edge response predictions to field observations. A tally of observed edge responses separated by habitat type and species where negative (-), neutral (0), and positive (+) edge response predictions were made. Model performance is separated into cases where it was correct (C - shaded columns), neutral (N - no response observed when one was expected) and wrong (W - an unpredicted negative or positive edge response). The proportion of times observed edge responses were in the predicted direction is shown, and when n>=10, is compared to a null expectation of 50% using a Chi-square goodness-of-fit test (*P<0.1, **P<0.05, ***P<0.01). Data from cottonwood habitat were omitted from species summaries due to poor performance in that habitat type. Evaluations of overall model performance are illustrated in figures 3.7 and 3.8.

Prediction:	-			0			+			Direction Test		
Observation:	-	0	+	-	0	+	-	0	+	%Corr	n	P
Model Performance	C	N	W	W	C	W	W	N	C			
All habitats	19	57	5	8	68	9	13	93	22	70	59	***
Cottonwood	0	2	0	6	22	2	5	32	1	16.7	6	
Grass	6	26	4	0	3	1	2	12	8	70	20	*
Mix	10	23	0	0	11	3	2	10	3	87	15	**
Mesquite	3	6	0	1	19	1	0	3	0	100	3	
Desert Scrub	0	0	1	1	13	2	4	36	10	66.7	15	ns
Species summaries												
All species	19	55	5	2	46	7	8	61	21	76	53	***
Battus philenor	0	7	0	0	0	0	3	6	1	25	4	
Brephidium exilis	2	7	0	0	1	0	0	0	1	100	3	
Chlosyne lacinia	0	10	1	0	1	1	0	5	1	50	2	
Colias cesonia	1	3	0	1	9	0	0	2	0	100	1	
Colias eurytheme	2	6	0	0	5	0	0	5	1	100	3	
Danaus gilippus	1	5	0	0	2	0	0	6	0	100	1	
Euptoieta claudia	4	0	0	1	3	0	0	0	0	100	4	
Eurema nicippe	0	0	0	0	3	2	1	7	4	80	5	
Eurema proterpia	0	0	0	0	5	0	1	1	2	66.7	3	
Libytheana carinenta	0	2	1	0	3	3	2	12	0	0	3	
Nathalis iole	0	2	2	0	8	0	0	2	0	0	2	
Pholisora catullus	0	1	0	0	2	1	1	4	2	66.7	3	
Phoebis sennae	1	3	0	0	4	0	0	4	9	100	10	***
Pieris protodice	1	1	0	0	0	0	0	0	0	100	1	
Pyrgus communis	7	8	1	0	0	0	0	6	0	87.5	8	

Figure Legends

Figure 3.1. A model to generate predictions for edge responses based on habitat preferences and resource distribution. This diagram shows how predictions are generated on each side of the edge. Resource distribution is separated into the cases where resources are divided between habitats (complementary) or available in both habitats (supplementary).

Figure 3.2. Two of the six study edges showing different degrees of edge contrast. The cottonwood-grassland habitat edge illustrated on the left is classified as a high contrast edge while the grassland-desert scrub edge illustrated on the right is classified as a low contrast edge. All twelve edge types included in this study are classified as having low, medium or high edge contrast (see Figure 3).

Figure 3.3. Classifications of riparian habitat along the San Pedro River. Habitat was divided into five types: the cottonwood-dominated floodplain (CW); an upland riparian zone that was divided into open grasslands (GRASS); mesquite-dominated forests (MES); and an intermediate type characterized by a mixture of mesquite and grassland (MIX); and finally the surrounding desert scrub (DS). The juxtaposition of these five habitat types result in twelve edge types (considering habitat separately on either side of the edge). The shading here is indicative of the general height of vegetation in that habitat type (darker shades indicate taller vegetation). Based on differences in overall vegetation height, each edge type was classified (see superscript) as to the degree of edge contrast: high=1; medium=2 and low=3. Transects composed of contiguous 10 x 10 m plots were established in several study areas for each edge type as illustrated here. Transect length in most study areas for each edge type is also shown.

Figure 3.4. The boundaries of the San Pedro National Conservation Area and the location of study sites. The cottonwood zone is shown in black, upland riparian in gray and surrounding desert scrub in white. Black dots (each scaled to 1km in diameter) show study area locations. One study area was located north of the boundary and is not shown.

Figure 3.5. Evaluation of model performance. A 3 x 3 contingency table illustrates cases where the model is correct (the predicted edge response was observed) or incorrect. Cases where the model was incorrect are divided into two categories: “wrong” (an unpredicted positive or negative response was observed) and “neutral” (a neutral response was observed when a positive or negative response was predicted).

Figure 3.6. An example of generation of edge response predictions and comparisons to observed edge responses for one species (*Phoebis sennae*) at the boundary of cottonwood (CW) and grassland (GRASS) habitat. In order to generate predictions from the model (Fig. 1), we needed to first determine if one of the habitats was preferred. In this case grassland was preferred over cottonwood (a). Next, we needed to determine if either host (b) or nectar sources (c) were largely concentrated in the less-preffered habitat, which was the case for this species’ host plant (b). Therefore, a positive edge response was predicted for both sides of the edge (d). Finally, actual edge responses measured in the

field show that a neutral response was seen within cottonwood habitat at the grassland edge (e), while the predicted positive response was seen within grassland habitat at the cottonwood edge (f).

Figure 3.7. An evaluation of model performance for all habitat types. The residuals (adjusted to cell totals to make them comparable), indicate whether each type of response (correct, neutral, or wrong – see figure 5) were observed more or less frequently than expected by chance. Positive values indicate outcomes that were observed more often and negative values indicate outcomes that were observed less often. P-values are based on Fisher's Exact Test. ***P< 0.01, **P<0.05, *P<0.10.

Figure 3.8. An evaluation of model performance for all species. Results from the cottonwood habitat were excluded due to poor model performance in that habitat type (Fig. 7). The residuals (adjusted to cell totals to make them comparable), indicate whether each type of response (correct, neutral, or wrong – see figure 5) were observed more or less frequently than expected by chance. Positive values indicate outcomes that were observed more often and negative values indicate outcomes that were observed less often.

Figure 3.1

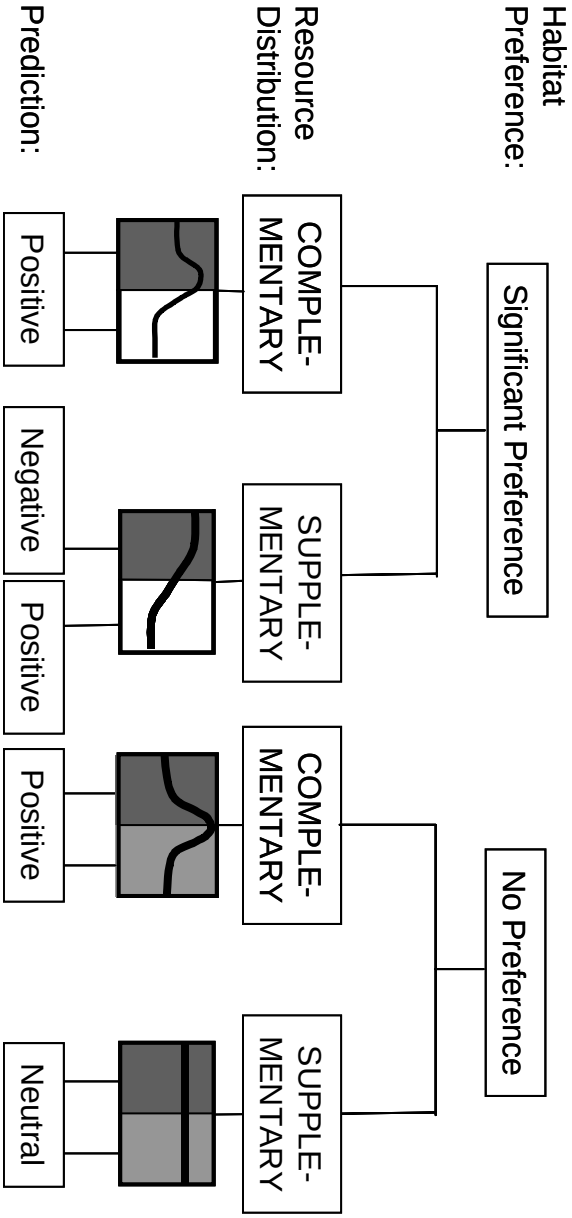

Habitat Preference:
Significant Preference
No Preference
Resource Distribution:
COMPLE-MENTARY
SUPPLE-MENTARY
COMPLE-MENTARY
SUPPLE-MENTARY
Prediction:
Positive
Negative
Positive
Positive
Neutral

Figure 3.2

Figure 3.3

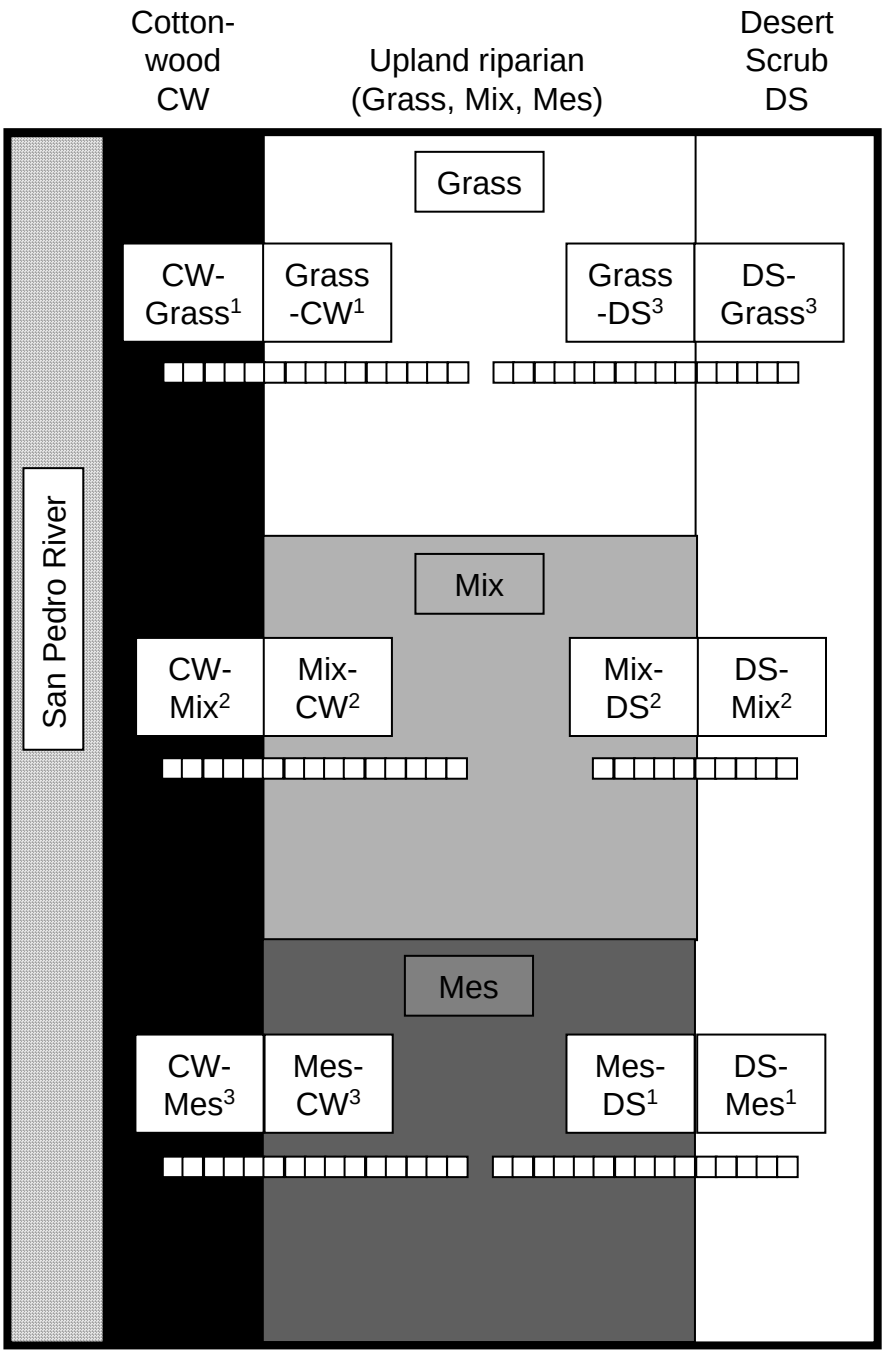

Cotton-
wood
CW
Upland riparian
(Grass, Mix, Mes)
Desert
Scrub
DS
San Pedro River
Grass
CW-
Grass1
Grass
-CW1
Grass
-DS3
DS-
Grass3
Mix
CW-
Mix2
Mix-
CW2
Mix-
DS2
DS-
Mix2
Mes
CW-
Mes3
Mes-
CW3
Mes-
DS1
DS-
Mes1

Figure 3.4

Figure 3.5

ANALYSIS OF MODEL PERFORMANCE			
	Observation		
Prediction	-	0	+
-	Correct	Neutral	Wrong
0	Wrong	Correct	Wrong
+	Wrong	Neutral	Correct

Figure 3.6

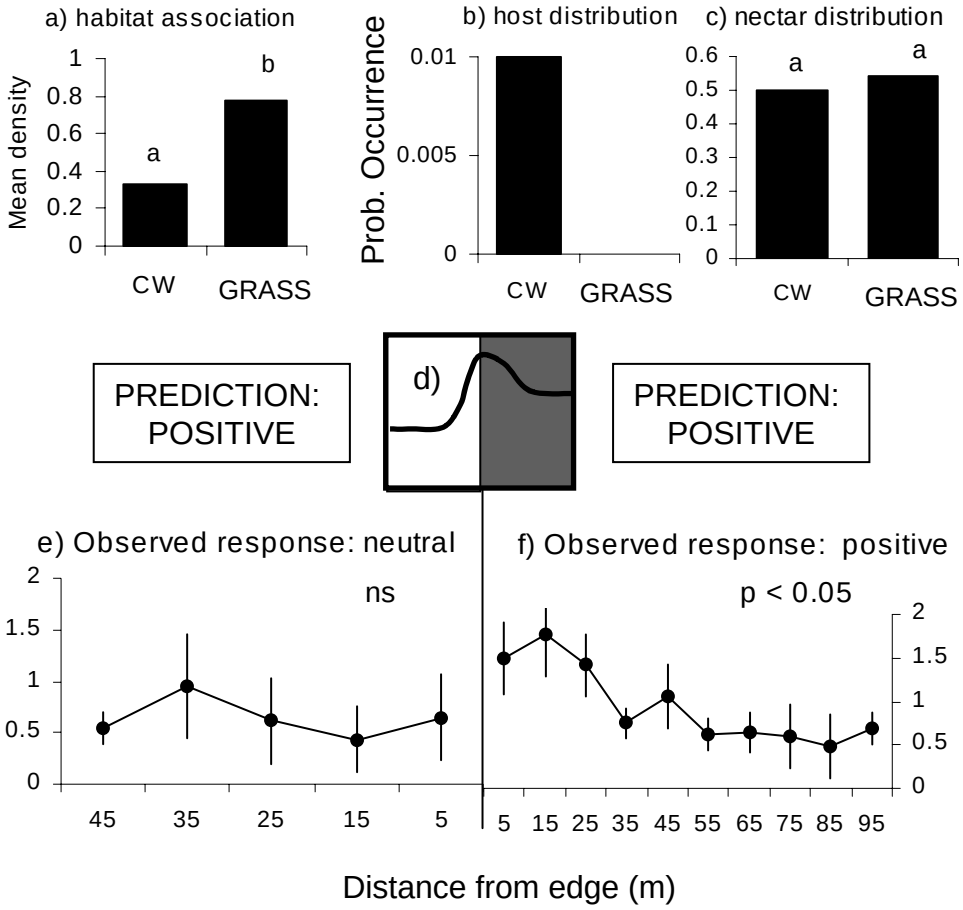

a) habitat association
Mean density
1
0.8
0.6
0.4
0.2
0
a
b
CW
GRASS
b) host distribution
Prob. Occurrence
0.01
0.005
0
CW
GRASS
c) nectar distribution
0.6
0.5
0.4
0.3
0.2
0.1
0
a
a
CW
GRASS
PREDICTION: POSITIVE
d)
PREDICTION: POSITIVE
e) Observed response: neutral
ns
2
1.5
1
0.5
0
45
35
25
15
5
f) Observed response: positive
p < 0.05
2
1.5
1
0.5
0
5
15
25
35
45
55
65
75
85
95
Distance from edge (m)

Figure 3.7

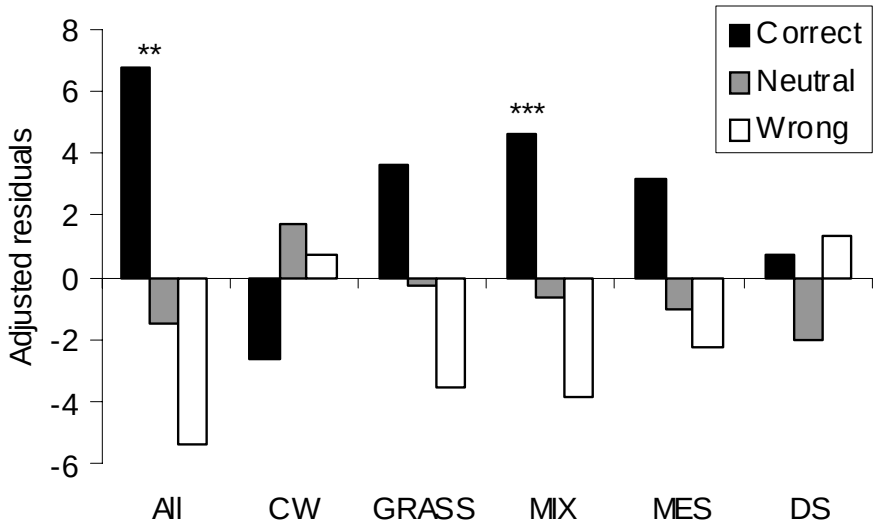
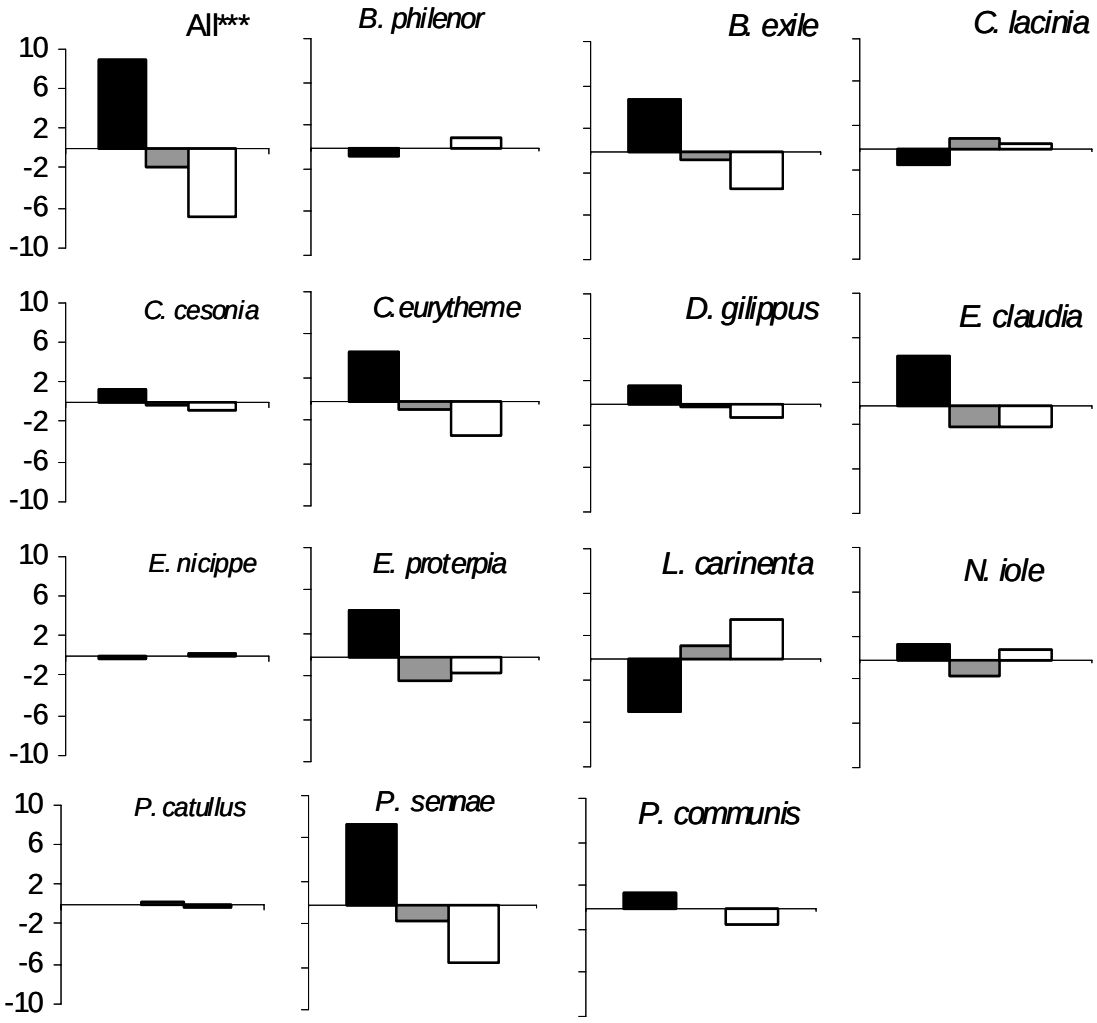

Correct
Neutral
Wrong
Adjusted residuals
8
6
4
2
0
-2
-4
-6
**
***
All
CW
GRASS
MIX
MES
DS

Figure 3.8


All***
B. philenor
B. exile
C. lacinia
C. cesonia
C. eurytheme
D. gilippus
E. claudia
E. nicippe
E. proterpia
L. carinenta
N. iole
P. catullus
P. sennae
P. communis
10
6
2
-2
-6
-10

EXTRAPOLATING EDGE RESPONSES TO LANDSCAPE PATTERNS: LESSONS LEARNED FROM AN EMPIRICAL TEST OF THE EFFECTIVE AREA MODEL

By Leslie Ries

Abstract

Edge responses have been studied extensively for decades, yet tools to extrapolate measured edge patterns to heterogeneous landscapes have been slow to develop. Core-Area models that effectively remove edge zones from the landscape so that only interior areas can be considered are deficient because many important ecological dynamics occur near edges. Additionally, as landscapes become increasingly fragmented, core areas may disappear. The Effective Area Model (EAM) is an alternative to the core area model that allows any measured edge response at all unique edge types to be extrapolated to the entire landscape. We tested the ability of the EAM to predict of butterfly densities in a complex desert riparian landscape. We compared predictions at several independent sites to those of a null model that ignores edge and context effects. The EAM was an improvement over the null model in only one of three patch types. We examine three factors that could explain poor performance and lead to improvements in future applications: the incorporation of local habitat variables, the identification of factors that underlie the variable expression of edge responses, and the development of techniques for dealing with complex edge geometry and the convergence of multiple habitat types. This last factor of how known edge responses manifest within the complex geometry of real landscapes has received little theoretical and even less empirical treatment. Our results suggest that some species may respond to these factors in consistent ways, indicating that general approaches are possible. The known importance of edge responses suggests that their inclusion in landscape-level models is an appropriate goal in many circumstances.

The Effective Area Model is the best tool available to extrapolate the full range of known edge patterns to the landscape, and therefore is not only currently useful to help consider the potential ecological consequences of different conservation or management decisions, but is worthy of further development.

Introduction

Understanding the factors that influence species distributions across heterogeneous landscapes is an important goal for determining how communities may shift under different conservation or management regimes (Wilcox and Murphy 1985, Burkey 1989, Starfield 1997, Stauffer 2002, Van Horne 2002) or in response to global climate change (Parsons 1991, Halpin 1997, Laurance and Williamson 2001). Accordingly, numerous models have been developed to predict species distributions, based on either local habitat variables, landscape-level variables, or both (Stauffer 2002). One of the main goals of landscape-level models is to deal specifically with the subject of how organisms respond to the fragmentation of landscapes. Understanding the impacts of fragmentation has become a major focus within the fields of conservation and management as human-induced changes to landscape structure have become more prevalent (Harris 1984, Faaborg et al. 1985, Wilcox and Murphy 1985, Wilcove et al. 1986), although there remains controversy about the relative importance of fragmentation effects compared to those of habitat loss (Fahrig 1997, Harrison and Bruna 1999).

The effects of fragmentation include increased isolation, reduced average patch size, and increased exposure to the influence of adjacent habitat through edge effects (Saunders et al. 1991). Models that predict the landscape-level impacts of reduced patch size and isolation have a theoretical basis in Island Biogeography Theory (MacArthur and

Wilson 1963) and metapopulation models (Hanski 1999). Island Biogeography Theory, though critical in highlighting issues of fragmentation has been limited in its application to terrestrial systems in contrast to metapopulation models, which have become widely used for making specific predictions of species occurrences in fragmented landscapes (Hanski 1999). Another popular approach to considering the impacts of fragmentation is to use spatially explicit population models (Dunning et al. 1995), which have been extensively used to model the dynamics of species of conservation concern such as the spotted owl (e.g., Lamberson et al. 1994). Partial differential equations have been used to explore the interaction of edge responses and patch structure in a more theoretical context (Fagan et al. 1999, Fagan et al. 2003). Another approach has based predictions on life-history characteristics associated with sensitivity to fragmentation (Hansen and Urban 1992, MacNally and Bennet 1997). Although predictive ability varies between models (Van Horne 2002), their continued use and improvement has led to a better understanding of the ecological processes driving distribution patterns (Starfield 1997, Stauffer 2002). However, landscape-level models that consider how organisms respond to edge-associated gradients in habitat quality have received less attention (Sisk and Haddad 2002) despite the fact that poor performance in some models has been ascribed to not considering edge or context effects (MacNally et al. 2000, Debinski et al. 2001).

There is a strong link between how organisms respond to the presence of habitat edges and how they respond to habitat fragmentation (Brittingham and Temple 1983, Sisk and Margules 1993, Faaborg et al. 1995, Laurence 1997, Gascon and Lovejoy 1998) and the interaction of patches within a landscape mosaic (Wiens et al. 1985, Dunning et al. 1992, Cadenasso et al. 2003). Largely because of this link, there have been hundreds

of studies over the past several decades on ecological responses to the presence of habitat edges (for reviews, see Paton 1994, Murcia 1995, Risser 1995, McCollin 1998, Chen et al. 1999, Lidicker 1999, Lahti 2001, Chalfoun et al. 2002, Sisk and Battin 2002). Studies that are designed specifically to determine the role of edges as a mechanism underlying fragmentation-related patterns have often been able to demonstrate a direct link (Rosenberg and Raphael 1986, Roland 1993, Bolger et al. 1997, Burke and Nol 1998, Didham et al. 1998, Jules 1998, Laurance et al. 1998, Bolger et al. 2000, Davies et al. 2001, Harrington et al. 2001, Beier et al. 2002, Fletcher and Koford 2002). Further, a formal meta-analysis of patch size effects shows that species that avoid edges show increased densities in larger patches, edge-attracted species show the opposite effect, while species that do not respond to edges show weak or no patch-size effects (Bender et al. 1998). This suggests that edge responses are one of the main factors driving area sensitivity. Accordingly, the consideration of the amount of edge is increasingly being incorporated into conservation decisions and landscape-level planning (Schonewald-Cox and Bayless 1986, Sisk and Haddad 2002, Bassett and Edwards 2003, Battin and Sisk 2003, Goldstein et al. 2003). Usually, this involves considering the amount of edge with the landscape. However, the extrapolation of empirical descriptions of edge responses to generate predictions of a species' distribution across a larger landscape has seldom been attempted (but see Ranney et al. 1981, Sisk et al. 1997). This may be due to a limited number of tools that allow the complicated range of edge patterns described to be integrated and interpreted at the landscape level (Sisk et al. 2002). Furthermore, in the cases where known edge responses have been used to predict or infer landscape patterns, determining whether this leads to more accurate predictions of distribution patterns has

received scant attention.

The most common type of model that has been used to incorporate edge patterns into landscape-level dynamics is the Core-Area Model. One of the first demonstrations of the Core-Area Model was by Temple (1986), who showed that the abundance of fragmentation-sensitive, "interior" birds more strongly correlated to the "core area" of a patch (calculated after removing a 100 m zone along the boundary) compared to the patch's total area. The idea of the Core-Area Model was extended by Laurence and Yensen (1991), who suggested that the width of the "edge zone" will vary depending on the ecological parameter being measured. They developed a formula that calculated core area based on depth of edge penetration, that could vary by species, and the shape of the patch of interest. Current software packages, such as Fragstats (McGarigal and Marks 1995), allow users to enter in a depth of edge influence and easily calculate the amount of "core area" in their landscape. As a result of the development of these tools, several authors include measures of core area in their studies (Zipperer 1993, Ohman and Eriksson 1998, Clark et al. 1999, Burke and Nol 2000, Ohman 2000, McGarigal et al. 2001, Honnay et al. 2002).

The main limitation of Core-Area Models is that the "edge zone" is effectively removed, despite the fact that there may be important ecological dynamics that occur there. This patch-centered view may lend itself to the study of highly habitat-specific species, but does not promote the consideration of the mosaic of patches usually present in a landscape. Core-Area Models address only species that avoid edges even though many species show their highest abundance near edges (Brittingham and Temple 1983, Baker et al. 2002, Imbeau 2003). Also, applications of the Core-Area Model do not

allow the consideration of the *type* of edge, which is defined by the type of bordering habitat. Edge effects are known to vary depending on the type of habitat in the adjacent patch (Sisk and Margules 1993, Murcia 1995, Fletcher and Koford 2003, Chapts. 1 and 2). Furthermore, as landscapes become increasingly fragmented, true "core" areas may effectively disappear as the real area of the remaining patches become smaller and more irregularly shaped (Sisk and Margules 1993). In many cases, however, populations often persist in highly fragmented landscapes, even those of so-called "interior" species (Daily et al. 2000), suggesting that modeling habitat by focusing only on "core area" has distinct limitations. In order to more fully account for the spatial context of each patch, the Effective Area Model (Sisk et al. 1997) was developed to allow consideration of all habitats in a heterogeneous landscape and adjust habitat quality within each patch according to the distance to and type of the adjacent patches.

The Effective Area Model

As originally conceived (Sisk et al. 1997), the Effective Area Model (EAM) divided a patch into bands, or edge zones, and applied a uniform density to each zone, based on the type of habitat surrounding that patch, which was then integrated to arrive at an abundance estimate for each patch within a landscape (Fig. 4.1). The term "effective area" refers to the fact that patches of equal area may support larger or smaller populations of a particular organism depending on how that organism responds to habitat edges. Therefore a patch may be effectively larger or smaller from that organism's point of view. Considering the influences of each unique edge type captures many of the structural attributes of a patch, including size, shape, and context. For applications in more complicated landscapes, the model has been developed as an Avenue extension in

Arc View (Sisk et al. 2002). In this version, digital landscape maps are combined with edge response functions to model the density of an organism throughout a heterogeneous landscape.

The model operates by taking a landscape map made up of patches of different habitat types and rendering it into a grid-based coverage. Each unique type of edge in the landscape is identified and located. Then, the edge density, interior density, and depth of edge influence (D_{max}) for each unique edge type can be specified for each species. If no alternate function is entered, the model applies a linear function from the edge to interior densities between 0m and D_{max} for each unique edge type. Applying this approach on an edge-by-edge basis raises two complicating factors that are poorly understood. First, edge influence for each pixel is based solely on its spatial relationship to the nearest point of the closest, adjacent patch and therefore assumes that the complex geometry of a patch edge (i.e. Malcolm 1994, Fernandez et al. 2002) will not strongly influence edge dynamics. For example, edge effects may be stronger near corners than straight edges (Benitez-Malvido 1998, Clark and Kuehl 2002, Fletcher and Koford, *in review*). Second, many points on the landscape may be near two or more types of edges. The EAM provides an averaging filter to smooth predictions near areas where multiple edge types converge at a single point, assuming effects are additive since there is no empirical evidence to suggest otherwise. Once D_{max} is reached, a uniform density (the interior density) is applied. After the model has assigned a density value to each pixel, the predicted density or abundance can be calculated for the entire landscape or for specified areas or patches.

The objective of this study was to determine if the inclusion of edge effects (using

the EAM) in a basic habitat model led to better predictions of butterfly densities in a fragmented landscape. The basic habitat model (henceforth called the "null" model), uses only information on habitat type to make predictions. We took this approach in lieu of constructing a more complex model that included other landscape-level factors, such as isolation, or variables related to local habitat quality because our goal was to determine to what extent including edge response information in predictions can result in improved model performance rather than to most accurately predict densities in a specific place or time. We did not compare our model to a "core-area" approach because our test system consisted of contiguous, narrow stretches of habitat rather than discrete patches (described below), so there is no easily defined "core area" for any of our test sites.

Test system: butterflies in desert riparian habitat

Butterflies in desert riparian habitat present an appropriate system to test the benefits of including edge responses into distribution models. Butterflies are a speciose, common, easily identifiable group whose biology is well described (Scott 1986), so they are an amenable subject for modeling efforts. There is a growing number of studies showing that many butterfly species either avoid (Shultz 1998, Haddad and Baum 1999) or are attracted (Ravenscroft 1994, Bergmann 1999, Wahlberg 2001, Ide 2002) to edges and, more importantly, that those edge responses are predictable (Chapt. 2). Additionally, butterflies have been the primary focal taxa for the development of metapopulation models (Hanski et al. 1994, Hanski 1999, Harrison et al. 1988), one of the cornerstones for understanding landscape-level patterns of distribution. Finally, butterflies are often used as indicators for purposes of conservation (Kremen 1994, Pearson and Carroll 1998, Ricketts et al. 2002). Desert riparian habitat represents areas of critical conservation

concern because it provides crucial habitat for the majority of regional wildlife (Naiman et al. 1993) despite the fact that it has been seriously degraded due to water diversions, agriculture and development (Krueper et al. 2003). Furthermore, once-contiguous, expansive networks of rivers and washes are being separated into isolated patches that are not only changing in quality, but are becoming increasingly narrow, maximizing the edge-to-interior ratio of this habitat. Riparian habitat once accounted for 5% of the landscape in the desert Southwest, but now comprises less than 1% of the total landscape (Krueper et al. 2003), so is experiencing both habitat loss and fragmentation.

Our study was centered on the Upper San Pedro River in southeastern Arizona, which is a center of butterfly diversity in North America (Bailowitz and Brock 1991). The Upper San Pedro has received a high level of protection compared to other riparian areas in the Southwest. It is undammed (although both ground and surface water are diverted), and has been protected from grazing and agriculture since 1987 when it was made into the first Riparian National Conservation Area in the United States (Kreuper et al. 2003). It supports a well-developed gallery forest dominated by cottonwood (*Populus fremontii*) in the primary floodplain (hereafter called cottonwood). The cottonwood zone also contains other woody vegetation, including willow (*Salix goodingii*) and the exotic salt cedar (*Tamarix chinensis*), which is rare in our study region but common in more degraded areas. Adjacent to the cottonwood zone there is an upland riparian zone consisting of a heterogeneous mix of grasslands, dominated by sacaton (*Sporobolus wrighti*), and woody vegetation, dominated by mesquite (*Prosopis velutina*) which, although native, is nevertheless encroaching into what were once predominantly open areas (Stromberg 1998). This upland riparian zone displays a high degree of

heterogeneity, from open grasslands to closed-canopy mesquite woodlands. To reduce variation in site-to-site quality, we restricted our surveys to areas where mesquite was common, but was sufficiently spaced to allow the formation of a well-developed herbaceous layer (hereafter called mesquite). The surrounding desert scrub is dominated by widely-spaced, low shrubs, including *Larrea tridentata, Acacia sp., Prosopis velutina, Ephedra sp., and Fouquieria splendens*, with a rocky ground cover and a usually sparse herbaceous layer. The riparian area varies considerably in width, from no more than 100 m wide in some areas to at least one kilometer in others (Fig. 4.2).

We selected the widest areas of the Upper San Pedro (Fig. 4.2) to collect data on edge responses to be used to parameterize the EAM (Fig. 4.3a). We then used the EAM to generate butterfly density predictions in three types of fragmented test sites (Fig. 4.3b) in three regions located at increasing distances from the San Pedro (Fig. 4.2). We then compared the predictions of both the EAM and the null model to observed densities in all test sites. We tested the model in three types of patches to determine how well edge responses extrapolated to landscapes of different complexity and structure, and we selected sites in three distinct regions to determine the ability of the model to make predictions at increasing distances from where parameterization data were collected. The three types of test sites (illustrated in Fig. 4.3b) were: 1) cottonwood stands surrounded by mesquite (CW), 2) mesquite washes surrounded on both sides by desert scrub (MES-DS), and 3) mesquite zones with cottonwood on one side and desert scrub on the other (MES-CW/DS). The three test regions were chosen due to accessability and because they contained at least two of the three test site types (Fig. 4.3b) that we had targeted. The three regions (Fig. 4.2) were: 1) the San Pedro, including narrow reaches of the main

river corridor or washes within 1 km of the main channel, 2) Ft. Huachuca, a military base located within the San Pedro watershed, approximately 14 km from the San Pedro River channel, and 3) Empire Cienega, a National Conservation Area in the adjacent watershed, approximately 40 km from the San Pedro River. Empire Cienega supports a slightly different desert scrub habitat. This region is dominated by desert grasslands, which have a similar structure to that of desert scrub surrounding the San Pedro, although the herbaceous vegetation is more abundant and the shrubs are more widely scattered and dominated by low mesquite. However, there is still a stark difference between our mesquite test sites (Fig. 4.3c) which were relatively lush, and these surrounding desert grasslands, which have lower, sparser vegetation with a rockier ground. For simplicity in describing our test sites, we will continue to refer to Empire Cienega desert grasslands as "desert scrub".

Materials and Methods

Data on butterfly distributions were collected to parameterize and test the model in separate locations and using different designs. Surveys were conducted at both types of study sites during the same time period over two years. Analyses were run separately for each year due to high year-to-year variability in butterfly abundance. We separated the descriptions of study design for model parameterization and model testing below. Butterfly survey methods are the same for both types of sites.

Model Parameterization

In order to parameterize the EAM, it was necessary to describe edge responses at three edge types (Fig. 4.3a): 1) within cottonwood habitat at mesquite edges, 2) within mesquite habitat at cottonwood edges, and 3) within mesquite habitat at desert scrub edges. Nine study areas were established in 2000 throughout the 70 km extent of the

National Conservation Area (Fig. 4.2), although only six of these areas were surveyed in 2001 due to losses to fire and other logistical considerations. Most study areas were at least 1 km from the next closest area (Fig. 4.2), although in one case, two study areas were only 300 m apart (in 2000 only). Study areas were located by using aerial photographs to find sites with focal edge types that were reasonably accessible, and where habitat was sufficiently wide to accommodate at least a 40 m transect. In each study area, all focal edge types (cottonwood near mesquite, mesquite near cottonwood, and mesquite near desert scrub) were identified, with each area containing from one to three of the focal edge types. For purposes of analysis, each of the study areas was considered to be one independent sample area within the boundaries of the National Conservation Area. There were five independent areas established for each edge type in 2000. In 2001, we surveyed five areas for mesquite near cottonwood edges and three areas for the remaining two edge types.

For each edge type within a study area, the point along the edge where transects were established was chosen using a random number generator, subject to the restriction that the edge was well-defined at that point. Transects consisting of contiguous 10 x 10 m plots were placed perpendicular to the edge (Fig. 4.3a). Cottonwood transects were restricted to 50 m, due to the generally narrow width of cottonwood habitat, while mesquite (near cottonwood) transects were from 40-100 m depending on the width of the area, and mesquite (near desert scrub) transects were from 40-50 m, because a railroad generally restricted the length we could make these transects. There were one to three transects established for each edge type within each area, with all transects for the same edge type located within 50 to 100 m of each other. Multiple transects for one edge type

within an area were not considered independent and were pooled later for analysis. Transects were placed so that they were never closer to any another edge type (including roads and railways) than the focal edge type. Each edge type had 7-8 transects established in 2000 and from 5-8 transects in 2001.

Model Testing

To test the predictions of the model, we established 39 model testing sites (Fig. 4.3b) over a two-year study period that were independent of where data were collected to parameterize the models (Fig. 4.2). In 2000, there were a total of 13 test sites established on the San Pedro and in Ft. Huachuca. We established five cottonwood (CW) test sites (three in washes near the San Pedro, as illustrated in Figure 4.2, and two on Ft. Huachuca). We established five mesquite sites with desert scrub on both sides (MES-DS), all on Ft. Huachuca and three mesquite with cottonwood bordering one side and desert scrub bordering the other (MES-CW/DS), all in washes near the San Pedro. In 2001, an additional 26 test sites were established for a total of 38 test sites (one site from 2000 was not revisted in 2001 due to logistical considerations). In 2001, there were 15 CW sites (7 on or near the San Pedro, 4 on Ft. Huachuca, 4 in Empire Cienega), 16 MES-DS sites (8 on or near the San Pedro, 4 on Ft. Huachuca, 4 in Empire Cienega), and 7 MES-CW/DS sites, all on or near the San Pedro. In all cases, test sites were not discrete patches, but were part of continuous washes or riparian corridors and so a section of those areas were delineated for surveys (Fig. 4.3b).

Multiple sites of the same type tended to be clumped in space due to biogeographical factors and logistical considerations, with two as close as 250 m, but most of the sites within the three regions were separated by at least 500 m and many by 1

km or more (Fig. 4.2). Sites delineated for surveys (Fig. 4.3b) were chosen haphazardly, mostly based on logistical considerations, such as ease of access. In each test site, three 30 m transects composed of contiguous 10 x 10 m plots were established with 5 m separating each transect (Fig. 4.3b). The start point of the first transect was chosen using a random number generator. The three transects were "zig-zagged" so that both edges and interiors of the site would be equally sampled (Fig. 4.3b). The boundaries of the test sites were delineated by including the area that contained the transects, as well as a 5 m buffer on each side (Fig. 4.3b). The boundaries of each test site were mapped using a GPS unit (GeoExplorer II, Trimble). Points were differentially corrected, then imported into Arc View (ver. 3.2) to create spatially explicit maps of all test sites.

Butterfly surveys

Butterfly surveys were conducted from mid-August through mid-September in 2000 and 2001. Each transect was visited twice in 2000 and 2001, except for test sites in 2000, which were visited three times. Surveys were begun in the morning after the dew had dried in unshaded areas and ended when the afternoon became overcast due to the seasonal monsoon weather pattern. Surveys began at one end of the transect, with an observer surveying alternate plots to the end of the transect, then reversing direction and surveying plots that had been skipped on the way back. This ensured that patterns of abundance along the transect were not associated with time of day. The start point of the transect was alternated between rounds. Surveys were only begun when the sun was not obscured by clouds. Each 10 x 10 m plot was searched for 3 minutes and all butterflies seen were recorded and, if necessary, caught for identification. Care was taken not to count the same butterfly twice, although double counting may have occurred, particularly

when butterflies were abundant.

Parameterizing the models

Models were parameterized separately for each year to account for year-to-year variability in butterfly abundances, which is substantial. We used data collected from the three types of edge transects established along the San Pedro River (Fig. 4.3a) to parameterize both the EAM and the null models. Data from the 17 most abundant species were analyzed to determine if they showed significant edge responses. The models were only run for each species in each of the three test site types (CW, MES-DS, MES-CW/DS) if we found a significant edge response in at least one of the edge types present at that test site. For example, if a species showed a significant edge response only within the cottonwood edge transects, the EAM and null models were only run for CW test sites. In all cases, we used the interior density estimate to parameterize the null model (described below) because that model ignores the influence of edges.

We used two methods of testing for significant edge responses. Linear regressions were used to determine if there were gradients in density within the three edge zones. Mixed models were used to account for the non-independence of plots within transects (Diggle et al. 1994) and the number of transects in each area (1-3) was used as a weighting factor. For a coarser-scale measure of edge effects, T-tests were performed using the average value of plots in the two types of mesquite edge transects. This determined if there was a context effect (i.e. overall densities were different in mesquite habitat near cottonwood edges compared to mesquite near desert scrub edges) even if there was not a fine-scale gradient in density within the edge transects themselves. An alpha level of 0.10 was used to consider edge responses significant, and in those cases

predictions were generated for both the EAM and null models. However, when comparing predictions of the EAM and null models using goodness-of-fit tests (see below), the magnitude of those p-values can be considered separately.

In order to parameterize the EAM, we specified densities at the edge, interior as well as the depth of edge penetration (D_{max}). There have been several suggestions on a formal method of determining D_{max} for edge responses (Manke and Gavin 2000, Zheng and Chen 2000, Brand and George 2001, Harper and MacDonald 2001, Toms and Lesperance 2003), most involving some type of non-linear modeling. An exploratory analysis using an information-theoretic approach (Burnham and Anderson 1998) revealed that non-linear models were never chosen over simple linear models. We therefore set D_{max} at 50m, the length to which we can estimate our data at all edge types without extrapolation beyond our field measurements (because transect lengths were either 50 or 100 m depending on the edge type). This assumption should have little impact on our predictions because none of our test sites were greater than 100 m in width, meaning that had D_{max} been greater than 50 m, our predictions would not have differed because D_{max} was never reached in our model runs.

Parameterization was straightforward for cottonwood test sites. If there was a significant slope parameter for the cottonwood edge regressions, then we used the slope and intercept values to estimate densities at 0 and 50m. The null model was always the same as the interior density estimate (density at 50 m). Parameterization for mesquite patches was more complex because there were two types of edge transects that contributed to the predictions (ones near cottonwood and ones near desert scrub) and two types of analysis were used to determine if there were edge effects (regressions for fine-

scale edge effects and t-tests for coarse-scale effects). This resulted in four different cases, each of which resulted in a different parameterization of the EAM and null models. When the slopes at both mesquite edge types were significant, we ignored the results of the t-test and used the parameters for each model to determine edge and interior densities separately at both types of mesquite edges. The null model was the mean interior density calculated at both edge types. When only one edge type showed a significant slope parameter and the t-test was not significant, we used the parameters from the regression to calculate edge and interior densities at the edge type with the significant slope parameter, and applied the interior density (the same as the null density) uniformly at the other edge type. When one slope was significant and the t-test was also significant, we used the regression model to calculate the edge and interior density at the edge with the significant slope and the mean density of all plots at the other edge type. The null model was the mean of both interior densities. Finally, when neither slope was significant but the t-test was significant, density values from each edge type were applied uniformly across all distances and the null model was the mean of both densities. The EAM was run and estimated density values were calculated for each individual test site.

In order to examine the issue of multiple edge types present in the MES-CW/DS sites (Fig. 4.3b), the EAM was run in three different ways. In one set of runs, we allowed the EAM to find both edge types and estimate densities accordingly so the predicted density for each pixel was based solely on responses to the nearest of the two edges. In another set, we ran the EAM in a manner that assumed that cottonwood edges overwhelm the influence of desert scrub edges. Then we reversed those rules so the EAM would assume desert scrub edges would overwhelm the influence of cottonwood edges. We

took this approach because even though the only theoretical treatment of this issue suggests multiple edges should have an additive influence (Fernandez et al. 2002), no data are available from any study to demonstrate this. Furthermore, it seems plausible that in some circumstances the influence of one edge could overwhelm the influence of the other, so we decided to explore both additive and non-additive possibilities.

Comparing EAM and NULL predictions

To compare the predictions of both the EAM and null models to observed values we simply compared both predictions to densities measured in the field and determined which prediction was closer. However, we first eliminated those cases where the EAM and null models were so close as to be indistinguishable (effectively a tie) and cases where the values of both were so far from the observed values that neither could be considered to have reasonably predicted the outcome. To identify cases where the EAM and null models tied, we used the standard error of the mean of observed densities of the multiple test sites (calculated separately for each of the three test site types) to establish a threshold of how different the EAM and null models should be in order to claim that the predictions differed to a biologically meaningful extent. When both the EAM and null models' density predictions differed from observed values by more than 2 individuals per 100 square meters, we concluded that neither model was reasonably able to predict the observed densities. To compare the EAM and null models in the remaining cases, we simply determined which prediction was closer, then identified either the EAM or the null model as the "winner" in that case. To determine if one model significantly outperformed the other, we compared the proportion of times each model "won" to 50%, the value expected by chance alone, using a chi-square analysis. Model performance was

also explored on a region-by-region and species-by-species basis for each of the three test site types. For MES-CW/DS test sites, we also separately compared the observed values to the three different predictions of the EAM (where the closest edge, or just one of the two edge types were used in modeling patch densities). For these comparisons, we didn't use any criteria to determine a "tie", but still eliminated cases where all models were off by more than 2 individuals per 100 m^2.

Results

Fourteen out of the 17 species showed significant edge responses in 2000, 2001 or both years. Results of edge response tests, as well as the parameters used for each model in each year for each of the three edge types are shown in Table 4.1. Based on the number of observed edge responses, we had 253 separate opportunities to compare the predictions of the EAM and null models across all species in all model testing sites over two years. In general, the predictions of the EAM and null models were distinguishable, with ties being called in only 48 cases (19%). Also, the predictions of both models were within a reasonable range of the observed values (<2 individuals per 100 m^2) in 234 of the cases (92%). This left 186 opportunities to directly compare the predictions of the EAM and null models with values observed in the field. The EAM outperformed the null only in the cottonwood habitat patches in 2001 ($p < 0.0001$; Fig. 4.4a). There were no significant differences in the other test site types, although in 2000 the EAM performed marginally better in MES-CW/DS patch types (Fig. 4.4c) while the null model performed marginally better in MES-DS patch types (Fig. 4.4b). There was no indication that model performance was better in sites closer to locations where data were collected to parameterize the models. The EAM performed equally or marginally better in all three regions (San Pedro sites, Ft. Huachuca, and Empire Cienega), with the best proportional

performance actually occurring at the farthest test region (Empire Cienega).

To examine results on a species by species basis, we present the number of times the EAM or null model "won" direct comparisons, for all species in all test site types (Table 4.2). Where there were greater than five opportunities to compare the EAM and null model, we determined when the EAM or null model was the consistent winner. Those cases are illustrated in Figure 4.5, which shows the EAM did better at predicting the observed outcomes for six species (Fig. 4.5a), with most of those cases occurring in cottonwood habitat. For another six species, the null model appeared to perform better (Fig. 5b). In the remaining cases, model performance was roughly equivalent (Table 4.2).

In the MES-CW/DS habitat which had two bordering edge types (cottonwood and desert scrub), the EAM was run in three different ways, considering both edge types or assuming that the influences of one edge type would overshadow the other. To compare the predictions of these three runs with observed densities, we combined 2000 and 2001 data because there were only three sites in 2000 making it difficult to evaluate trends. For these comparisons, we ignored the null model because our primary goal here was to explore the issue of multiple edge types. Overall, the model did better when either desert scrub (42 out of 84 cases) or cottonwood (29 out of 84 cases) edges were assumed to dominate. In only 11 out of 84 cases (13%) did predictions improve when both edges were taken into account. When examining model performance on a species-by-species basis, the model performed better for four species when assuming desert scrub dominated (Fig. 6a) and for two species when assuming cottonwood dominated (Fig. 4.6b). The models were indistinguishable for three species (Fig. 4.6c).

Discussion

The results of this study suggest that, for butterflies in desert riparian habitat, including edge responses in predictions of landscape-level densities resulted in only marginal improvements in model performance. The only other study that attempted to validate the predictions of the Effective Area Model by comparing observations to predictions in independent sites found that the EAM was better able to predict avian community composition compared to a null model that ignored edge and context effects (Sisk et al. 1997). These results suggest that, given the current formulation of the EAM, the inclusion of edge responses in landscape-scale predictive models may only be valuable in certain situations. However, a legacy of studies showing that edge responses are common, often strong, and closely linked to observed responses to fragmentation (reviewed earlier) suggest that edge responses are an important factor in understanding landscape-level dynamics. Therefore, their inclusion in landscape-level predictions warrants further development. Based on only two studies that tested this approach at the landscape level, focusing on very different taxa, it is difficult to draw any strong conclusions about the model's general applicability. Instead, we explore three factors that we feel contributed to variable model performance in this study: 1) site-to-site variability, 2) the variable expression of edge responses, and 3) convergent, multiple habitat types and complex patch geometry. Further, we suggest how those factors could be addressed to improve future applications of this, or any model, that seeks to incorporate edge responses into landscape-level predictions.

Site-to-site variability

Because of the complex, interacting nature of all the ecological factors that contribute to habitat quality (Stauffer 2002), the success of modelers in predicting animal

densities has, at best, been mixed (Van Horne 2002). In this study, we dealt with site-to-site variability by using an estimate of the standard error among test sites to set a threshold for how different we determined the predictions of the EAM and null models should be in order to effectively compare their predictions. In cases where the difference between the predictions was less than the estimated standard error, we declared the outcome a "tie" (Fig. 4.4), which occurred in about 20% of cases. However, site-to-site variability likely also contributed to cases where "ties" were not declared, but the EAM and null models performed equally well. Using a more conservative measure of site to site variability, such as the standard deviation, would have resulted in many more "ties" and fewer opportunities to compare model predictions (which is why we chose not to use it). Setting some minimum proportion of overall variation explained by edge responses as a guideline to decide when they are "biologically meaningful" may be useful for some applications of the model. Determining what that measurement should be and when it should be used is worthy of further development.

Another approach to dealing with site to site variation is to incorporate variables that contribute to local habitat quality into the predictive model. To explore that option in the context of this study, it is worthy to discuss the factors that contribute to local variability in habitat quality for butterflies, and how valuable it may be to include those factors into a more complex model. Dennis (2003) describes the minimum resource requirements for adult butterflies as access to host plants, feeding materials, mates, resting and roosting sites, and protection from predators. Several studies have shown correlations with butterfly distribution and the presence of their host and nectar plants (Elmes et al. 1996, Schultz and Crone 1998, Bergmann 1999, Edge 2002). However, the

strength of those associations vary and *quality* of host and nectar plants have been shown to be better predictors of butterfly distributions (Schultz and Dlugosh 1999). Some factors are family specific. For instance, there is a whole group of butterflies (Lycaenidae) who have obligate ant hosts, and for those species the presence of ants tends to be the best predictor of habitat quality (Elmes et al. 1996, Clarke et al. 1997, Griebeler and Seitz 2002). Other local habitat factors that have been shown to be important determinants of habitat quality for butterflies include fire history (Swengle 1996, Schultz and Crone 1998, Edge 2002), topography (Luto et al. 2002, Fleishman et al. 2003), moisture gradients (Debinski et al. 2002), and microclimate (Greatorex-Davies et al. 1993, Bergmann 1999).

For use in the EAM, one potential approach to incorporating this site-to-site variability is to determine some measure of overall habitat quality that can be used to adjust the estimates of "interior" density numbers up or down, then scaling the predicted edge response to the variation in predicted densities in each site. Although this assumes that edge responses are conserved at different population densities (explored below), it is one method that could help improve predictions and deal with the issue of spatial variability in habitat quality. Ultimately, the degree to which local habitat factors should be incorporated are related to the goals for the model in the first place (Starfield 1997). Here, our goal was to determine how well including edge responses improved predictions of species distributions. Including measures of habitat quality may have allowed us to more easily distinguish between the predictions of the EAM and null models, however this is far from certain. Had our goal been to build a model to most accurately predict butterfly density in specific places (as may often be the case for reaching species-specific

management goals), then inclusion of site-specific habitat variables would likely be warranted. In that case, selection of variables to be included might be based on how strongly each correlates with a species' distribution, as well as the availability of data to parameterize that model over a larger landscape. In general, data on host and nectar plant distribution, fire history, distribution of ant colonies, etc. is not available at a landscape scale. In addition, butterflies show a great deal of temporal variability due to climate (Hill 1999, Fischer and Fiedler 2001), so any model that spanned multiple years would have to somehow take that fact into account. However, if the goal is to explore the potential ecological consequences of different landscape structures resulting, for instance, from alternative management scenarios (e.g., Sisk et al. 2002), then incorporating site-to-site variation may not be necessary.

The Variable Expression of Edge Responses

For this test, we extrapolated edge responses to several independent sites and found some species for which the EAM made better predictions (Fig. 4.5a) and some for which the null model's predictions were closer to observed values (Fig. 4.5b). In some cases, the null may have made better predictions because the edge responses we had measured along the San Pedro were simply not operating in some sites where we tested predictions. Edge responses are known to be variable (Murcia 1995, Villard 1998, Sisk and Battin 2002). However, in most cases, when a significant edge response is observed, it is in a consistent and predictable direction (Chapt. 1 and 2). Therefore, the variability in edge responses can be seen as a binary process where, in some cases, a consistent uni-directional response is observed (positive *or* negative) and in some cases no edge response is observed. Of course, in reality edge responses are not binary, but range along

a continuum of strength, and when responses are stronger they are more likely to be detected compared to when they are weak. Therefore, it is important to understand the factors that may strengthen, weaken or entirely nullify the expression of known edge responses. Edge orientation has received the most attention relative to its influence on the variable strength of edge responses. Several studies have shown how edge orientation influences both the strength and/or depth of penetration (but never direction) of edge responses for plants (Wales 1972, Fraver 1994, Honnay et al. 2002,) and for insects (Stiles and Jones 1998, Meyer and Sisk 2001). Edge abruptness has also been shown to have an influence (Young et al. 1995, Suarez et al. 1997) although not in all cases (Kingston and Morris 2001). The changing structure of edges over time (e.g. edge sealing) can influence edge responses (Lovejoy et al. 1986). Other factors that have been considered include temporal variability due to season and the extent of internal patch heterogeneity (Noss 1991). Edge contrast has also received some attention, but we do not consider it here because the EAM considers each unique edge type separately, so differences in edge contrast are accounted for.

As research continues to focus on factors that most strongly influence the variable strength and expression of edge responses, our ability to make predictions across landscapes will improve. However, the fact that edge responses for the same species at the same edge type tend to be in a consistent and predictable direction when they are observed (Chapts. 1 and 2), means that edge responses are likely to have a predictable influence when integrated over large landscapes or time frames (Kolbe and Janzen 2002), although that influence may be dampened depending on how consistently each edge response is expressed throughout the landscape. Of course, there may be many factors

that influence the variable expression of edge responses, and these may not be easily described or incorporated into models. One solution is to maximize the number of independent sites where edge response data are collected for model parameterization. This may capture at least some variability and allow more realistic extrapolation of edge responses over a complex landscape. However, if the goal is to test model predictions in specific sites (as was done here), incorporating site-specific factors that underlie cases where edge responses are weakened or not operative is vital to understanding why including edge responses improves predictions in some cases but not others.

Multiple habitats and complex geometry

Complicated patch structure leads to areas where edge influences may be increased (Fig. 4.7a) or decreased (Fig. 4.7b) depending on local geometry. Malcolm (1994) presents a model that integrates edge influences among every point along a patch border and then shows that measured edge responses fit better to this more complicated model than a model based solely on the distance to the closest edge. Fernandez et al. (2002) extend this idea, but allow for non-linear dynamics that account for both complex geometry at a single edge type (i.e. Figs. 4.7a,b) and different types of edges influencing a single point (i.e. Fig. 4.7c). However, this theoretical study presents no evidence that the mathematical models that they use (drawn from electrical engineering) are appropriate to describe these ecological dynamics. Another approach that has been taken is to measure multiple distances at either two (Fletcher and Koford, *in review*) or four (Manke and Gavin 2001) set directions from the survey point. Similarly, there is little empirical evidence of how these complex edge responses are realized in actual landscapes, although some studies have shown stronger edge effects in corners compared to along

straight edges (Benitez-Malvido 1998, Clark and Kuehl 2002, Fletcher and Koford, *in review*). We have found no studies that empirically examine how the presence of multiple types of bordering patches (Fig. 4.7c) influence realized edge effects, and our data suggest that this factor may make direct applications of these models challenging.

In our study, we found no obvious evidence of increased edge influence due to complex geometry (i.e. Fig. 4.7b) because the EAM did not consistently underestimate the magnitude of edge influence. This would be expected in our narrow sites where any point will be close to an edge on two sides rather than just one, although this factor may have been swamped by local differences in habitat quality or the variability of expressed edge responses. However, we do present the first consideration (that we are aware of) of how the influence of convergent, multiple edge types (Fig. 4.7c) may have interacted. Although our data do not provide consistent answers to the question of how multiple edges interact, they do suggest that complex dynamics may result from the interaction of multiple edge types. Although our following points can be seen as largely speculative, we feel that they are ecologically plausible and show the need for both theoretical and empirical treatment of this issue.

The EAM performed best in the cottonwood habitat (Fig. 4.4a). The cottonwood test sites were largely free of the multiple edge effects that may have been an issue for mesquite sites. This is because cottonwood sites were bordered solely by one habitat type (mesquite), both in areas where response data were collected (Fig. 4.3a) and sites where predictions were tested (Fig. 4.3b). This suggests that edge responses may extrapolate more easily to situations where there are not other patch types that may be directly exerting an influence. Past tests of the EAM that took place in simple landscapes

such as these were largely successful. Sisk et al. (1997) showed the EAM was better able to predict bird community composition in woodland patches depending on whether those patches were surrounded solely by grassland or chaparral, compared to a null model that did not include those contextual effects. Haddad and Baum (1999) found that the EAM was able to explain some variation in patch density of four butterfly species in clearcut patches surrounded solely by pine forests.

The EAM performed most poorly compared to the null model in the mesquite habitat with only desert scrub edges (Fig. 4.4b). Although this test site type was not itself being influenced by multiple edges (Fig. 4.3b), data collected to parameterize the model may have been influenced by nearby cottonwood edges (Fig. 4.3a) and therefore may not have extrapolated well to sites where cottonwood was absent. As an illustrative example, *Phoebis sennae* showed particularly poor performance in these sites (Fig. 4.5b). *P. sennae* consistently shows increased abundance near cottonwood edges (Table 4.1), and results of another study suggest that this is due to the presence of its hostplant being found exclusively within cottonwood habitat (Chapt. 2). In fact, in 2001, no individuals were recorded within mesquite edge transects near desert scrub (Table 4.1) suggesting that cottonwood edges may have exerted an influence on the desert scrub edges by drawing individuals away. However, our mesquite test sites that were surrounded by desert scrub were usually far from cottonwood habitat found along the main river, completely imbedded in a matrix of desert scrub. Within a landscape dominated by desert scrub (the least preferred habitat for *P. sennae* in this landscape, see Chapt. 2), those strips of mesquite may have constituted the best local habitat, while close to the river, they constituted the worst. *P. sennae* showed consistently higher abundance in

these mesquite sites than predicted by the EAM, which may have systematically under-predicted densities due to this influence of cottonwood edges being found only where model parameterization data were collected. We also noted that MES-DS test sites showed the highest proportion of cases where neither model was able to adequately predict densities (Fig. 4.4b), which also suggests that data from the San Pedro did not extrapolate well to these sites. Although speculative, this demonstrates that edge responses may not extrapolate directly to novel sites that have a different context than where edge responses were measured.

Results were mixed in the mesquite test sites that had both cottonwood and desert scrub edges (Fig. 4.3b), with the EAM performing marginally better in 2000 and the null in 2001 (Fig. 4.4c). These were sites where multiple edge types were always present (Fig. 4.3b) and we specifically examined how accounting for the effects of both or each edge separately may influence the performance of the model. Runs where the EAM considered both edge types equally rarely outperformed runs where either the cottonwood or desert scrub edges were considered to dominate. For four of the nine species examined, the model performed best when desert scrub edges were assumed to dominate (Fig. 4.6a), while for two species it performed best when cottonwood edges were assumed to dominate (Fig. 4.6b). Although two species showed no real trends (Fig. 4.6c), in no case did the runs considering both edges outperform the other two. The fact that there was some consistency within species suggests that, in some situations, the influence of one edge dominates the other, rather than their effects being additive (as suggested by Fernandez et al. 2002 and assumed in the current structure of the EAM). Our results suggest that, in some cases, where more than one edge type abuts a focal

habitat, the influence of one edge may predominate. Furthermore, the dominating edge may vary by species. This makes some ecological sense, because there is no reason to believe that one edge type should consistently dominate the influence of another edge type across all species; instead relative effects will likely depend on the ecological factors underlying each species' response to each edge type (Chapt. 1). There is currently no ecologically-based framework to determine if and when multiple edges should have some combined effect, or if the influences of one edge should dominate the effects of other edges present in the landscape. The fact that the convergence of multiple edges are common features in most landscapes suggests that this issue needs both theoretical and empirical attention.

Conclusions

To date, the Effective Area Model has been shown to improve predictions only in structurally simple landscapes. However, the widespread recognition that edge responses underlie many of the complex patterns of organismal response to habitat fragmentation suggests that, when considering how different landscape structures may impact ecological communities, including known edge responses is a valuable approach that deserves continued attention. Based on the results of this study however, we conclude that significant work remains to be done. We suggest three factors that may allow for improved extrapolation of edge responses to the landscape. Increasing model complexity to include local habitat variables that are known to influence site quality may be appropriate in some cases. More importantly, determining the circumstances under which known edge responses are expressed throughout a complex, heterogeneous landscape is critical for being able to modify predictions to account for the specific types of known variability in the expression of edge responses. Finally, real landscapes have

complex patch geometry and typically include numerous places where multiple habitat types converge. Given this spatial complexity, considering only the distance to and type of the closest edge may be overly simplistic and limit our ability to extrapolate edge responses to larger landscapes. Instead, an ecologically-based framework for understanding how the presence of different edge types are expected to interact is necessary. While the EAM is perhaps the best tool that is currently available to model the full range of known edge responses, its ability to predict distributions in complex landscapes is limited and it should therefore be used with caution.

Ultimately, the challenge of determining the best way to extrapolate from known edge responses to complex landscapes will require further theoretical and empirical treatment. In the meantime, there remains a strong theoretical and practical impetus to consider edge responses as one factor that influences how changing landscapes may impact ecological communities.

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Table 4.2. Performance of the Effective Area Model compared to a null model that ignored edge effects. The tally of times the EAM or NULL model predictions were closer to observed values for 14 butterfly species in three types of model test sites, illustrated in Fig. 4.3b. Cases where the models "tied" or both were greater than 2 ind/100m2 are not illustrated (see text). Cases where the EAM or NULL model performed consistently better are illustrated in Figure 4.5.

		Cottonwood sites		Mesquite sites			
				MES-DS		MES-CW/DS	
Species	Year	EAM	NULL	EAM	NULL	EAM	NULL
Battus philenor	2001					2	4
Brephidium exilis	2001					7	0
Chlosyne lacinia	2001	11	4				
Colias cesonia	2000	1	5	2	3		
Colias eurytheme	2001	15	0	10	6	1	2
Euptoieta claudia	2000					2	0
Eurema mexicanum	2000					3	0
	2001					3	3
Eurema proterpia	2000					3	0
	2001					0	7
Libytheana carinenta	2000			1	4	0	2
	2001			11	4		
Liminitis archippus	2000	4	2				
	2001	8	7				
Phoebis sennae	2000	3	3			0	3
	2001			4	12	4	3
Pholisorus catullus	2001					0	7
Pieris protodice	2001			1	3	1	0
Pyrgus communis	2000			2	3	3	0
Total		42	21	31	35	29	31

Figure Legends

Figure 4.1. Schematic version of the Effective Area Model. Each patch is separated into zones based on distance to and type of nearest edge. Each zone has a density estimate applied based on field data (in this example, the spotted towhee). Abundances are calculated for each zone, then integrated over the entire patch to arrive at a single abundance estimate. The model is currently implemented within a GIS framework. (Reprinted from Sisk and Haddad 2002).

Figure 4.2. Map of our study regions and detail of the San Pedro Study Sites. All edge response data were collected in study sites (black circles) along the San Pedro River within the National Conservation Area (area shown in detail). Model tests were carried out in several sites in three regions: along the San Pedro river (grey circles), in Ft. Huachuca and Empire Cienega National Conservation Area. One test site along the San Pedro River is shown using remotely sensed imagery. The detail of the San Pedro National Conservation Area shows the cottonwood zone in black, the upland riparian zone in grey and the surrounding desert scrub in white.

Figure 4.3. Study design for both model parameterization and model testing. For model parameterization (a), edge transects were established in the widest sections of the San Pedro River (see Fig. 4.2). Transects were perpendicular to the edge and made up of 10 x 10 m plots. Average transect length at each edge type is also shown (each square represents a 10 x 10 m plot). For model testing (b), cottonwood (CW) sites (1) are surrounded by mesquite on both sides. There are two types of mesquite sites, one (MES-DS) has desert scrub along both edges (2), and the other (MES-CW/DS) with a cottonwood edge on one side and a desert scrub edge on the other (3). Study sites had 30m transects composed of 10 x 10 m plots. Study sites were delineated by the two bordering edges and with 5 m buffers around transects.

Figure 4.4. The outcome of each comparison of the predictions of the EAM and null models in the cottonwood test sites (a), mesquite sites with desert scrub edges (b), and mesquite sites with both cottonwood and desert scrub edges (c). Results are shown separately for 2000 (left-hand panel) and 2001 (right-hand panel). For each species in each of 38 separate sites, the proportion of times the EAM or null made the prediction closest to observed values is shown. Also shown is the number of times the models tied (were within a standard error of each other) or where neither model had a prediction close to the measured value (off by more than 2 indiv. per 100 m^2). P-values are based on a chi-square analysis testing whether the proportion of times the EAM and null models won deviated significantly from 50% (***$P < 0.0001$). The test did not include “ties” or “neither” outcomes.

Figure 4.5. Examples where species' densities were consistently predicted better by either the EAM (a) or null model (b). The number of times each model most closely predicted observed outcomes is separated by species, year, and test site type. The species and year for each illustrated comparison is identified. Full species names are in Table 4.1.

Figure 4.6. Model performance by species for mesquite test sites with one cottonwood and one desert scrub edge. The EAM was run in three different ways: considering the both edges (white bars), assuming the desert scrub edges dominated the influences of the cottonwood (black bars) and assuming that cottonwood edges dominated (gray bars). Model performance is compared on a species-by-species basis and shown where the model does better when desert scrub edges are assumed to dominate (a), cottonwood edges are assumed to dominate (b), and species where no model does consistently better(c).

Figure 4.7. Complex and multiple edge effects. In most published studies, the influence of edge is almost always described for a point based on the distance to the nearest edge, which would be the same for all three panels in this figure (a,b,c). However, the type and strength of edge influence is likely to be different for each situation. Even at the same edge type (a,b), the geometry of the patch shape is likely to exhibit complex effects that cause edge influences to be either greater (a) or lesser (b) on points equidistant from the edge. A further complication that has received no empirical treatment is when multiple edge types converge at one point (c).

Figure 4.1

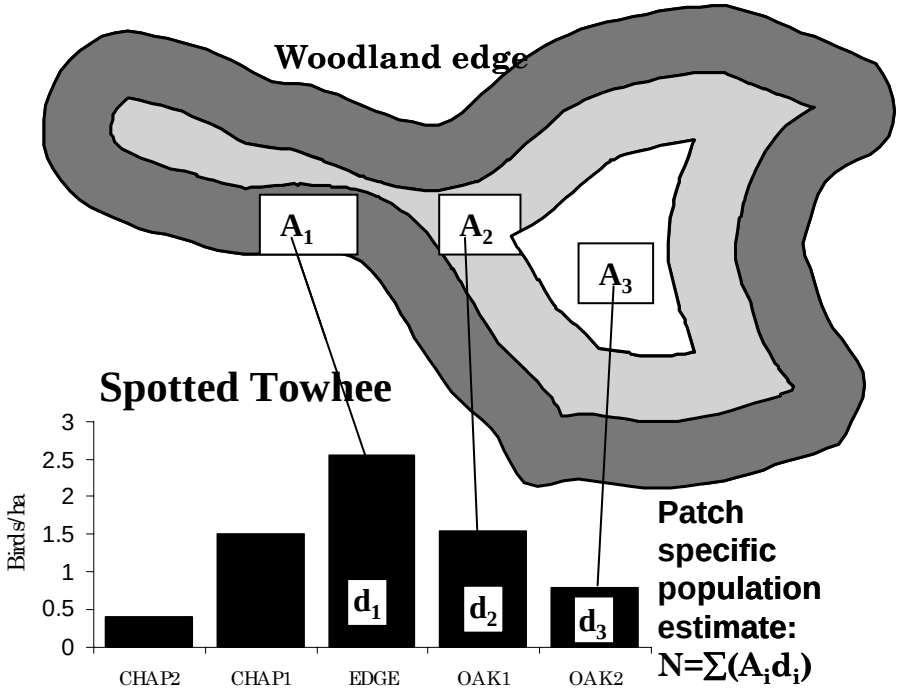
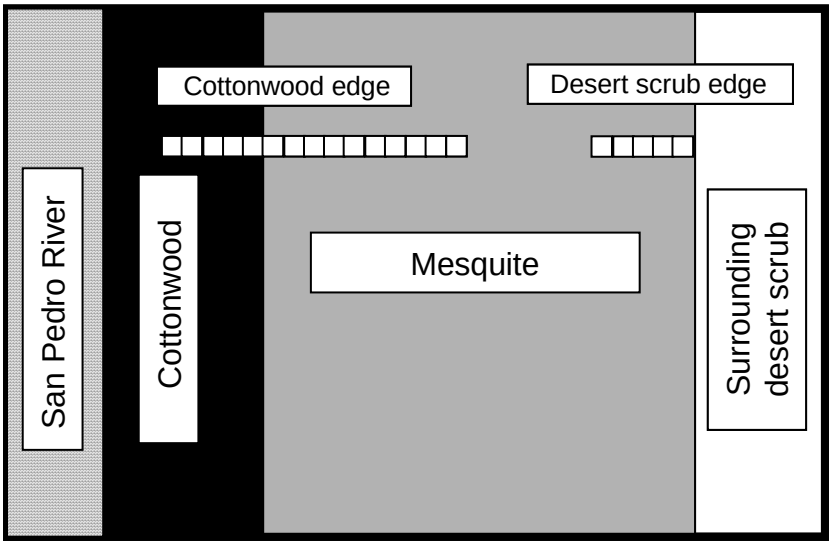

Woodland edge
A1
A2
A3
Spotted Towhee
Birds/ha
3
2.5
2
1.5
1
0.5
0
d1
d2
d3
CHAP2
CHAP1
EDGE
OAK1
OAK2
Patch specific population estimate:
N=∑(Ai di)

Figure 4.2

Figure 4.3

a) Model parameterization: measuring edge responses



b) Model testing: three types of test sites

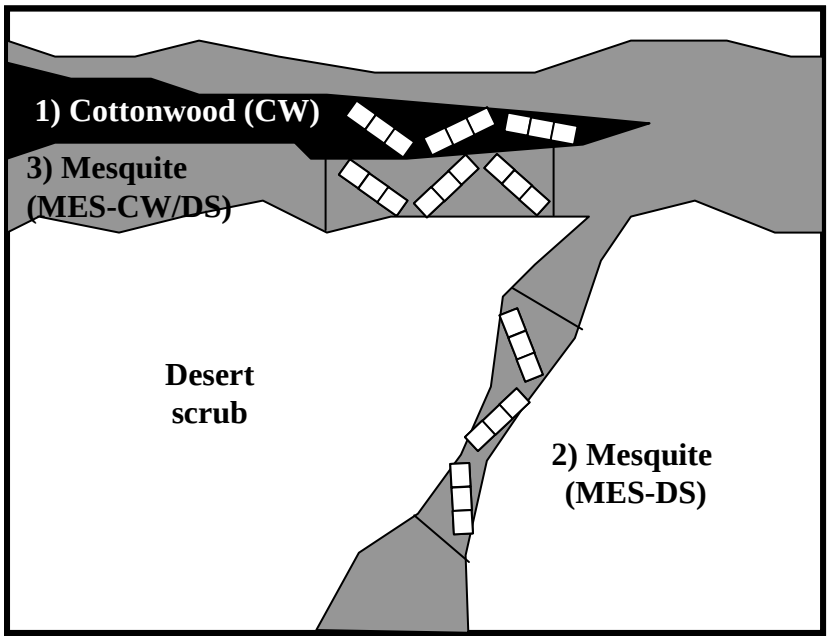


Figure 4.4

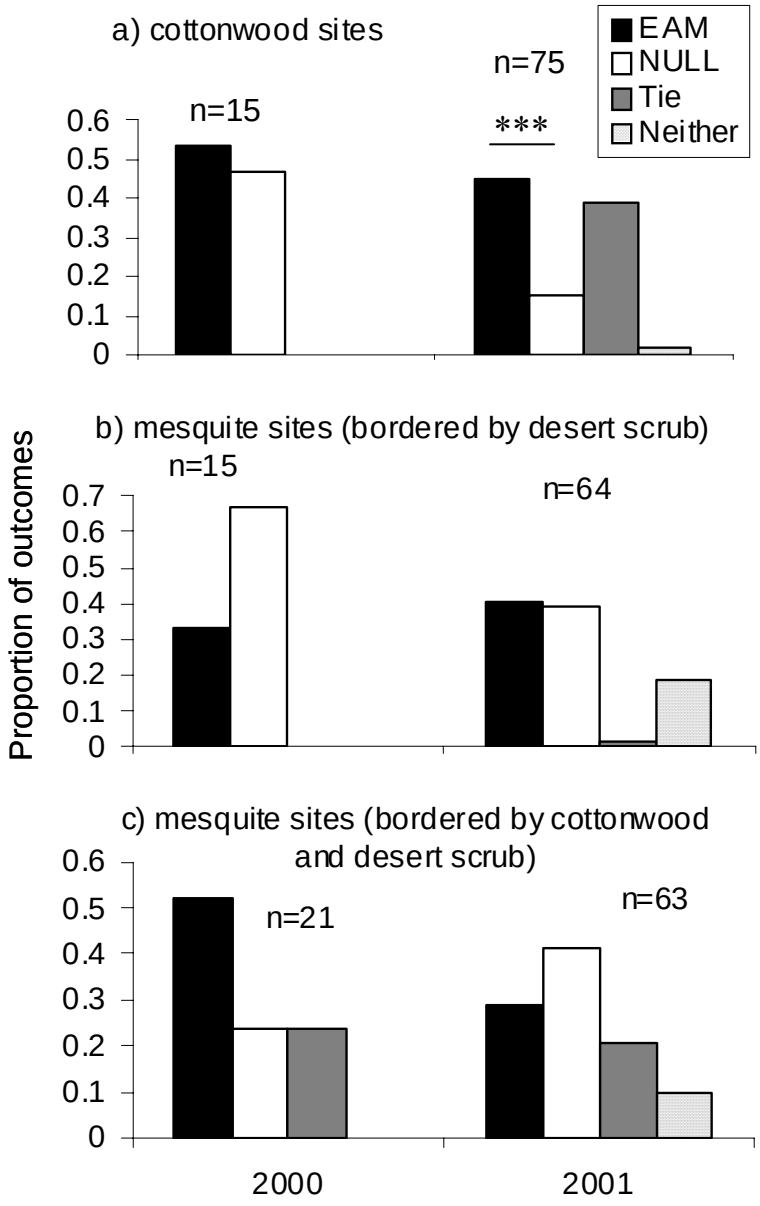

a) cottonwood sites
EAM
NULL
Tie
Neither
n=15
n=75
***
0.6
0.5
0.4
0.3
0.2
0.1
0
b) mesquite sites (bordered by desert scrub)
Proportion of outcomes
n=15
n=64
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
c) mesquite sites (bordered by cottonwood and desert scrub)
n=21
n=63
0.6
0.5
0.4
0.3
0.2
0.1
0
2000
2001

Figure 4.5

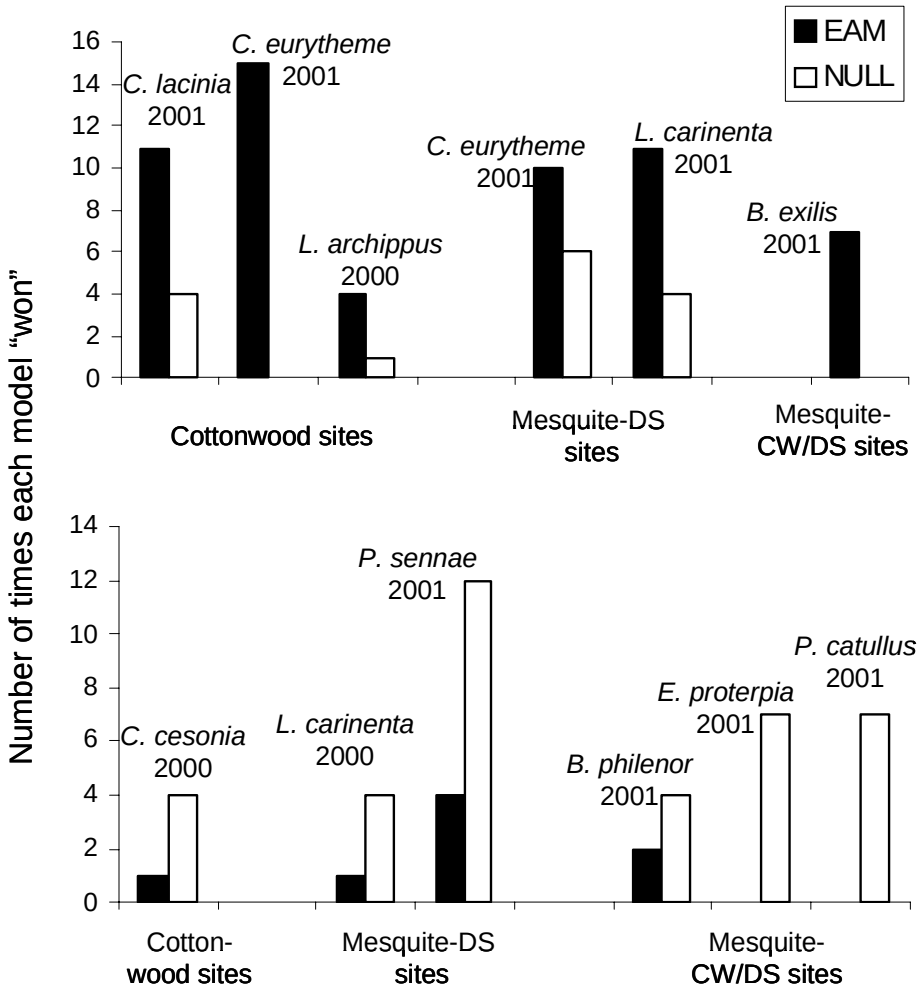

EAM
NULL
Number of times each model "won"
16
14
12
10
8
6
4
2
0
C. lacinia 2001
C. eurytheme 2001
L. archippus 2000
C. eurytheme 2001
L. carinenta 2001
B. exilis 2001
Cottonwood sites
Mesquite-DS sites
Mesquite-CW/DS sites
14
12
10
8
6
4
2
0
C. cesonia 2000
L. carinenta 2000
P. sennae 2001
B. philenor 2001
E. proterpia 2001
P. catullus 2001
Cotton-wood sites
Mesquite-DS sites
Mesquite-CW/DS sites

Figure 4.6

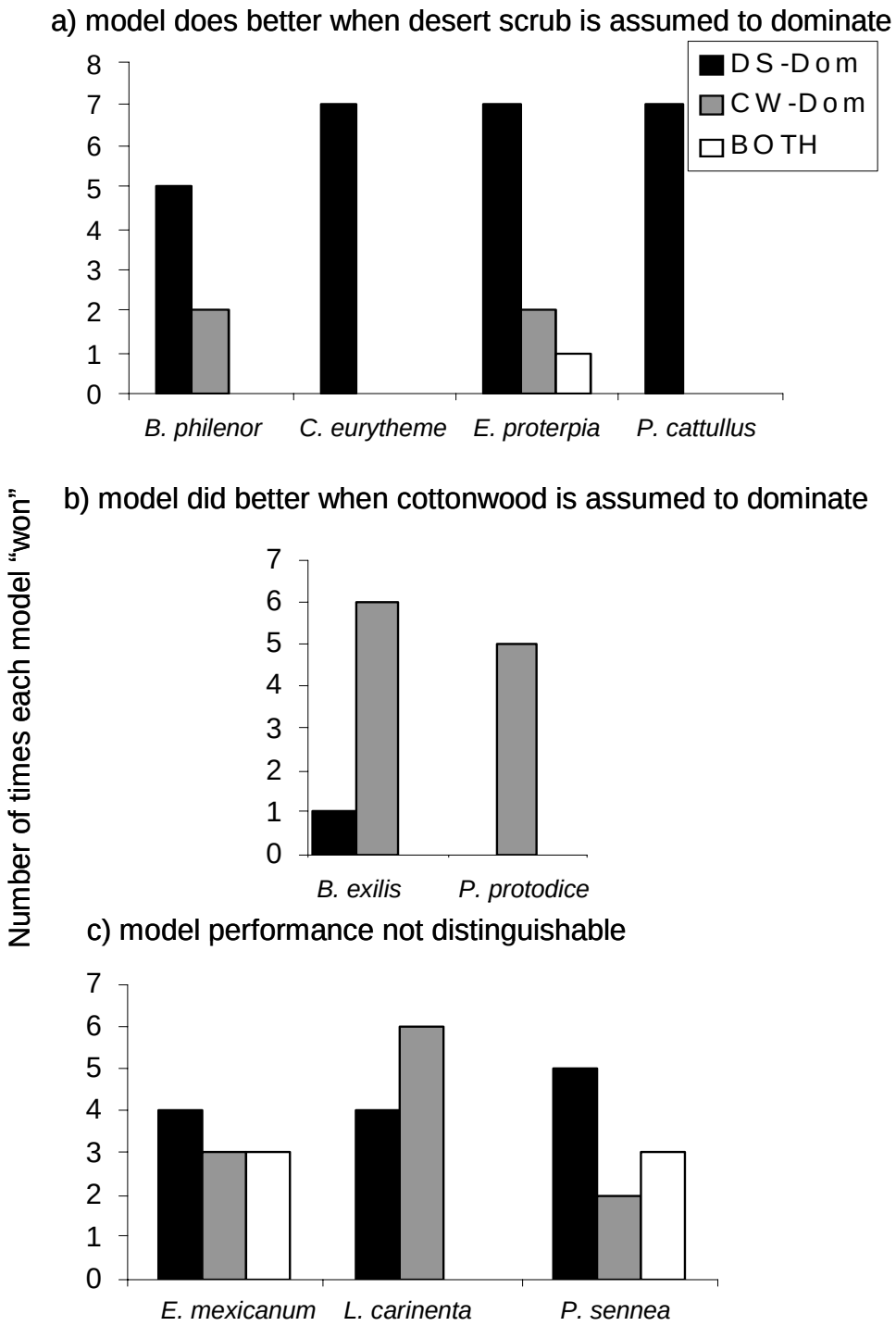
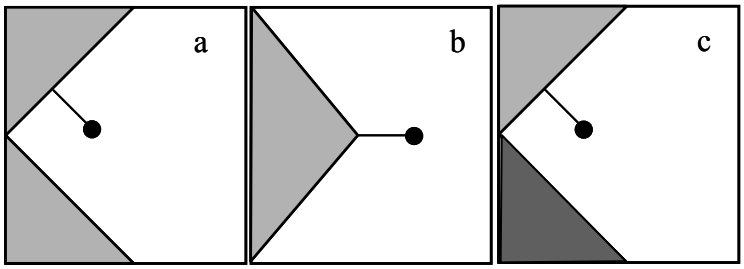

a) model does better when desert scrub is assumed to dominate
DS-Dom
CW-Dom
BOTH
8
7
6
5
4
3
2
1
0
B. philenor
C. eurytheme
E. proterpia
P. cattullus
Number of times each model "won"
b) model did better when cottonwood is assumed to dominate
7
6
5
4
3
2
1
0
B. exilis
P. protodice
c) model performance not distinguishable
7
6
5
4
3
2
1
0
E. mexicanum
L. carinenta
P. sennea

Figure 4.7



CHAPTER 5

CONCLUSION

The research reported in this dissertation represents several important advancements in the understanding of edge responses and how that information can be used to understand distributions across heterogeneous landscapes. The model presented in Chapter 2 and the tests of that model in both Chapter 2 and Chapter 3 suggest that, when present, edge responses are largely consistent and predictable based on habitat preferences and resource distribution. This research suggests that an important component to understanding variability in edge responses is to identify factors that predictably influence the strength and detectability of edge responses. The results presented in Chapter 4 highlight many of the difficulties in extrapolating known edge responses to heterogeneous landscapes, and demonstrate many deficiencies in the theoretical and empirical edge literature. The model used to extrapolate known edge responses was successful in only one of three patch types. Three issues were explored that may have led to poor model performance: site-to-site variability, the variable expression of edge responses and complex patch geometry. Despite current limitations, models that include known edge responses in their predictions likely present a better picture of distributions across landscapes compared to models that ignore edge and context effects. Hopefully, the results of these studies will influence future edge studies by suggesting new avenues of research that will allow a more realistic picture of how a wide range of organisms respond to complex, changing landscapes.