DISSERTATION

PREDICTION AND ASSESSMENT OF EDGE RESPONSE AND ABUNDANCE FOR DESERT RIPARIAN BIRDS IN SOUTHEASTERN ARIZONA

Submitted by

L. Arriana Brand

Graduate Degree Program in Ecology

In partial fulfillment of the requirements
For the Degree of Doctor of Philosophy
Colorado State University
Fort Collins, Colorado
Spring 2004

ProQuest Information and Learning Company
300 North Zeeb Road
P.O. Box 1346
Ann Arbor, MI 48106-1346

COLORADO STATE UNIVERSITY

March 2, 2004

WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY L. ARRIANA BRAND ENTITLED PREDICTION AND ASSESSMENT OF EDGE RESPONSE AND ABUNDANCE FOR DESERT RIPARIAN BIRDS IN SOUTHEASTERN ARIZONA BE ACCEPTED AS FULLFILING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

Committee on Graduate Work

Kenneth P. Burnham

Barry R. Noon
Advisor

Department Head

ABSTRACT OF DISSERTATION

PREDICTION AND ASSESSMENT OF EDGE RESPONSE AND ABUNDANCE FOR DESERT RIPARIAN BIRDS IN SOUTHEASTERN ARIZONA

The ability to reliably predict the impacts of habitat loss and fragmentation for many species in diverse environments is necessary to identify conservation priorities and to accelerate conservation planning. However, no general relationship has emerged that will allow *a priori* predictions of the expected abundance response of a given species to edges, or to reliably predict absolute abundance in novel locations. The overall objectives of my dissertation were to predict and assess edge response and abundance in novel locations to aid in conservation planning. In Chapter 1, I used a meta-analytic approach and AICc model selection to predict positive and negative edge response for birds on both sides of forest edges with ecological and life-history trait information readily available from the literature. Using Receiver and Operating Characteristic (ROC) analysis to compare observed versus predicted edge response on the same dataset in which the models were developed, I found that the percent of observations correctly classified for positive and negative edge prediction models ranged from 74-78% for the forest-open edge type and from 82-89% for the open-forest edge type. In Chapter 2, I applied the prediction models to 25 previously unstudied species in 8 sub-edge types in the San Pedro River riparian corridor to assess model robustness to novel locations, edge types, and species. The models performed well for predicting negative edge response in both forest-open and open-forest edge types (80-91% correct classification), adequately for positive edge response in the forest-open edge type (64-77% correct classification), but poorly for positive edge response in the open-forest edge type (38-44% correct classification). Using logistic regression analysis I found that classification success was robust to novel edge and habitat types, and that positive prediction models in the open-forest edge type may have failed due to a different set of mechanisms occurring on the San Pedro River compared with the meta-analysis dataset. In Chapter 3, I validated and calibrated a landscape ecological model that uses change in both habitat composition and geometry to predict change in species abundance at novel locations (Effective Area Model; EAM). For model validation, I compared the EAM to a null model in terms of its ability to accurately predict observed species abundance in 50 validation sites different from those in which the model was parameterized. The EAM outperformed the null model when considering all validation sites as well as subsets of validation sites categorized on the basis of four variables (isolation, presence of water, region, and focal habitat). For model calibration, I explored a framework to decrease prediction error given inherent temporal and spatial variability in abundance in an attempt to improve the ability of the EAM to predict absolute abundance in novel landscapes. I calibrated the EAM to new locations using a linear regression between observed and predicted EAM abundance with and without additional habitat covariates. I found that model calibration used to account for unexplained variability in time and space, as well as variability that can be explained by incorporating additional covariates, improved EAM prediction of absolute abundance in novel locations.

L. Arriana Brand
Graduate Degree Program
in Ecology
Colorado State University
Fort Collins, CO 80523
Spring 2004

ACKNOWLEDGEMENTS

I would like to express my sincere gratitude for the support and help of my committee: Drs. Barry R. Noon (advisor), Kenneth P. Burnham, Kenneth R. Wilson, and John A. Wiens. Data collection and project development was funded by the Strategic Environment Research and Development (SERDP) project CS-1100. This funding was supplemented with a CSU College of Natural Resources Oscar and Isabel Anderson Fellowship, Cooper Society Travel Award, a grant for work study data entry from M. M. Jeanes and R. J. Brand, as well as by teaching FW 371/471 (Wildlife Data Collection and Analysis) for the Fishery and Wildlife Biology Department during Fall 2001 and Spring 2002. I appreciate the enthusiasm and hard work of the field crew that collected data on the San Pedro River: Seth Factor, Devin Biggs, Carey Hill, Mark Faherty, Brian Acord, Dolly Crawford, Christopher Putnum, Janine McCabe, and Brynne Langan. The Bureau of Land Management San Pedro Project Office was particularly helpful during all stages of the data collection effort. In particular I would like to thank Bill Childress, Dave Krueper, and Jack Whetstone for all of their help as well as access to the San Pedro Riparian National Conservation Area (SPRNCA) and Empire Cienega Riparian National Conservation Area. Edward Wilk, naturalist with The Nature Conservancy, was very helpful in showing me around and granting permission to establish study sites on the Patagonia / Sonoita Creek Preserve. Sheridan Stone, Wildlife Biologist of Fort Huachuca, granted permission to work on the east and west ranges of Fort Huachuca. Permission to work on particular study areas was also granted by Mr. and Mrs. Hughes, Steinman, Bennett, and Dewells, Barbara Clark, and Quinteen Miller. The BLM San Pedro Project Office also helped immensely by providing housing at Boquillas Ranch on

the SPRNCA for 4 summers of data collection. Thomas Sisk, Rocky Coleman, and Brian Cade loaned field equipment, for which I am grateful. I would also like to thank Thomas Sisk, Leslie Ries, James Battin, and Haydee Hampton of Northern Arizona University as well as Ronnie Estelle for their collaboration during the course of this project. Brett Dickson helped me to edit shapefiles as efficiently as possible using ArcView 3.2. I have also appreciated the many friends and colleagues from the Department of Fishery and Wildlife Biology as well as the Graduate Degree Program in Ecology. Finally, I am very thankful for the love and support of my parents, Richard and Karen Brand, and the love, patience, humor, and understanding of my husband, Henry Jeanes. I also owe much to my sons, Sebastian and Gavin Jeanes, for helping me to be efficient at work and fully present at home.

Dedicated to Gavin and Sebastian

TABLE OF CONTENTS

Ecological and Life-History Traits Predict Avian Edge Response: A Meta-Analysis 1
- Abstract 1
- Introduction 2
- Methods 7
  - Selection of Papers 7
  - Data Collection from Edge Response Papers 8
  - Candidate Model Development 10
    - Environmental Factors 12
    - Biotic Interactions 16
    - Stochastic Processes 19
    - Fitness Consequences 20
    - Adjustment Factors 21
  - Analytic Methods 23
- Results 27
  - Descriptive Results 27
  - Model Selection Results 29
  - Predictive Edge Models 29
    - Forest-Open Edge Type 30
    - Open-Forest Edge Type 31
  - Internal Validation of Predictive Edge Models 32
- Discussion 33
- Literature Cited 41
- Figures 50
- Tables 54
- Appendix 1 66
- Appendix 2 69

Empirical Validation of a Method for Predicting Species-Specific Edge Response for Birds in Forested Landscapes 70
- Abstract 70
- Introduction 71
- Methods 75
  - Predicted Edge Response 75
    - Ecological and Life-history Trait Database 75
    - Predicting Probability of Edge Response 78
  - Observed Edge Response 80
  - Field Protocol 80
    - Distance Sampling Analysis 83
    - Edge Response Functions 84

        Comparison of Observed with Predicted 86
    Results 87
        Observed Edge Response 87
        Predicted Edge Response 88
        Comparison of Observed with Predicted 89
            Environmental Factors 89
            Ecological and Life-history Traits 90
    Discussion 91
    Literature Cited 96
    Figures 101
    Tables 102
    Appendix 3 113

Predicting Abundance of Desert Riparian Birds: Validation and Calibration of the Effective Area Model 120
    Abstract 120
    Introduction 121
    Methods 125
        Predicted Abundance 125
            Field Protocol 126
            Distance Sampling Analysis 128
            EAM and Null Model Parameterization 130
            Validation Study Sites 132
        Observed Abundance 133
        Comparison of Observed and Predicted 135
            Model Validation 135
            Model Calibration 137
    Results 139
        Model Validation 139
        Model Calibration 140
    Discussion 142
    Literature Cited 148
    Figures 152
    Tables 158

CHAPTER 1

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

Abstract

Despite 70 years of research addressing avian abundance in relation to distance from habitat edges, no general relationship exists that enables *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, Receiver and Operating Characteristic (ROC) analysis was used to compare observed versus predicted edge response by calculating the area under the ROC curve, % 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 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 allows *a priori* predictions of the expected edge response for 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 about mechanisms that may structure how various bird species respond to edges. Further, there is a general perception that predicting how unstudied species will respond to edges is impossible (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 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 insufficient time and resources to study each species in each habitat for which conservation decisions are necessary (Côté and Reynolds 2002).

Various approaches have been attempted in the effort to use surrogate species whose status and trends provide insights into the state of the larger ecological system (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 must be identified in each new location or system of interest. For example, while a focal species may serve as an indicator for a system in which 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 ecological theory currently exists to guide the selection of such species (Noon et al. 1997, Flather et al. 1997, MacNally and Fleishman 2002).

Of these various approaches, 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 the 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 affect many regions and may apply to many species occupying diverse ecosystems.

It also 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 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, potentially enables movement 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 considered how best to identify predictive traits for this threat. Habitat fragmentation studies typically measure patch size, patch shape, or distance from edge (Flaspohler et al. 2001, George and Brand 2002). A focus on edges has a number of 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 scale, effects of edge can also be used in a predictive capacity more readily than patch size (Sisk et al. 1997). Given the interest in both positive and negative results in edge studies since the late-1930's, edge studies are also less likely 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 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 edge is viewed as a selective environment arising from a unique set of physical and biological drivers that occur at the edge, then traits associated with edge species should differ from interior species to the extent that the two selective environments differ. I hypothesized that environment at the edge is characterized by 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 edge results in a unique selection regime, the biotic, abiotic, and stochastic factors that operate at the edge environment differently from the interior environment serve as mechanisms of edge habitat selection or avoidance, and in turn, shape the evolutionary history of an organism through natural selection. Notwithstanding cautions set forth by Van Horne (1983), my assumption is that greater 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 lead to an increase in the population (central tenant of natural selection).

Selection regimes or mechanisms operating on birds at edges may influence multiple traits, e.g. increased predation could impact 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 and allows predictions about how species will be affected at edges.

Ecological and life-history traits have been related to sensitivity to habitat fragmentation. Most often these have been based on qualitative observations, although a few attempts to identify traits related to vulnerability to fragmentation have been 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 (i.e., change in density or abundance as a function of distance from edge). Best et al. (1990) found a relationship between edge response and diet, foraging substrate, and nesting substrate. 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 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 explored a diverse set of ecological and life-history traits to identify those traits that allow prediction of how species respond to edges. I used the following basic approach: given a particular stressor such as the creation of edges due to habitat fragmentation, 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) highlight the importance of using quantitative analyses that are ecosystem and taxon specific (Kolar and Lodge 2002). Similarly, I focus 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 using readily available information on life-history and ecological traits of birds from the literature. I hope that as a result, reliable conservation decisions can still be made when detailed edge response studies are not possible.

Methods

Selection of Papers

The selection of papers to include in the meta-analysis was based literature reviews by Sisk and Battin (2002) and additional literature searches that I conducted.

Sisk and Battin (2002) reviewed 90 studies that presented original research addressing avian response to edges in primarily forested landscapes. From searches of the literature, I identified 71 potential papers that estimated bird density, abundance, or nest density in relation to distance from the forest edge, and assessed each paper according to set of selection criteria as outlined below.

A number of criteria were used for the selection of papers included in the meta-analysis. Topics of papers were limited to breeding bird species in North America, where the response to edge was species-specific. 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 this criteria studied abrupt edges, regardless of whether they were human-caused or naturally occurring, and presented original data analysis 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 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 this 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 the appropriate effect size is difficult with edge studies because of differences in methods of data collection and analysis, and variability of published information. For example, some studies report density and some report abundance, and some report only relative measures estimated without a detection function, which may vary with distance from edge. 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 were surveyed, may also affect data quality. These issues were resolved here 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 used 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 and 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 some 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 13 traits were used in the four candidate model sets (Table 2), with three 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 that decreased humidity, found to be lower at edges compared with the forest interior (Chen 1995, Lehtinen et al. 2003), would 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 (Whitcomb et al. 1981, Brand and George 2001). 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 (De Graaf 1992, Lopez de Casenave et al. 1998). 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 (Gates and Gysel 1978, De Graaf 1992, Marini et al. 1995, Germaine et al. 1997). 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., Whitcomb et al. 1981, Restrepo and Gomez 1998). 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 hypothesized that omnivores may be more abundant at the edge because they may benefit from cross-boundary subsidies (Fagan et al. 1999, Cantrell et al. 2001) in both 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 (De Graaf 1992, Yahner 1995, Jokimaeki et al. 1998, Van Wilgenburg et al. 2001). 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 (De Graaf 1992, Yahner 1995). 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, 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 (Ehrlich et al. 1988, National Geographic 1992). 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, Donovan et al. 1997, Chalfoun 2002). 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 The Birds of North America series 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 (Brittingham and Temple 1983, Evans and Gates 1997, Hobson and Villard 1998). 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.

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 (Galli et al. 1976, Crawford et al. 1981, Whitcomb et al.1981, Rich et al. 1994). 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 (Johnston 1947, Whitcomb et al. 1981, Chasko and Gates 1982, Kroodsma 1987, Gates and Giffen 1991, O'Connell et al. 1998). 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 plasticity 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 The Birds of North America series for 17 species; longevity obtained from bird banding 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 with 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 the mechanisms operating on birds at edges (Table 4). I selected 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, respectively (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, calculated the area under the ROC curve along with the associated standard error and confidence intervals, and calculated 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 studied 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 (Appendix 1,2). 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. Eight 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 had $P < 0.1$ (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 birds 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 (Table 7). The best prediction model for negative edge response had an Akaike weight $w_i = 19.1\%$, and the best model to predict positive edge response had an Akaike weight $w_i = 28.3\%$ (Table 7). Model selection uncertainty was observed with ΔAICc value < 2 for 4 and 3 models in negative and positive candidate models sets, respectively (Table 7). Despite model selection uncertainty, the first model had about twice the support of the second model in terms w_i values for both positive and negative edge response models (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). The first model had 160 and 80 times the support of the second model in terms w_i values for both positive and negative edge response models (Table 8).

Multi-trait Predictive Edge Models

I 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 had $P < 0.1$. 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, however, lifetime reproductive effort had $P < 0.1$ (Table 5, Figure 2), and thus may be 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 (Table 10). 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 host was in the best model but was not significant ($P = 0.432$; Table 10) though it had $P < 0.1$ 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 (Table 10). 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).

Internal 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 SE and Confidence Intervals. Additionally, I calculated the sensitivity, specificity, and % correct classification associated with a particular cut point (Table 11). Cut points along the logistic function were determined by maximizing the % 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 on 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 (DeGraaf 1992, Yahner 1995). 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 (Whitcomb et al. 1981, Restrepo and Gomez 1998), 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 model selection. 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). 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 demonstrable 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 4 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 (De Graaf 1992, Flaspohler et al. 2001). Similarly, I 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 sense based on available nesting substrate being higher in forest edges than in 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 (Whitcomb et al. 1981, Peters 1983, Lima 1986, O'Connell et al. 1998), I found smaller, more specialized 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 generalized 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. This result possibly reflects compensation for the negative fitness consequences of nesting at the edge. There is likely some fitness advantage of nesting at the edge for particular species (increased nesting resources, increased food) but possibly 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 short and long times scales.

I considered three adjustment factors to account for intra-specific variability in edge response. No adjustment variable 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.

One of the primary limitations of this approach is that edge response predictions are qualitative (positive, neutral, or negative) rather than quantitative. Further study would be needed to assess whether quantitative edge response predictions would be possible. Further, it should be recognized that the validation of these models using ROC analysis was done with the same data used to develop the models. As such, the success of the predictions may be overestimated. Predictions of these models should be tested with an independent data set, which is the topic of Chapter 2.

Literature Cited

Anderson, S. H., K. Mann, and J. Shugart, Herman H. 1977. The effect of transmission-line corridors on bird populations. *American Midland Naturalist* 97: 216-221.

Arnqvist, G. and D. Wooster. 1995. Meta-analysis: Synthesizing research findings in ecology and evolution. *Trends in Ecology and Evolution* 10: 236-240.

Best, L. B., R. C. Whitmore, and G. M. Booth. 1990. Use of cornfields by birds during the breeding season: the importance of edge habitat. *American Midland Naturalist* 123:84-99.

Brand, L. A., and T. L. George. 2000. Predation risks for nesting birds in fragmented coast redwood forest. *Journal of Wildlife Management* 64: 42-51.

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

Brant, R. 1990. Assessing Proportionality in the Proportional Odds Model for Ordinal Logistic Regression. *Biometrics* 46: 1171-1178.

Brittingham, M. C., and S. A. Temple. 1983. Have cowbirds caused forest songbirds to decline? *Bioscience* 33: 31-35.

Burnham, K. P., and D. A. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach, 2nd edition. Springer-Verlag, Inc. New York. 488 pp.

Cantrell, R. S., C. Cosner, and W. F. Fagan. 2001. How Predator Incursions Affect Critical Patch Size: The Role of the Functional Response. *American Naturalist* 158: 368-375.

Chalfoun, A. D., F. R. Thompson III, and M. J. Ratnaswamy. 2002. Nest predators and fragmentation: a review and meta-analysis. *Conservation Biology* 16: 306-318.

Chasko, G. G., and J. E. Gates. 1982. Avian habitat suitability along a transmission-line corridor in an oak-hickory forest region. *Wildlife Monographs* 82: 1-41.

Chen, J., J. F. Franklin, and T. A. Spies. 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. *Ecological Applications* 2: 387-396.

Chen, J., J. F. Franklin, and T. A. Spies. 1995. Growing-season microclimatic gradients from clearcut edges into old-growth Douglas-fir forests. *Ecological Applications* 5: 74-86.

Clapp, R. B., M. K. Klimkiewicz, and A. G. Futcher. 1983. Longevity records of North American Birds: Columbidae through Paridae. *Journal of Field Ornithology* 54:123-137.

Clapp, R. B., M. K. Klimkiewicz, and J. H. Kennard. 1982. Longevity records of North American Birds: Gaviidae through Alcidae. *Journal of Field Ornithology* 53:81-208.

Collins, P. W. 1999. Rufous-crowned Sparrow (*Aimophila ruficeps*) in A. Poole and F. Gill, eds The Birds of North America, No. 472. The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

Conway, C. J. 1999. Canada Warbler (*Wilsonia canadensis*) in A. Poole and F. Gill, eds. The Birds of North America , No. 421. The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

Côté, I. M., and J. D. Reynolds. 2002. Predictive ecology to the rescue? *Science* 298: 1181-1182.

Crawford, H. S., R. G. Hooper, and R. W. Titterington. 1981. Songbird population response to silviculture practices in cetnral Appalachian hardwoods. *Journal of Wildlife Management* 45:680-692.

Davis, J. N. 1995. Hutton's vireo (*Vireo huttoni*) in A. Poole and F. Gill, eds The Birds of North America, No. 189. The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

DeGraaf, R. M. 1992. Effects of even-aged management on forest birds at northern hardwood stand interfaces. *Forest Ecology and Management* 46: 95-110.

DeLong, E. R., D. M. DeLong, and D. L. Clarke-Pearson. 1988. Comparing the Areas under Two or More Correlated Receiver Operating Characteristic Curves: A Nonparametric Approach. *Biometrics* 44: 837-845.

DeLong, E. R., W. B. Vernon, and R. R. Bollinger. 1985. Sensitivity and Specificity of a Monitoring Test. *Biometrics* 41: 947-958.

Donovan, T. M., P. W. Jones, E. M. Annand, and F. R. Thompson III. 1997. Variation in local-scale edge effects: Mechanisms and landscape context. Ecology 78: 2064-2075.

Dunning, Jr., J. B. 1992. CRC Handbook of Avian Body Masses. Dunning (editor) CRC Press.

Ehrlich, P. R., D. S. Dobkin, and D. Wheye. 1988. The Birder's Handbook: A field guide to the natural history of North American Birds. Simon and Schuster Inc.

Evans, D. R., and J. E. Gates. 1997. Cowbird selection of breeding areas: the role of habitat and bird species abundance. *Wilson Bulletin* 109:470-480.

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

Fahrig, L. 2002. Effect of habitat fragmentation on the extinction threshold: A synthesis. *Ecological Applications* 12: 346-353.

Ferris, C. R. 1979. Effects of Interstate 95 on breeding birds in northern Maine. *Journal of Wildlife Management* 43: 421-427.

Flaspohler, D. J., S. A. Temple, and R. N. Rosenfield. 2001. Species-specific edge effects on nest success and breeding bird density in a forested landscape. *Ecological Applications* 11: 32-46.

Flather, C. H., K. R. Wilson, D. J. Dean, and W. C. McComb. 1997. Identifying gaps in conservation networks: Of indicators and uncertainty in geographic-based analyses. Ecological Applications 7: 531-542.

Galli, A. E., C. F. Leck, and R. T. Forman. 1976. Avian distribution patterns in forest islands of different sizes in central New Jersey. Auk 93: 356-364.

Gates, J. E., and N. R. Giffen. 1991. Neotropical migrant birds and edge effects at a forest-stream ecotone. *Wilson Bulletin* 103: 204-217.

Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* 59: 871-883.

George, T. L. 2000. Varied Thrush (*Ixoreus naevius*) in A. Poole and F. Gill, eds The Birds of North America, No. 541. The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

George, T. L., and L. A. Brand. 2002. The effects of habitat fragmentation on birds in coast redwood forests. *Studies in Avian Biology* No. 25: 92-102.

Germaine, S. S., S. H. Vessey, and D. E. Capen. 1997. Effects of small forest openings on the breeding bird community in a Vermont hardwood forest. *The Condor* 99: 708-718.

Greene, E., W. Davison, and V. R. Muehter. 1998. Steller's Jay (*Cyanocitta stelleri*) in A. Poole and F. Gill, eds The Birds of North America, No. 343. The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

Guinan, J. A., P. A. Gowaty, and E. K. Eltzroth. 2000. Western Bluebird (*Sialia mexicana*) in A. Poole and F. Gill, eds The Birds of North America, No. 510. The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

Hall, G. A. 1994. Magnolia warbler (*Dendroica magnolia*) in A. Poole and F. Gill, eds The Birds of North America, No. 136. The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

Hall, G. A. 1996. Yellow-throated warbler (*Dendroica dominica*) in A. Poole and F. Gill, eds The Birds of North America, No. 16. The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

Hamel, P. B. 2000. Cerulean Warbler (*Dendroica cerulea*) in A. Poole and F. Gill, eds The Birds of North America, No. 511. The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

Hobson, K. A., and M-A Villard. 1998. Forest fragmentation affects the behavioral response of American redstarts to the threat of cowbird. *The Condor* 100: 389-394.

Hopp, S. L., A. Kirby, and C. A. Boone. 1995. White-eyed vireo (*Vireo griseus*) in A. Poole and F. Gill, eds The Birds of North America, No. 168. The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

Ingold, J. L., and G. E. Wallace. 1994. Ruby-crowned kinglet (*Regulus calendula*) in A. Poole and F. Gill, eds The Birds of North America, No. 119. The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

Johnston, V. R. 1947. Breeding birds of the forest edge in Illinois. *The Condor* 49: 45-52.

Jokimaeki, J., E. Huhta, J. Itaemies, and P. Rahko. 1998. Distribution of arthropods in relation to forest patch size, edge, and stand characteristics. *Canadian Journal of Forest Research* 7: 1068-1072.

Keller, M. E., and S. H. Anderson. 1992. Avian use of habitat configurations created by forest cutting in southeastern Wyoming. *The Condor* 94:55-65.

King, D. I., C. R. Griffin, and R. M. DeGraaf. 1997. Effect of clearcut borders on distribution and abundance of forest birds in northern New Hampshire. *Wilson Bulletin* 109: 239-245.

Klimkiewicz, M. K., and A. G. Futcher. 1987. Longevity records of North American Birds: Coerebinae through Estrilididae. *Journal of Field Ornithology* 58: 318-333.

Klimkiewicz, M. K., R. B. Clapp, and A. G. Futcher. 1983. Longevity records of North American Birds: Remizidae through Parulinae. *Journal of Field Ornithology* 54: 287-294.

Kolar, C. S., and D. M. Lodge. 2002. Ecological predictions and risk assessment for alien fishes in North America. *Science* 298: 1233-1236.

Kroodsma, R. L. 1982. Ege effect on breeding forest birds along a powerline corridor. *Journal of Applied Ecology* 19:361-370.

Kroodsma, R. L. 1984a. Ecological factors associated with degree of edge effect in breeding birds. *Journal of Wildlife Management* 48: 418-425.

Kroodsma, R. L. 1984b. Effect of edge on breeding forest bird species. *Wilson Bulletin* 96: 426-436.

Kroodsma, R. L. 1987. Edge effect on breeding birds along power-line corridors in east Tennessee. *American Midland Naturalist* 118: 275-283.

Lambeck, R. J. 1997. Focal species: a multi-species umbrella for nature conservation. *Conservation Biology* 11: 849-856.

Landres, P. B., J. Verner, and J. W. Thomas. 1988. Ecological use of vertebrate indicator species: a critique. *Conservation Biology* 2: 316-328.

Lay, D. W. 1938. How valuable are woodland clearings to birdlife? *Wilson Bulletin* 50: 254-256.

Lehtinen, R. M., J. B. Ramanamanjato, and J. G. Raveloarison. 2003. Edge effects and extinction proneness in a herpetofauna from Madagascar. Biodiversity and Conservation 12: 1357-1370.

Lens, L., S. Van Dongen, K. Norris, M. Githuru, and E. Matthysen. 2002. Avian persistence in fragmented rainforest. *Science* 298: 1236-1238.

Lima, S. L. 1986. Predation risk and unpredictable feeding conditions: Determinants of body mass in birds. *Ecology* 67: 377-385.

Lopez de Casenave, J., J. P. Pelotto, S. M. Caziani, M. Mermoz, and J. Protomastro. 1998. Responses of avian assemblages to a natural edge in a chaco semiarid forest in Argentina. *Auk* 115: 425-435.

Lowther, P. E. 2000. Nuttall's Woodpecker (*Picoides nuttallii*) in A. Poole and F. Gill, eds The Birds of North America, No. 555. The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

Lowther, P. E. 2000. Pacific-slope Flycatcher (*Empidonax difficilis*) and Cordilleran Flycatcher (*Empidonax occidentalis*) in A. Poole and F. Gill, eds The Birds of North America, No. 556. The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

MacNally, R., and E. Fleishman. 2002. Using "indicator" species to model species richness: Model development and predictions. *Ecological Applications* 12: 79-92.

Mac Nally, R., and A. F. Bennett. 1997. Species-specific predations of the impact of habitat fragmentation: Local extinction of birds in the box-ironbark forests of central Victoria, Australia. *Biological Conservation* 82: 147-155.

Mac Nally, R., A. F. Bennett, and G. Horrocks. 2000. Forecasting the impacts of habitat fragmentation. Evaluation of species-specific predictions of the impact of habitat fragmentation on birds in the box-ironbox forests of central Victoria, Australia. *Biological Conservation* 95: 7-29.

Marini, M. A., S. K. Robinson, and E. J. Heske. 1995. Edge effects on nest predation in the Shawnee National Forest, southern Illinois. *Biological Conservation* 74: 203-213.

Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65(1):101-127.

Mills, L. S, M. E. Soulé, and D. F. Doak. 1993. The keystone-species concept in ecology and conservation. *Bioscience* 43: 219-224.

Moldenhauer, R. R., and D. J. Regelski. 1996. Northern Parula (*Parula americana*) in A. Poole and F. Gill, eds The Birds of North America, No. 215. The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

Morse, D. H. 1994. Blackburnian warbler (*Dendroica fusca*) in A. Poole and F. Gill, eds The Birds of North America, No. 102. The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

Morse, D. H. 1993. Black-throated green warbler (*Dendroica virens*) in A. Poole and F. Gill, eds The Birds of North America, No. 55. The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

Moskoff, W., and S. K. Robinson. 1996. Philadelphia vireo (*Vireo philadelphicus*) in A. Poole and F. Gill, eds The Birds of North America, No. 214. The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

National Geographic Society. 1992. Field guide to the birds of North America, 3rd edition.

Newmark, W. D. 2001. Tanzanian Forest Edge Microclimatic Gradients: Dynamic Patterns. *Biotropica* 33: 2-11.

Niemuth, N. D., and M. S. Boyce. 1997. Edge-related nest losses in Wisconsin pine barrens. *Journal of Wildlife Management* 61:1234-1239.

Noon, B. R., K. McKelvey, and D. Murphy. 1997. Developing an analytical context for multispecies conservation planning. Pages 43-59 in S. T. A. Pickett, R. S. Ostfeld, M Shackak, and G. E. Likens (eds.). The Ecological Basis of Conservation: Heterogeneity, Ecosystems and Biodiversity. Chapman & Hall, New York.

Noss, R. F. 1991. Effects of edge and internal patchiness on avian habitat use in an old-growth Florida hammock. *Natural Areas Journal* 11: 34-47.

O'Connell, T. J., L. E. Jackson, and R. P. Brooks. 1998. A bird community index of biotic integrity for the mid-atlantic highlands. *Environmental Monitoring and Assessment* 51:145-156.

Pearson, S. F. 1997. Hermit Warbler (*Dendroica occidentalis*) in A. Poole and F. Gill, eds The Birds of North America, No. 303. The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge. 329 pp.

Pidgeon, A. M., V. C. Radeloff, and N. E. Mathews. 2003. Landscape-scale patterns of black-throated sparrow (*Amphispiza bilineata*) abundance and nest success. *Ecological Applications* 13: 530-542.

Pitocchelli, J. 1993. Mourning warbler (*Oporornis philadelphia*) in A. Poole and F. Gill, eds The Birds of North America, No. 72. The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

Restrepo, C., and N. Gomez. 1998. Responses of understory birds to anthropogenic edges in a neotropical montane forest. *Ecological Applications* 8: 170-183.

Rich, A. C., D. S. Dobkin, and L. J. Niles. 1994. Defining forest fragmentation by corridor width: the influence of narrow forest dividing corridors on forest-nesting birds in southern New Jersey. *Conservation Biology* 8: 1109-1121.

Richardson, M., and D. Brauning. 1995. Chestnut-sided warbler (*Dendroica pensylvanica*) in A. Poole and F. Gill, eds The Birds of North America, No. 190. The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

Rimmer, C. C., and K. P. McFarland. 1998. Tennessee Warbler (*Vermivora peregrina*) in A. Poole and F. Gill, eds The Birds of North America, No. 350. The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

Robinson, W. D. 1996. Summer tanager (*Piranga rubra*) in A. Poole and F. Gill, eds. The Birds of North America, No. 248. The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

Rodewald, P. G., and R. D. James. 1996. Yellow-throated vireo (*Vireo flavifrons*) in A. Poole and F. Gill, eds The Birds of North America, No. 247. The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

Sisk, T. D., and J. Battin. 2002. Habitat edges and avian ecology: Geographic patterns and insights for western landscapes. *Studies in Avian Biology* No. 25: 30-48.

Sisk, T. D., N. M. Haddad, and P. R. Ehrlich. 1997. Bird assemblages in patchy woodlands: modeling the effects of edge and matrix habitats. *Ecological Applications* 7: 1170-1180.

Sisk, T. D., and C. R. Margules. 1993. Habitat edges and restoration: methods for quantifying edge effects and predicting the results of restoration efforts. Pages 57-69 in D. A. Saunders, R. J. Hobbs, and P. R. Ehrlich, eds. *Nature Conservation 3: Reconstruction of Fragmented Ecosystems*. Surrey, Beatty & Sons, Sydney, North Wales, Australia.

Small, M. F., and M. L. Hunter. 1989. Response of passerines to abrupt forest-river and forest-powerline edges in Maine. *Wilson Bulletin* 101:77-83.

Strelke, W. K., and J. G. Dickson. 1980. Effect of forest clear-cut edge on breeding birds in east Texas. *Journal of Wildlife Management* 44: 559-567.

Suding, K. N., D. E. Goldberg, and K. M. Hartman. 2003. Relationships among species traits: Separating levels of response and identifying linkages to abundance. *Ecology* 84: 1-16.

Tenney, C. R. 1997. Black-chinned sparrow (*Spizella atrogularis*) in A. Poole and F. Gill, eds The Birds of North America, No. 270. The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47: 893-901.

Van Wilgenburg, S. L., D. F. Mazerolle, and K. A. Hobson. 2001. Patterns of arthropod abundance, vegetation, and microclimate at boreal forest edge and interior in two landscapes: Implications for forest birds. *Ecoscience* 8: 454-461.

Vitousek, P. M. 1994. Beyond global warming: ecology and global change. *Ecology* 75:1861-1876.

Whitcomb, R. F., C. S. Robbins, J. F. Lynch, B. L. Whitcomb, M. K. Klimkiewicz, and D. Bystrak. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pp. 125-205 *in* Burgess, R. L. and D. M. Sharpe (eds). Forest island dynamics in man-dominated landscapes. Ecological Studies, vol. 41.

Wiens, J. A. 1989. The Ecology of Bird Communities Vol. 2: Processes and Variations. Cambridge University Press, New York, NY. 316 pp.

Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66: 1211-1214.

Williams, J. M. 1996. Bay-breasted warbler (*Dendroica castanea*) in A. Poole and F. Gill, eds The Birds of North America, No. 206. The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

Woodward, A. A., A. D. Fink, and F. R. Thompson. 2001. Edge effects and ecological traps: Effects on shrubland birds in Missouri. *Journal of Wildlife Management* 65: 668-675.

Yahner, R. H. 1995. Habitat use by wintering and breeding bird communities in relation to edge in an irrigated forest. *Wilson Bulletin* 107:365-371.

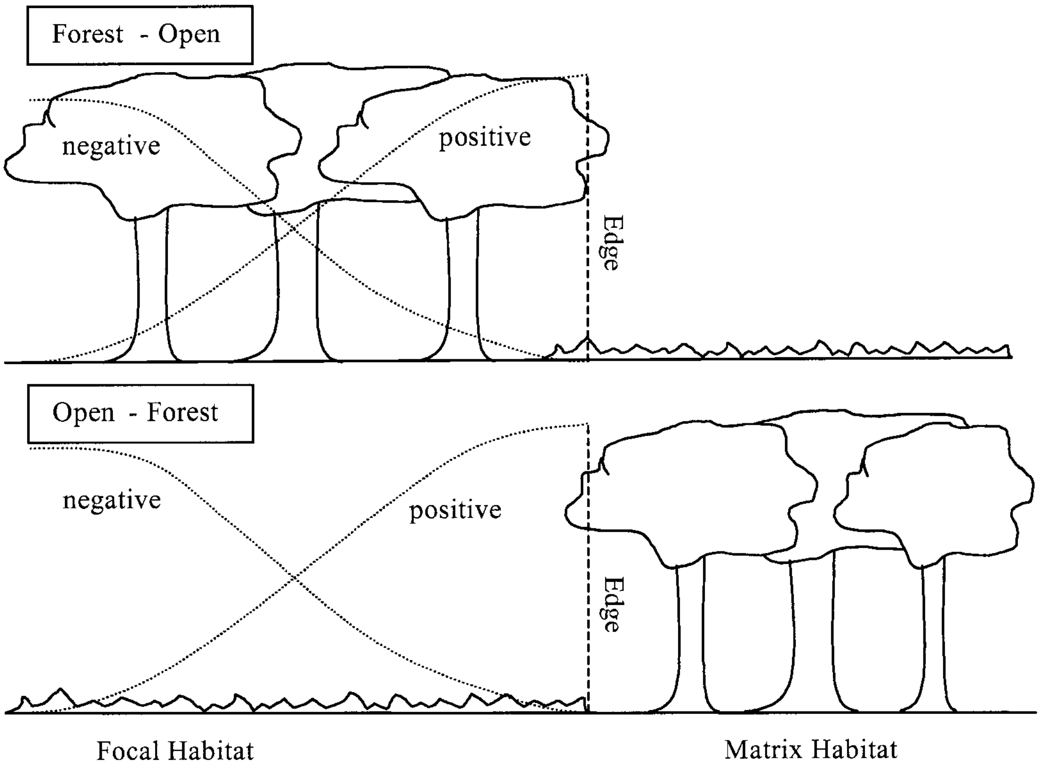


Figure 1. Positive and Negative Edge Response in Forest-Open and Open-Forest Edge Types

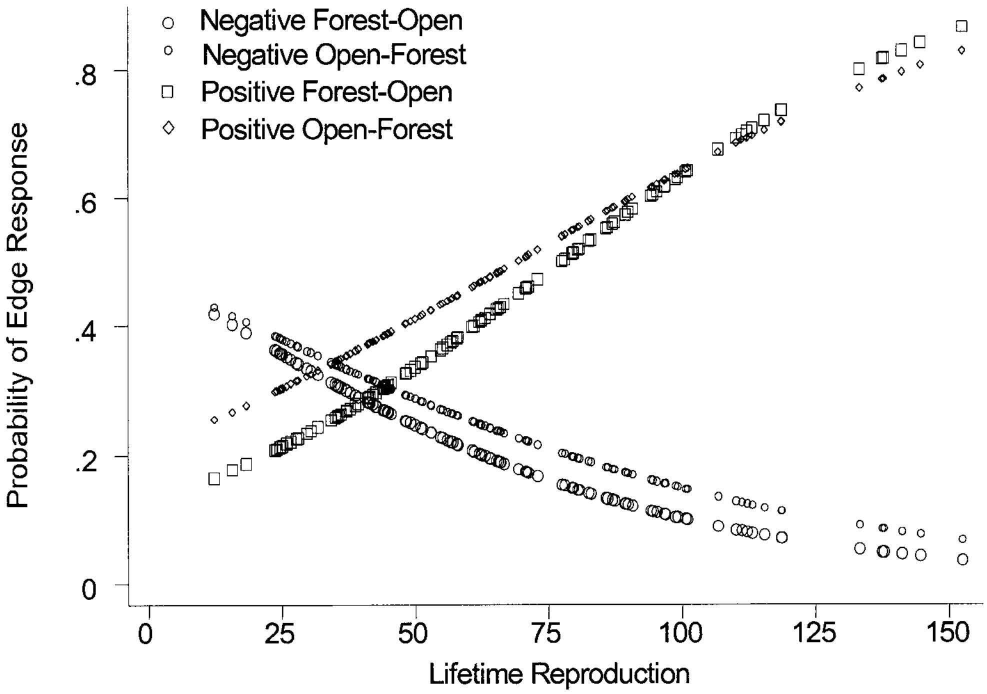


Figure 2. Probability of negative and positive edge response as a function of lifetime reproductive output in forest-open and open-forest edge types.

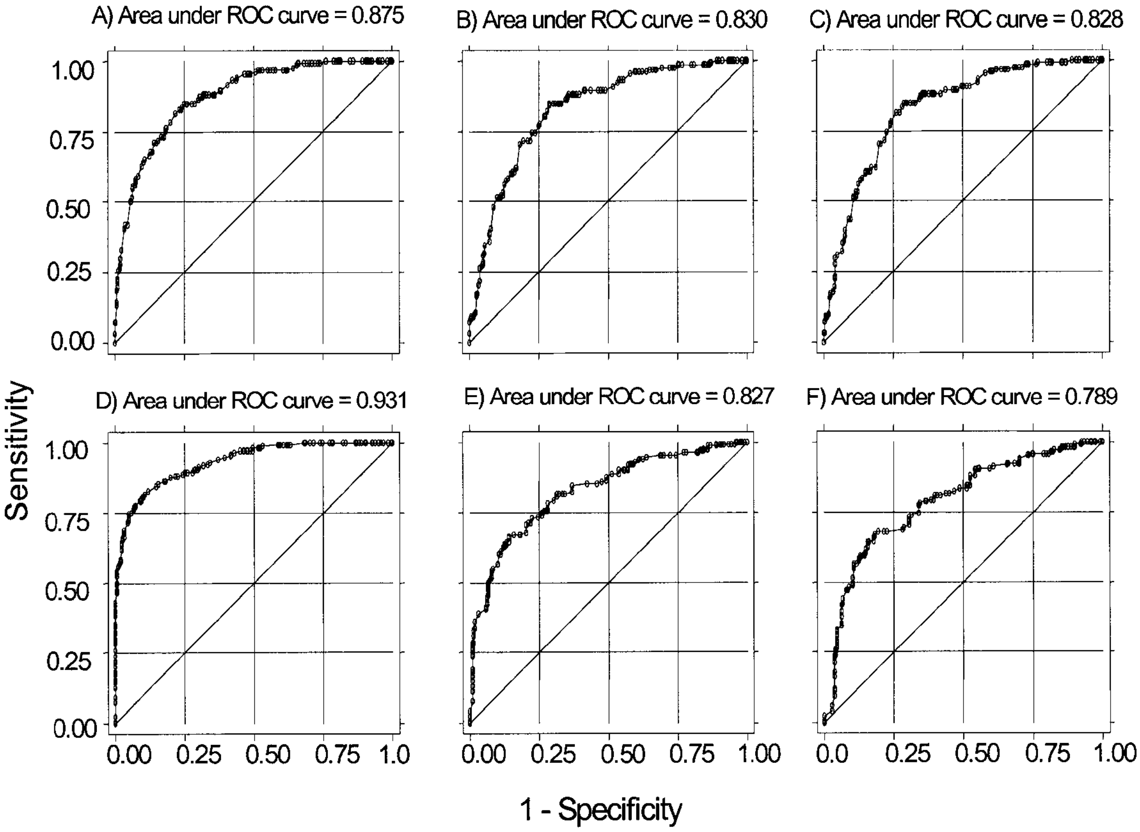


Figure 3. ROC analyses for Forest-Open Edge Type: Negative Edge Response with A) Species, B) Family and C) no Random Effect; Positive Edge Response with D) Species, E) Family, and F) no Random Effect.

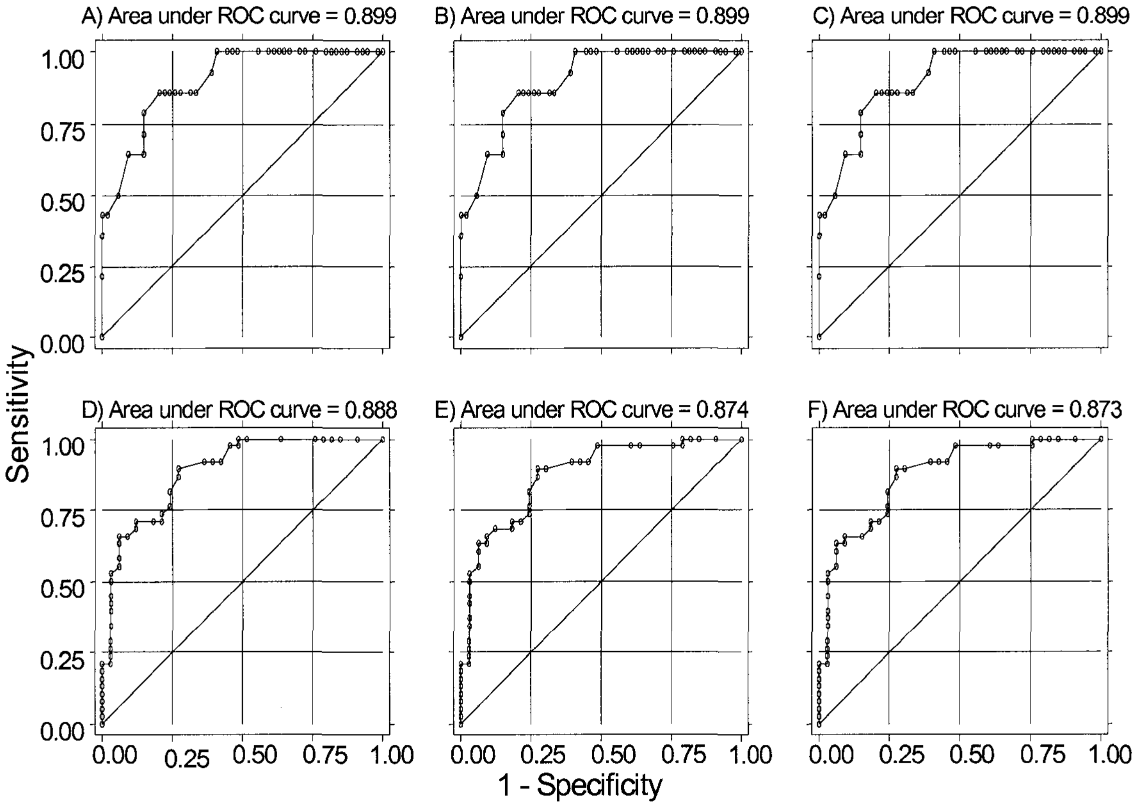


Figure 4. ROC analyses for Open-Forest Edge Type: Negative Edge Response with A) Species, B) Family, and C) no Random Effect; Positive Edge Response with D) Species, E) Family, and F) no Random Effect.

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	Code
Environmental Factors	Mesic habitat selection	MH
	Foraging Substrate	FS1,FS2
	Diet	DI1, DI2
	Habitat Utilization	HU1, HU2
Biotic Interactions	Nest Type	NT
	Incubation + Nesting period	IN
	Cowbird host frequency	CH
	Migratory Status	MS
Environmental Factors and Biotic Interactions	Nest Substrate	NS
	Nest Height	NH
Stochastic Processes	Ecological Plasticity	EP
	Body mass	BM

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	HU 1	forest habitat (C) vs. open / both (R)	forest -open	greater	lesser	1, 2
	HU 2	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 Frequency	CH	common host (C) vs. rare host (R)	both	lesser	NA	1
Ecological Plasticity	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 category 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.	SE	P	95% LCL	95% UCL	Reference [1]	Comparison [1]	Odds Ratio[1,2]
Negative Edge Response, Forest-Open								
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
Positive Edge Response, Forest-Open								
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
Negative Edge Response, Open-Forest								
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
Positive Edge Response, Open-Forest								
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.	SE	P	95% LCL	95% UCL	Reference[1]	Comparison[1]	Odds Ratio[1]
Negative, Forest-Open								
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
Positive, Forest-Open								
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
Negative, Open-Forest								
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
Positive, Open-Forest								
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[1]	AICc	ΔAICc	w_i[2]
Negative Edge Response							
HU+ME+IN+EP+BM+LR	422	119	-192.14	8	400.63	0.00	0.191
HU+ME+IN+LR+EP+BM+AN	422	119	-191.94	9	402.32	1.69	0.082
HU+ME+IN+LR+EP+BM+RE	422	119	-192.01	9	402.45	1.82	0.077
HU+ME+IN+LR+EP+BM+AG	422	119	-192.01	9	402.45	1.82	0.077
HU+IN+EP+BM+LR	422	119	-194.23	7	402.72	2.09	0.067
HU+ME+IN+BM+LR	422	119	-194.32	7	402.91	2.28	0.061
HU+CD+IN+EP+BM+LR	422	119	-193.35	8	403.05	2.42	0.057
HU+DI+IN+EP+BM+LR	422	119	-193.59	8	403.53	2.90	0.045
HU+ME+CD+IN+BM+LR	422	119	-193.61	8	403.57	2.94	0.044
HU+ME+DI+IN+BM+LR	422	119	-193.63	8	403.61	2.98	0.043
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

[1] K is the number of estimable parameters including both fixed and random components.

[2] w_i are Akaike weights (see Burnham and Anderson 2002).

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

model	num obs	num grps	log-lik	K[1]	AIC$_c$	ΔAIC$_c$	w$_i$[2]
		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

[1] K is the number of estimable parameters including both fixed and random components.

[2] w$_i$ are Akaike weights (see Burnham and Anderson 2002).

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

Trait	Coef.	SE	P	95% LCL	95% UCL	Reference[1]	Comparison[1]	Odds Ratio[3]
			Negative Edge Response, Species Random Effect					
HUI	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.	SE	P	95% LCL	95% UCL	Reference[1]	Comparison[1]	Odds Ratio[1]
Negative Edge Response, Species and 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	SE	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	≥ 0.532	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

Appendix 1. Edge response by species for forest-open edge type obtained from 30 journal articles included in the meta-analysis data set.

Species Name (Scientific Name)	Species	Edge Response			Total
	Code	Negative	Neutral	Positive	
Acadian Flycatcher *Empidonax virescens*	ACFL	6	0	0	6
Allen's Hummingbird *Selasphorus sasin*	ALHU	1	0	0	1
American Crow *Corvus brachyrhynchos*	AMCR	0	0	3	3
American Goldfinch *Carduelis tristis*	AMGO	0	0	3	3
American Redstart *Setophaga ruticilla*	AMRE	3	2	2	7
American Robin *Turdus migratorius*	AMRO	0	3	7	10
Anna's Hummingbird *Calypte anna*	ANHU	1	1	0	2
Ash-throated Flycatcher *Myiarchus cinerascens*	ATFL	0	0	2	2
Bay-breasted Warbler *Dendroica castanea*	BBWA	1	0	0	1
Bewick's Wren *Thryomanes bewickii*	BEWR	0	2	0	2
Black-and-white Warbler *Mniotilta varia*	BWWA	2	2	1	5
Black-capped Chickadee *Poecile atricapilla*	BCCH	0	3	0	3
Black-throated Blue Warbler *Dendroica caerulescens*	BTBW	1	1	1	3
Black-throated Green Warbler *Dendroica virens*	BTGW	2	2	0	4
Blackburnian Warbler *Dendroica fusca*	BLWA	1	2	0	3
Blue Grosbeak *Guiraca caerulea*	BLGR	0	0	3	3
Blue Jay *Cyanocitta cristata*	BLJA	3	4	3	10
Blue-gray Gnatcatcher *Polioptila caerulea*	BGGN	1	5	1	7
Blue-winged Warbler *Vermivora pinus*	BLUW	0	0	1	1
Brown Creeper *Certhia americana*	BRCR	4	1	0	5
Brown Thrasher *Toxostoma rufum*	BRTH	0	0	1	1
Brown-headed Cowbird *Molothrus ater*	BHCO	0	1	9	10
Brown-headed Nuthatch *Sitta pusilla*	BHNU	1	0	0	1
California Quail *Callipepla californica*	CAQU	0	1	1	2
California Thrasher *Toxostoma redivivum*	CATH	0	1	0	1
California Towhee *Pipilo crissalis*	CATO	0	0	2	2
Canada Warbler *Wilsonia canadensis*	CAWA	2	0	1	3
Carolina Chickadee *Poecile carolinensis*	CACH	0	3	2	5
Carolina Wren *Thryothorus ludovicianus*	CAWR	1	3	1	5
Cassin's Finch *Carpodacus cassinii*	CAFI	1	0	1	2
Cedar Waxwing *Bombycilla cedrorum*	CWAX	0	0	1	1
Cerulean Warbler *Dendroica cerulea*	CEWA	1	0	0	1
Chestnut-backed Chickadee *Poecile rufescens*	CBCH	2	1	0	3
Chestnut-sided Warbler *Dendroica pensylvanica*	CSWA	0	0	5	5
Chipping Sparrow *Spizella passerina*	CHSP	0	1	1	2
Common Bushtit *Psaltriparus minimus*	COBU	1	0	1	2
Common Grackle *Quiscalus quiscula*	COGR	0	0	3	3
Common Raven *Corvus corax*	CORA	0	1	0	1
Common Yellowthroat *Geothlypis trichas*	COYE	0	0	8	8
Dark-eyed Junco *Junco hyemalis*	DEJU	2	3	1	6
Downy Woodpecker *Picoides pubescens*	DOWO	2	3	1	6
Eastern Kingbird *Tyrannus tyrannus*	EAKI	0	0	1	1
Eastern Phoebe *Sayornis phoebe*	EAPH	1	1	0	2
Eastern Wood-pewee *Contopus virens*	EAWP	5	2	2	9

European Starling *Sturnus vulgaris*	EUST	0	1	2	3
Field Sparrow *Spizella pusilla*	FISP	0	0	4	4
Fish Crow *Corvus ossifragus*	FICR	0	0	1	1
Golden-crowned Kinglet *Regulus satrapa*	GCKI	0	1	0	1
Gray Catbird *Dumetella carolinensis*	GRCA	0	0	3	3
Gray Jay *Perisoreus canadensis*	GRJA	0	0	2	2
Great Crested Flycatcher *Myiarchus crinitus*	GCFL	2	3	2	7
Hairy Woodpecker *Picoides villosus*	HAWO	4	1	0	5
Hermit Thrush *Catharus guttatus*	HETH	4	1	1	6
Hermit Warbler *Dendroica occidentalis*	HEWA	1	0	0	1
Hooded Warbler *Wilsonia citrina*	HOWA	4	1	0	5
House Sparrow *Passer domesticus*	HOSP	0	0	1	1
House Wren *Troglodytes aedon*	HOWR	0	0	2	2
Hutton's Vireo *Vireo huttoni*	HUVI	0	1	1	2
Indigo Bunting *Passerina cyanea*	INBU	0	0	6	6
Kentucky Warbler *Oporornis formosus*	KEWA	6	0	0	6
Least Flycatcher *Empidonax minimus*	LEFL	1	1	2	4
Lesser Goldfinch *Carduelis psaltria*	LEGO	0	2	0	2
Loggerhead Shrike *Lanius ludovicianus*	LOSH	0	0	1	1
Louisiana Waterthrush *Seiurus motacilla*	LOWA	1	0	0	1
Magnolia Warbler *Dendroica magnolia*	MAWA	0	0	2	2
Mountain Chickadee *Poecile gambeli*	MOCH	1	1	0	2
Mourning Dove *Zenaida macroura*	MODO	0	1	4	5
Mourning Warbler *Oporornis philadelphia*	MOWA	0	0	2	2
Nashville Warbler *Vermivora ruficapilla*	NAWA	0	1	0	1
Northern Bobwhite *Colinus virginianus*	NOBO	0	0	2	2
Northern Cardinal *Cardinalis cardinalis*	NOCA	0	2	6	8
Northern Flicker *Colaptes auratus*	NOFL	0	1	5	6
Northern Mockingbird *Mimus polyglottos*	NOMO	0	0	3	3
Northern Oriole *Icterus galbula*	NOOR	0	0	1	1
Northern Parula *Parula americana*	NOPA	2	0	1	3
Nuttall's Woodpecker *Picoides nuttallii*	NUWO	0	0	2	2
Orange-crowned Warbler *Vermivora celata*	OCWA	1	1	0	2
Orchard Oriole *Icterus spurius*	OROR	0	0	2	2
Ovenbird *Seiurus aurocapillus*	OVBI	8	1	0	9
Pacific-slope Flycatcher *Empidonax difficilis*	PSFL	1	0	0	1
Philadelphia Vireo *Vireo philadelphicus*	PHVI	0	0	1	1
Pileated Woodpecker *Dryocopus pileatus*	PIWO	2	2	0	4
Pine Grosbeak *Pinicola enucleator*	PIGR	2	0	0	2
Pine Siskin *Carduelis pinus*	PISI	0	1	1	2
Pine Warbler *Dendroica pinus*	PIWA	3	1	1	5
Plain Titmouse *Parus inornatus*	PLTI	1	1	0	2
Prairie Warbler *Dendroica discolor*	PRWA	0	0	1	1
Prothonotary Warbler *Protonotaria citrea*	PROW	1	1	0	2
Purple Finch *Carpodacus purpureus*	PUFI	0	1	1	2
Red-bellied Woodpecker *Melanerpes carolinus*	RBWO	1	4	1	6
Red-breasted Nuthatch *Sitta canadensis*	RBNU	3	0	0	3
Red-cockaded Woodpecker *Picoides borealis*	RCWO	0	0	1	1
Red-eyed Vireo *Vireo olivaceus*	REVI	11	2	1	14
Red-headed Woodpecker *Melanerpes erythrocephalus*	RHWO	0	0	2	2

Red-winged Blackbird *Agelaius phoeniceus*	RWBL	0	0	3	3
Rose-breasted Grosbeak *Pheucticus ludovicianus*	RBGR	0	0	3	3
Ruby-crowned Kinglet *Regulus calendula*	RCKI	1	1	0	2
Ruby-throated Hummingbird *Archilochus colubris*	RTHU	0	0	2	2
Ruffed Grouse *Bonasa umbellus*	RUGR	0	0	1	1
Rufous-sided Towhee *Pipilo erythrophthalmus*	RSTO	2	2	6	10
Scarlet Tanager *Piranga olivacea*	SCTA	4	5	0	9
Scissor-tailed Flycatcher *Tyrannus forficatus*	STFL	0	0	1	1
Scrub Jay *Aphelocoma californica*	SCJA	0	1	1	2
Solitary Vireo *Vireo solitarius*	SOVI	1	0	0	1
Song Sparrow *Melospiza melodia*	SOSP	0	0	4	4
Steller's Jay *Cyanocitta stelleri*	STJA	0	0	1	1
Summer Tanager *Piranga rubra*	SUTA	0	0	4	4
Swainson's Thrush *Catharus ustulatus*	SWTH	0	0	2	2
Tennessee Warbler *Vermivora peregrina*	TEWA	0	0	1	1
Tufted Titmouse *Baeolophus bicolor*	TUTI	2	4	1	7
Varied Thrush *Ixoreus naevius*	VATH	1	0	0	1
Veery *Catharus fuscescens*	VEER	1	2	0	3
Violet-green Swallow *Tachycineta thalassina*	VGSW	0	0	1	1
Western Bluebird *Sialia mexicana*	WEBL	0	1	0	1
Western Wood-pewee *Contopus sordidulus*	WEWP	1	1	0	2
White-breasted Nuthatch *Sitta carolinensis*	WBNU	2	3	2	7
White-eyed Vireo *Vireo griseus*	WEVI	0	1	1	2
White-throated Sparrow *Zonotrichia albicollis*	WTSP	0	0	3	3
Willow Flycatcher *Empidonax traillii*	WIFL	0	0	1	1
Wilson's Warbler *Wilsonia pusilla*	WIWA	0	1	0	1
Winter Wren *Troglodytes troglodytes*	WIWR	4	0	0	4
Wood Thrush *Hylocichla mustelina*	WOTH	10	2	1	13
Worm-eating Warbler *Helmitheros vermivorus*	WEWA	3	0	0	3
Wrentit *Chamaea fasciata*	WREN	0	1	2	3
Yellow-bellied Sapsucker *Sphyrapicus varius*	YBSA	0	2	0	2
Yellow-billed Cuckoo *Coccyzus americanus*	YBCU	1	3	3	7
Yellow-breasted Chat *Icteria virens*	YBCH	0	0	3	3
Yellow-rumped Warbler *Dendroica coronata*	YRWA	2	1	0	3
Yellow-throated Vireo *Vireo flavifrons*	YTVI	1	2	0	3
Yellow-throated Warbler *Dendroica dominica*	YTWA	2	0	0	2
Total		143	115	184	442

Appendix 2. Edge response by species for open-forest edge type obtained from 30 journal articles included in the meta-analysis data set.

Species Name	Species Code	Edge Response Negative	Neutral	Positive	Total
American Crow *Corvus brachyrhynchos*	AMCR	0	0	1	1
American Goldfinch *Carduelis tristis*	AMGO	0	1	1	2
American Robin *Turdus migratorius*	AMRO	0	0	2	2
Blue Grosbeak *Guiraca caerulea*	BLGR	0	2	0	2
Blue Jay *Cyanocitta cristata*	BLJA	0	1	1	2
Brown Thrasher *Toxostoma rufum*	BRTH	1	0	0	1
Brown-headed Cowbird *Molothrus ater*	BHCO	1	0	2	3
California Thrasher *Toxostoma redivivum*	CATH	1	0	0	1
Carolina Chickadee *Poecile carolinensis*	CACH	0	0	2	2
Carolina Wren *Thryothorus ludovicianus*	CAWR	0	1	0	1
Chestnut-sided Warbler *Dendroica pensylvanica*	CSWA	0	0	1	1
Common Grackle *Quiscalus quiscula*	COGR	0	0	1	1
Common Yellowthroat *Geothlypis trichas*	COYE	2	0	1	3
Dark-eyed Junco *Junco hyemalis*	DEJU	0	1	1	2
Eastern Kingbird *Tyrannus tyrannus*	EAKI	0	0	1	1
Eastern Wood-pewee *Contopus virens*	EAWP	0	0	1	1
Field Sparrow *Spizella pusilla*	FISP	3	1	0	4
Gray Catbird *Dumetella carolinensis*	GRCA	0	0	1	1
Great Crested Flycatcher *Myiarchus crinitus*	GCFL	0	0	1	1
Horned Lark *Eremophila alpestris*	HOLA	0	1	0	1
House Sparrow *Passer domesticus*	HOSP	0	0	1	1
Indigo Bunting *Passerina cyanea*	INBU	1	2	3	6
Killdeer *Charadrius vociferus*	KILL	0	1	0	1
Northern Bobwhite *Colinus virginianus*	NOBO	0	0	1	1
Northern Cardinal *Cardinalis cardinalis*	NOCA	0	1	4	5
Prairie Warbler *Dendroica discolor*	PRWA	1	3	0	4
Red-eyed Vireo *Vireo olivaceus*	REVI	0	0	2	2
Red-headed Woodpecker *Melanerpes erythrocephalus*	RHWO	0	0	1	1
Red-winged Blackbird *Agelaius phoeniceus*	RWBL	1	0	1	2
Rufous-sided Towhee *Pipilo erythrophthalmus*	RSTO	1	0	3	4
Scarlet Tanager *Piranga olivacea*	SCTA	0	0	1	1
Scrub Jay *Aphelocoma californica*	SCJA	0	0	2	2
Song Sparrow *Melospiza melodia*	SOSP	0	1	1	2
White-crowned Sparrow *Zonotrichia leucophrys*	WCSP	0	0	1	1
White-eyed Vireo *Vireo griseus*	WEVI	1	0	0	1
Yellow-breasted Chat *Icteria virens*	YBCH	2	2	0	4
Total		15	18	38	71

CHAPTER 2

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

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. In Chapter 1, I 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, I have compared the predicted edge response of 25 species using models developed in a meta-analysis (Chapter 1) 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, I 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 8 cases (80-91% correct classification), adequate in 4 cases (64-77% correct classification), and poorly in 4 cases (38-44% correct classification). Generally the 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 used 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 (Mac Nally et al. 1997, 2000, Côté and Reynolds 2002). While there are numerous studies that attempt to explain abundance or presence / absence of species based on patch size or distance from edge (Germaine et al. 1997, King et al. 1997, Brand and George 2000) there are 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 (MacNally and Bennett 1997, Côté and Reynolds 2002).

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 decides which parcels of land to purchase and restore. Environmental consultants often 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 studies have attempted 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 (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 Chapter 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 the environmental factors as well as species' traits used as edge predictor variables that most affected 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" vegetation type 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 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). 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.

I used nest height and duration of the incubation and nesting period as continuous variables. Average nest height was taken as the average of minimum and maximum nest heights (Ehrlich et al. 1988). 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 Ehrlich et al. (1988) for the duration of nesting 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, Edwards and Schnell 2000, Johnson et al. 2002). Because this information was not available in the above sources, the duration of the nestling period for Lucy's Warbler and Lesser Goldfinch was obtained, respectively, by averaging the average nestling period for the 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 (Lowther 1993, Tweit and Finch 1994, Robinson 1996, Lowther et al. 1999, Cardiff and Dittmann 2000, Cardiff and Dittmann 2002). Longevity, defined here as maximum observed adult lifespan, was obtained from published records (Klimkiewicz et al. 1983, Clapp et al. 1983, Klimkiewicz and Futcher 1987). 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 three *Contopus* flycatchers, two *Tyrannus* kingbirds, seven *Vermivora* warblers, and one *Archilochus* hummingbird for which longevity was reported (Klimkiewicz et al. 1983, Clapp et al. 1983, Klimkiewicz and Futcher 1987).

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 region 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 models 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 models are provided in Appendix 3. For example, the equation to predict negative edge response in forest-open edge type is:

$$\log odds = \ln\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 \cdot HU1 + \beta_2 \cdot IN + \beta_3 \cdot EP + \beta_4 \cdot MH + \beta_5 \cdot BM + \beta_6 \cdot LR + \alpha_i \qquad \text{(eqn. 1)}$$

where,

p = probability of positive or negative edge response

α_i is the random effect, and

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

Given a prediction model, 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 Appendix 3. 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 3 for coding of binary variables). The random effect played the role of an addition or subtraction from the log odds, depending on the species being modeled (see eqn. 1). If species or family was included in the meta-analysis (Chapter 1) then the numerical value for that random effect is available in Appendix 3. 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:

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

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 Appendix 3. 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 whether the predictive edge models could be successfully applied to birds 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 mostly natural edges between adjacent habitats and to test the predictive edge 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.

I investigated eight edge types within the riparian corridor. Each edge type represented one side 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 eight 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 prediction equations (Chapter 1) were cottonwood adjacent to grassland, and grassland 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 prediction 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 the validation, I 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 with a more open canopy and was considered "open" habitat. When adjacent to grassland, mesquite is relatively taller with greater canopy cover, 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, 289 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 stations located on 2-3 transects depending on the width of the riparian corridor at that site. 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. Point count locations occurred at varying distances from habitat edges and 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 bird 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. Point count locations were surveyed for 5 min after an initial 1 minute wait period. Additionally, in order to meet the distance sampling assumption of perfect detection at the point (i.e., $g(0) = 1$), and in order to reduce potential bias resulting from evasive movement in response to an observer, birds were also recorded as an observer approached a point. Movement of those birds detected at the point was then recorded during the subsequent wait period and survey period in order to avoid double counting. Surveys were conducted from 10 minutes before sunrise until 3 hrs after sunrise. The order in which transects were walked was varied systematically to avoid bias related to time of day.

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 experienced observers conducted surveys during the 4 year study. In a given field season, a minimum of two and a half 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).

Candidate detection function models for each species 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. Candidate detection functions included pooling desert scrub with grassland, cottonwood with mesquite, and pooling grassland, desert scrub and mesquite separately from cottonwood. Two detection functions were considered sufficiently similar to justify inclusion in the candidate model set when plant species composition differed but structure was relatively similar.

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 that species. 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 may 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. The per-point density estimates were then used along with the distances from edge of point-transect locations to estimate edge response functions.

Edge Response Functions

Edge response functions were implemented for 25 species in 8 edge types using random effects linear regression with density as a function of distance from edge in Stata

8.0 (StataCorp 2003). 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 18 to 42 locations per edge type ranging from 0 m to 330 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 in order to separate the edge response on opposite sides of the edge (Baker et al. 2002). Between 12-18 point count locations were clustered within each of the 23 sites, and the lack of independence in point count locations within sites, as well as the site-to-site variability, was accounted for by using site as a random effect.

In order to identify the edge response for each species in each edge type, I used the slope coefficient of the regression equation along with the P-value of the estimated slope parameter. If the slope was positive and the $P < 0.1$, the edge response was categorized as negative (lower density at the edge than in the interior). If the slope was negative and the P was < 0.1, the edge response was categorized as positive (higher density at the edge than in the interior). I used $\alpha = 0.1$ in order to minimize the probability of a Type II error. If the P was > 0.1, the edge response was categorized as neutral. Edge response was categorized for all species / edge type combination with > 4 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.

Some species / edge type combinations may have been better modeled by using a piecewise linear rather than a linear regression model with site as a random effect (Figure 1). If a breakpoint representing the maximum distance of edge influence exists, there tends to be a steeper slope between the edge and the breakpoint and thus increased ability to detect a positive or negative, rather than neutral edge response. However, with only 18 to 42 distances from edge within each of the 8 edge types, there was not sufficient replication per edge type per site to attain convergence for richly parameterized non-linear random effects models. When faced with the trade-off between using the piecewise linear regression without site as a random effect, and linear regression with site as the random effect, I felt that it was most important to properly account for the site-to-site variability and lack of independence within sites. By using random effects linear regression, the slope parameter may be biased low or high (depending on whether there is a positive or negative edge response) in approximately 10 % of the species / edge type combinations. However, the slope parameter is also estimated more reliably by using the random effect, which is very important for the method I am using to identify a qualitative edge response (positive, neutral, or negative) for each species / edge type combination.

Comparison of Observed with Predicted

In order to empirically assess the validity of the prediction models, I compared the observed edge response of 25 species (Table 2) in 8 edge types on the San Pedro River with predicted edge response obtained from predictive equations and trait information obtained from the literature (Chapter 1). I compared the observed with predicted edge response for each of the 8 sub-edge types in both 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 prediction models (positive and negative) in order to calculate the percent correctly classified as well as the number of observations (species) in each cell.

In order to better understand aspects of the models that were successful, I characterized classification outcomes with a binary variable (correct vs. not-correct) and used logisitic regression to identify environmental and trait factors related with the probability of correct classification. I used life-history and ecological traits as well as environmental factors each considered as predictors by themselves. Traits included as predictors of correct classification included those contained in each of the predictive models. 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). 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 effective in predicting edge responses in a desert riparian system in southeastern Arizona based on general patterns from previous studies in North America.

Results

Observed Edge Response

Edge response was categorized as positive, neutral, or negative for 25 species in a total of 8 edge types using linear regression with site as a random effect (Tables 3-6). Of the 8 edge types, 4 represented forest-open edge type with cottonwood or mesquite as the focal habitat (Tables 3 and 4 respectively), and 4 represented the open-forest edge type with cottonwood or mesquite as the matrix habitat (Tables 5 and 6 respectively).

In the forest-open edge type, I observed primarily neutral responses, with fewer positive and negative edge responses. For the forest-open edge type with cottonwood as the focal habitat, 11 % of the observed edge responses were negative, 15 % were positive, and 74 % were neutral (Table 3). For mesquite as the focal habitat, 15 % of the observed edge responses were negative, 9 % were positive, and 76 % were neutral (Table 4).

The open-forest edge type had more positive edge responses but fewer negative and neutral edge responses compared with the forest-open edge type. For the open-forest edge type with cottonwood as the matrix habitat, 6 % of the observed edge responses were negative, 27 % were positive, and 67 % were neutral (Table 5). For the open-forest edge type with mesquite as the matrix habitat, 4 % of the observed edge responses were negative, 22 % were positive, and 74 % were neutral (Table 6).

Predicted Edge Response

Using the logistic regression equation (eqn. 1) to predict a negative versus non-negative edge response in forest-open edge type, none of the 25 species were predicted to have a negative edge response (Table 7). Using the appropriate equation (see Appendix 3) to predict a negative versus non-negative edge response in open-forest edge type, I predicted that 3 particular species of 25 examined should show a negative edge response (12%; Table 8). I also predicted that 9 particular species of 25 examined should show a positive edge response (36%) in the forest-open edge type, and that 11 of 25 species should show a positive edge response (44%) in the open-forest edge type (Tables 9 and 10 respectively; see appropriate equations in Appendix 3).

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 non-negative) or incorrectly classified (observed negative but predicted non-negative, and observed non-negative but predicted negative); the analogous table was done for the positive predictive model (Table 11). Of 16 edge response / edge type combinations, the prediction models performed well in 8 cases (80-91 % correct classification), adequately in 4 cases (64-77 % correct classification), and poorly in 4 cases (38-44% correct classification). Generally the prediction models performed well for the negative edge response in both forest-open and open-forest edge types, adequately for the positive edge model in the forest-open edge type, but poorly in the positive open-forest (Table 11).

Environmental Factors

I used logistic regression to identify the environmental factors associated with correct classification. Four environmental factors were each considered as predictors for correct classification: edge type, sub edge type, focal habitat, and matrix habitat.

There was no difference in the probability of correct classification for the negative predictive models between the forest-open and open-forest edge type ($P = 0.573$). However for the positive models, the odds of correct classification was 3.0 times greater in forest-open than in the open-forest edge type ($P < 0.0001$).

Evaluating correct classification as a function of sub-edge types, focal and matrix habitats on the San Pedro helps to evaluate how robust the prediction models were for environmental conditions that differed from those in which the prediction models were developed in the meta-analysis (Chapter 1). Of the forest-open edge type, cottonwood adjacent to grassland was the most similar to the meta-analysis dataset and thus was used as a reference. For the negative and positive prediction models in both forest-open and open-forest edge types, there was no difference in probability of correct classification between any of the sub- edge types ($P > 0.3$). Likewise, probability of correct classification was unrelated with focal or matrix habitats for any of the prediction models ($P > 0.2$). Overall, the prediction models appear robust across environmental factors that differ substantially from those in which the models were developed.

Ecological and Life-history Traits

Relevant traits from each of the 4 prediction models were used as predictors of correct classification. This approach may provide insights into the different mechanisms operating on birds on the San Pedro as compared with multiple studies from across the U.S. in which the prediction models were developed (Chapter 1).

Of the 6 traits in the negative prediction model in forest-open edge type, none had any predictive value for the probability of correct classification ($P > 0.3$). However in the open-forest edge type, two of the 3 traits included in the negative prediction model were related with probability of correct classification: habitat utilization and nest height. For habitat utilization, the odds of correct classification for a bird that uses forest or both forest and open habitat was 10.3 times that of an open habitat bird ($P < 0.0001$). For nest height, the odds of correct classification for a nest 1-m high was 4.3 times that of a 10-m high nest (P = 0.005).

For the positive prediction models, traits were related with probability of correct classification in both edge types. In forest-open edge type, 3 of 6 traits were related with probability of correct classification: incubation + nesting duration, nest substrate, and nest type. A bird with a short incubation + nestling period duration (20 days) was 13.8 times more likely to be correctly classified than that of a bird with a long duration (35 days; P = 0.002). Ground or tree nesting birds were 5.4 times more likely to be correctly classified than shrub nesting birds (P = 0.004). Finally, cavity nesting species were 9.2 times more likely to be correctly classified than open-nesting species (P = 0.004). Of three traits included in the open-forest edge type positive prediction model, nest height and lifetime reproductive output were related with probability of correct classification. Birds with high nests (10-m) were 3.0 times more likely to be correctly classified than low nesting birds (1-m; P < 0.0001). Birds with low lifetime reproductive output (25 individuals) were 2.7 times more likely to be correctly classified than birds with high lifetime reproductive output (75 individuals; P = 0.023).

Discussion

The prediction models performed well for negative edge response predictions in both forest-open and open-forest edge types, adequately for positive edge response predictions in forest-open edge types, and poorly for positive edge response predictions in open-forest edge types. In order to shed light on aspects of these models that failed to predict edge response for birds on the San Pedro River, I evaluated environmental factors and traits related with probability of correct classification.

Three of four environmental factors -- sub-edge type, focal and matrix habitats -- had no relationship with probability of correct classification. That these environmental factors were not related with model performance seems to indicate that the prediction models were robust across environmental conditions unique to the San Pedro that differed from those in which the models were developed. For example, 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 thus it was not used in the development of the prediction models (Chapter 1). Yet the sub- edge types, focal and matrix habitats related with mesquite were as likely to be correctly classified as edge types that were more similar to the types of environments in which the prediction models were developed such as cottonwood adjacent to grassland.

Of the environmental factors that I considered, only edge type (forest-open vs. open-forest) was related with probability of correct classification for the positive prediction model. That the prediction model failed to predict positive edge response in the open-forest edge type may indicate that different mechanisms and related traits are occurring on the San Pedro compared with the meta-analysis (Chapter 1) as discussed below.

Ecological and life-history traits were related with probability of correct classification for three of the four prediction models. For the forest-open edge type, traits were related with probability of correct edge response classification for only the positive prediction model. The three traits that were significant predictors of correct classification in the positive prediction model -- duration of incubation plus nestling period, nest substrate, and nest type -- are all related with nesting biology. Increased predation and parasitism at edges has been found to detrimentally affect the nest success of numerous bird species (Brittingham and Temple 1983, Donovan et al. 1997, Chalfoun 2002). However, a study in a riparian system in Montana found that predation and parasitism rates were not related to the presence of edge and patch size (Tewksbury et al. 1998). If this is similar on the San Pedro, it may indicate that predation and parasitism rates do not increase at edges in riparian systems. In this study, the Brown-headed cowbird was found to have a positive edge response in only two of the eight edge types with a neutral edge response in the remaining six edge types. As such, the traits related with nesting biology used in the positive prediction model may have failed to properly predict edge response due to a different set of mechanisms operating on birds on the San Pedro or in riparian systems more generally.

Two traits were significantly related with probability of correct 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. Counter to predictions, all other species/subedgetype combinations showed a neutral or positive edge response. Perhaps due to the narrowness of the San Pedro riparian corridor, the majority of open-habitat species used more than one habitat type, rather than using the open habitat type exclusively, which may have affected the observed edge responses. In addition to habitat utilization, nest height was not a useful predictor in either the positive or negative edge-response models. Counter to prediction, 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 regularly utilize resources in the adjacent 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 perhaps due to their association with mesic habitat.

Lifetime reproductive output was related with probability of correct classification for the positive prediction model in the open-forest edge type. Birds with low lifetime reproductive output were more likely to be correctly classified than birds with high lifetime reproductive output. The three birds with the highest lifetime reproductive output: White-winged Dove, House Finch, and Northern Cardinal were all predicted to show a positive edge response in the open-forest edge type. However, in 11 of 12 species / edge type combinations, observed edge responses were non-positive. In the meta-analysis (Chapter 1), I found that birds with greater lifetime reproductive output had a higher probability of positive edge response, which I surmised to compensate for decreased nesting success at edges. If predation and parasitism by Brown-headed cowbirds are not higher at edges in riparian systems (Tewksbury et al. 1998), then this may illustrate another example of how different mechanisms operating on the San Pedro compared with other regions may lead to a different set of predictive traits for edge response.

That particular environmental factors and species' traits fail to predict edge response for some bird species on the San Pedro River is not surprising due to inherent differences between desert riparian ecosystems compared with the more contiguous forest landscapes of the west, Midwest, and eastern United States. In Chapter 1, I 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 the desert riparian system. Within my study area, edges on the San Pedro River result from 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 attain a density response to a possible edge influence. Finally, the riparian system on the San Pedro is spatially heterogeneous with relatively large gaps in the forest canopy and areas along the river channel without tree cover, and thus the spatial scale at which edges were defined may not have been appropriate for all of the species that I investigated.

Even though the models predicted poorly for a number of species / edge type combinations, overall 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 3 traits in the forest-open edge type and 4 traits in the open-forest edge type had little predictive ability, the majority of traits in the predictive models, and hypothesized to be related with mechanisms operating on birds at edges, contributed significantly to the correct classification of edge response for birds on the San Pedro River.

This work contributes to development of tools to predict bird species' responses to human-induced edges between habitat types using easily parameterized models based on widely available data. 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 (MacNally et al. 2003). These diverse, successful attempts to predict species response to changes in landscape pattern indicate that use of readily available information coupled with broad-scale habitat maps can predict the effects of landscape change on biodiversity.

Literature Cited

Baker, J., K. French, and R. J. Whelan. 2002. The edge effect and ecotonal species: Bird communities across a natural edge in Southeastern Australia. Ecology 83: 3048-3059.

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

Brand, L. A., and B. R. Noon. 2004. Ecological and life-history traits predict avian edge response: A meta-analysis. To be submitted to Ecology.

Bright, P. W. 1993. Toward 2000: The future of British mammals. Mammal Review. 23: 101-111.

Brittingham, M. C., and S. A. Temple. 1983. Have cowbirds caused forest songbirds to decline? *Bioscience* 33: 31-35.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, and L. Thomas. 2001. Introduction to distance sampling: Estimating abundance of biological populations. Oxford University Press, Oxford, U. K. 432 pp.

Burnham, K. P., and D. A. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach, 2nd edition. Springer-Verlag, Inc. New York. 488 pp.

Cardiff, S. W., and D. L. Dittmann. 2000. Brown-crested Flycatcher (*Myiarchus tyrannulus*). in A. Poole and F. Gill, eds. *The Birds of North America, no. 496.* The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

Cardiff, S. W., and D. L. Dittmann. (2002). Ash-throated flycatcher (*Myiarchus cinerascens*) in A. Poole and F. Gill, eds. *The Birds of North America, No. 664.* The Birds of North America, Inc., Philadelphia.

Chalfoun, A. D., F. R. Thompson III, and M. J. Ratnaswamy. 2002. Nest predators and fragmentation: a review and meta-analysis. *Conservation Biology* 16: 306-318.

Clapp, R. B., M. K. Klimkiewicz, and A. G. Futcher. 1983. Longevity records of North American birds: Columbidae through Paridae. Journal of Field Ornithology 54:123-137.

Côté, I. M., and J. D. Reynolds. 2002. Predictive Ecology to the Rescue? Science 298: 1181-1182.

Davies, K. F., C. R. Margules, and J. F. Lawrence. 2000. Which traits of species predict population declines in experimental forest fragments? Ecology 81: 1450-1461.

Donovan, T. M., P. W. Jones, E. M. Annand, and F. R. Thompson III. 1997. Variation in local-scale edge effects: Mechanisms and landscape context. Ecology 78: 2064-2075.

Dunning, Jr., J. B. 1992. CRC Handbook of Avian Body Masses. Dunning (editor) CRC Press.

Edwards, H.H. and G. D. Schnell. 2000. Gila Woodpecker (*Melanerpes uropygialis*) in A. Poole and F. Gill, eds. *The Birds of North America, no. 532.* The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

Ehrlich, P. R., D. S. Dobkin, and D. Wheye. 1988. The Birder's Handbook: A field guide to the natural history of North American Birds. Simon and Schuster Inc., New York.

Germaine, S. S., S. H. Vessey, and D. E. Capen. 1997. Effects of small forest openings on the breeding bird community in a Vermont hardwood forest. The Condor 99:708-718.

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

Johnson, M. J., C. Van Riper, III, and K. M. Pearson. 2002. Black-throated Sparrow (*Amphispiza bininеata*) in A. Poole and F. Gill, eds. *The Birds of North America, no. 637.* The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

Johnson, RR, H. K. Yard, and B. T. Brown. 1997. Lucy's Warbler (*Vermivora luciae*) in A. Poole and F. Gill, eds. *The Birds of North America, no. 318.* The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

King, D. I., C. R. Griffin, and R. M. DeGraaf. 1997. Effect of clearcut borders on distribution and abundance of forest birds in northern New Hampshire. Wilson Bulletin 109:239-245.

Klimkiewicz, M. K., R. B. Clapp, and A. G. Futcher. 1983. Longevity records of North American birds: Remizidae through Parulinae. Journal of Field Ornithology 54:287-294.

Klimkiewicz, M. K, and A. G. Futcher. 1987. Longevity records of North American Birds: Coerebinae through Estrildidae. Journal of Field Ornithology 58:318-333.

Kolar, C. S., and D. M. Lodge. 2002. Ecological Predictions and Risk Assessment for Alien Fishes in North America. Science 298: 1233-1236.

Kremen, C., R. K. Colwell, T. L. Erwin, D. D. Murphy, R. F. Noss, and M. A. Sanjayan. 1993. Terrestrial arthropod assemblages: Their use in conservation planning. Conservation Biology 7: 796-808.

Krueuper, D. J. 1997. Annotated checklist to the birds of the upper San Pedro river valley. BLM, San Pedro National Conservation Area.

Lens, L., S. Van Dongen, K. Norris, M. Githiru, and E. Matthysen. 2002. Avian persistence in fragmented rainforest. Science 298: 1236-1238.

Lowther, P. E. (1993). Brown-headed cowbird (*Molothrus ater*) in A. Poole and F. Gill, eds. *The Birds of North America, No. 47*. The Birds of North America, Inc., Philadelphia.

Lowther, P. E., C. Celada, N. K. Klein, C. C. Rimmer, and D. A. Spector. 1999. Yellow Warbler (*Dendroica petechia*) in A. Poole and F. Gill, eds. *The Birds of North America, no. 454*. The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

Mac Nally, R., E. Fleishman, J. P. Fay, and D. D. Murphy. 2003. Modelling butterfly species richness using mesoscale environmental variables: model construction and validation for mountain ranges in the Great Basin of western North America. Biological Conservation 110: 21-31.

Mac Nally, R., and A. F. Bennett. 1997. Species-specific predations of the impact of habitat fragmentation: Local extinction of birds in the box-ironbark forests of central Victoria, Australia. Biological Conservation 82: 147-155.

Mac Nally, R., A. F. Bennett, and G. Horrocks. 2000. Forecasting the impacts of habitat fragmentation. Evaluation of species-specific predictions of the impact of habitat fragmentation on birds in the box-ironbox forests of central Victoria, Australia. Biological Conservation vol?: 7-29.

McCullagh, P., and J.A. Nelder. 1989. Generalized linear models, 2nd Edition. Chapman and Hall, London, New York.

Pywell, R. F., J. M. Bullock, D. B. Roy, L. Warman, K. J. Walker, and P. Rothery. 2003. Plant traits as predictors of performance in ecological restoration. Journal of Applied Ecology 40:65-77.

National Geographic Society. 1992. Field guide to the birds of North America, 3rd edition.

Robinson, W. D. (1996). Summer tanager (*Piranga rubra*) in A. Poole and F. Gill, eds. *The Birds of North America, No. 248*. The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

Saab, V. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: A hierarchical analysis. Ecological Applications 9: 135-151.

Sisk, T. D., N. M. Haddad, and P. R. Ehrlich. 1997. Bird assemblages in patchy woodlands: modeling the effects of edge and matrix habitats. Ecological Applications 7(4): 1170-1180

Tewksbury, J. J., S. J. Hejl, and T. E. Martin. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. Ecology 79:2890-2903.

Tweit, RC; Finch, DM. 1994. Abert's towhee *(Pipilio aberti)* in A. Poole and F. Gill, eds. *The Birds of North America, no. 111.* The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

Watt, D.J., and E. J. Willoughby. 1999. Lesser Goldfinch (*Carduelis psaltria*) in A. Poole and F. Gill, eds. *The Birds of North America, no. 392.* The Birds of North America, Inc., Academy of Natural Sciences, Philadelphia, PA.

Watts, J. 1996. San Pedro River Vegetation Mapping Project. U. S. Army Engineer Research and Development Center, Topographic Engineering Center.

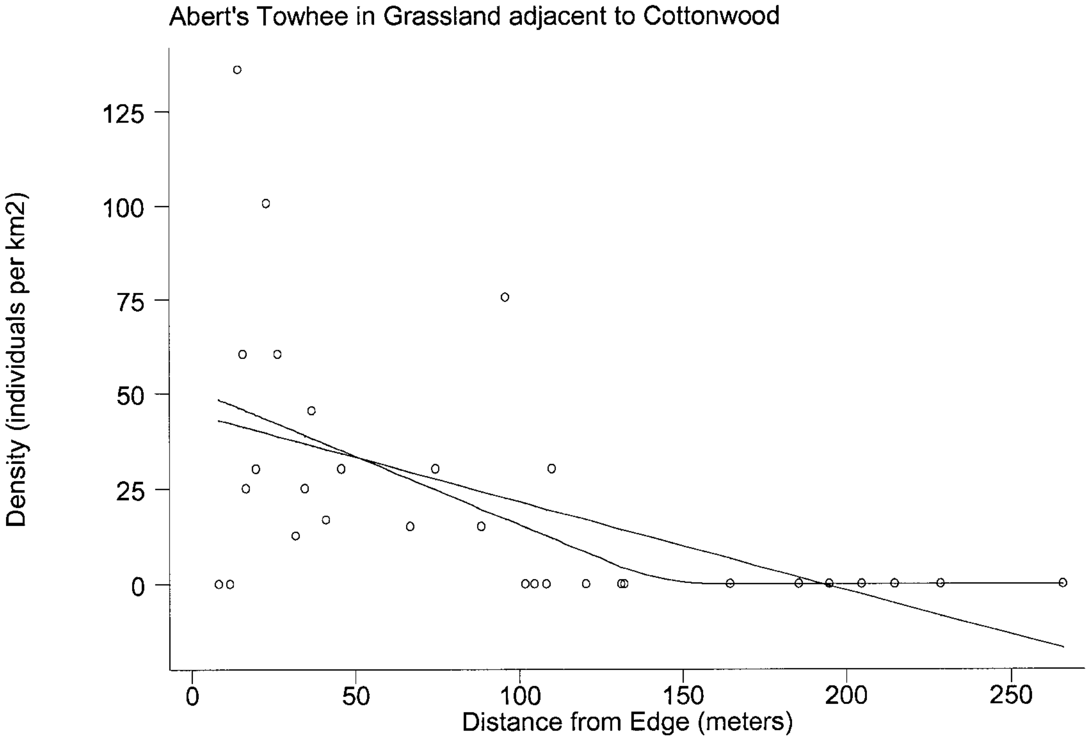


Figure 1. Density as a function of distance from edge using both linear and piecewise linear models (pooled across sites) for the Abert's Towhee in Grassland adjacent to Cottonwood.

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 Reproduction	LR	clutch size x number of broods x longevity	both positive	forest-open open-forest
Environmental Traits				
Region	RE	east vs. west	positive	forest-open
Agricultural Edge	AG	agriculture vs. non-agriculture	both	open-forest

Table 2. Total number of detections for 25 most common species encountered in avian surveys on the San Pedro River, Arizona 1998-2001.

Species Name	Species Code	Total number of detections
Abert's Towhee *Pipilo aberti*	ABTO	805
Ash-throated Flycatcher *Myiarchus cinerascens*	ATFL	544
Bell's Vireo *Vireo bellii*	BEVI	403
Bewick's Wren *Thryomanes bewickii*	BEWR	758
Black-chinned Hummingbird *Archilochus alexandri*	BCHU	231
Black-throated Sparrow *Amphispiza bilineata*	BTSP	581
Blue Grosbeak *Guiraca caerulea*	BLGR	430
Brown-crested Flycatcher *Myiarchus tyrannulus*	BCFL	259
Brown-headed Cowbird *Molothrus ater*	BHCO	893
Bullock's Oriole *Icterus bullockii*	BUOR	140
Cassin's Kingbird *Tyrannus vociferans*	CAKI	386
Common Yellowthroat *Geothlypis trichas*	COYE	348
Gila Woodpecker *Melanerpes uropygialis*	GIWO	402
House Finch *Carpodacus mexicanus*	HOFI	357
Lesser Goldfinch *Carduelis psaltria*	LEGO	178
Lucy's Warbler *Vermivora luciae*	LUWA	1232
Mourning Dove *Zenaida macroura*	MODO	439
Northern Cardinal *Cardinalis cardinalis*	NOCA	177
Song Sparrow *Melospiza melodia*	SOSP	303
Summer Tanager *Piranga rubra*	SUTA	434
Verdin *Auriparus flaviceps*	VERD	231
Vermillion Flycatcher *Pyrocephalus rubinus*	VEFL	306
White-winged Dove *Zenaida asiatica*	WWDO	507
Yellow Warbler *Dendroica petechia*	YWAR	659
Yellow-breasted Chat *Icteria virens*	YBCH	1688

Table 3. Observed edge response by species in forest-open edge type with cottonwood focal habitat based on linear regression of density as a function of distance from edge and site as a random effect from San Pedro River, Arizona for 1998-2001.

	Cottonwood / Grassland				Cottonwood / Mesquite			
Species	Coef	SE	P	Edge Resp	Coef	SE	P	Edge Resp
ABTO	0.037	0.172	0.829	neutral	-0.046	0.268	0.863	neutral
ATFL	0.303	0.164	0.065	negative	-0.208	0.194	0.284	neutral
BEVI	*insufficient observations*				-0.286	0.295	0.332	neutral
BEWR	0.075	0.162	0.645	neutral	-0.014	0.280	0.960	neutral
BCHU	-0.160	0.438	0.716	neutral	-0.767	0.779	0.325	neutral
BTSP	*insufficient observations*				*insufficient observations*			
BLGR	-0.103	0.075	0.173	neutral	-0.148	0.075	0.049	positive
BCFL	-0.056	0.117	0.635	neutral	0.046	0.140	0.739	neutral
BHCO	-0.273	0.125	0.029	positive	-0.298	0.246	0.225	neutral
BUOR	-0.017	0.313	0.957	neutral	0.136	0.173	0.429	neutral
CAKI	-0.076	0.140	0.588	neutral	0.115	0.170	0.496	neutral
COYE	0.457	0.268	0.088	negative	0.348	0.391	0.373	neutral
GIWO	-0.060	0.100	0.550	neutral	0.249	0.161	0.123	neutral
HOFI	0.015	0.090	0.879	neutral	-0.111	0.129	0.392	neutral
LEGO	-0.453	0.223	0.042	positive	0.271	0.229	0.238	neutral
LUWA	0.084	0.256	0.742	neutral	-1.364	0.775	0.078	positive
MODO	-0.151	0.081	0.064	positive	0.111	0.035	0.001	negative
NOCA	*insufficient observations*				-0.034	0.134	0.797	neutral
SOSP	-0.740	0.491	0.132	neutral	0.867	0.587	0.140	neutral
SUTA	0.146	0.165	0.379	neutral	0.263	0.157	0.095	negative
VERD	0.013	0.032	0.678	neutral	-0.213	0.128	0.095	positive
VEFL	0.337	0.323	0.296	neutral	0.650	0.218	0.003	negative
WWDO	-0.012	0.080	0.883	neutral	0.074	0.231	0.749	neutral
YWAR	-0.330	0.493	0.503	neutral	0.797	0.686	0.245	neutral
YBCH	-0.144	0.266	0.588	neutral	-0.760	0.275	0.006	positive

Table 4. Observed edge response by species in forest-open edge type with mesquite focal habitat based on linear regression of density as a function of distance from edge and site as a random effect from San Pedro River, Arizona for 1998-2001.

	Mesquite / Grassland				Mesquite / Desert Scrub			
Species	Coef	SE	P	Edge Resp	Coef	SE	P	Edge Resp
ABTO	0.240	0.215	0.265	neutral	0.441	0.094	0.000	negative
ATFL	0.104	0.208	0.615	neutral	0.289	0.281	0.304	neutral
BEVI	*insufficient observations*				0.239	0.240	0.319	neutral
BEWR	0.232	0.190	0.223	neutral	0.131	0.176	0.458	neutral
BCHU	-0.476	0.282	0.092	positive	-0.337	0.723	0.641	neutral
BTSP	-0.640	0.401	0.111	neutral	-0.810	0.370	0.029	positive
BLGR	0.024	0.075	0.753	neutral	0.243	0.111	0.029	negative
BCFL	-0.032	0.046	0.494	neutral	-0.010	0.107	0.929	neutral
BHCO	-0.268	0.147	0.068	positive	0.044	0.134	0.743	neutral
BUOR	*insufficient observations*				0.076	0.114	0.504	neutral
CAKI	-0.083	0.089	0.353	neutral	0.053	0.025	0.035	negative
COYE	0.027	0.027	0.320	neutral	-0.011	0.061	0.861	neutral
GIWO	0.001	0.052	0.982	neutral	-0.041	0.047	0.382	neutral
HOFI	-0.038	0.085	0.656	neutral	-0.187	0.090	0.037	positive
LEGO	0.248	0.087	0.004	negative	0.062	0.074	0.400	neutral
LUWA	-0.161	0.596	0.787	neutral	0.880	0.749	0.240	neutral
MODO	-0.049	0.052	0.354	neutral	0.031	0.064	0.633	neutral
NOCA	0.207	0.094	0.027	negative	0.038	0.033	0.249	neutral
SOSP	*insufficient observations*				0.046	0.043	0.281	neutral
SUTA	0.068	0.103	0.511	neutral	0.179	0.152	0.242	neutral
VERD	0.161	0.105	0.126	neutral	0.095	0.109	0.384	neutral
VEFL	-0.151	0.136	0.270	neutral	0.125	0.043	0.003	negative
WWDO	0.038	0.079	0.636	neutral	-0.028	0.024	0.247	neutral
YWAR	0.022	0.048	0.646	neutral	0.042	0.049	0.392	neutral
YBCH	0.204	0.137	0.135	neutral	0.386	0.182	0.034	negative

Table 5. Observed edge response by species in open-forest edge type with cottonwood matrix habitat based on linear regression of density as a function of distance from edge and site as a random effect from San Pedro River, Arizona for 1998-2001.

	Grassland / Cottonwood				Mesquite / Cottonwood			
Species	Coef	SE	P	Edge Resp	Coef	SE	P	Edge Resp
ABTO	-0.209	0.069	0.002	positive	-0.026	0.184	0.887	neutral
ATFL	-0.051	0.038	0.181	neutral	0.115	0.122	0.345	neutral
BEVI	*insufficient observations*				0.042	0.158	0.789	neutral
BEWR	-0.125	0.033	0.000	positive	-0.138	0.189	0.465	neutral
BCHU	-0.202	0.263	0.444	neutral	0.125	0.376	0.739	neutral
BTSP	-0.016	0.008	0.067	positive	-0.046	0.074	0.540	neutral
BLGR	-0.072	0.056	0.199	neutral	-0.057	0.073	0.435	neutral
BCFL	-0.015	0.010	0.116	neutral	-0.053	0.072	0.462	neutral
BHCO	-0.007	0.055	0.905	neutral	0.006	0.084	0.940	neutral
BUOR	-0.073	0.089	0.412	neutral	-0.164	0.204	0.422	neutral
CAKI	-0.066	0.049	0.174	neutral	-0.039	0.042	0.354	neutral
COYE	-0.286	0.109	0.009	positive	-0.106	0.057	0.063	positive
GIWO	-0.072	0.024	0.003	positive	-0.076	0.064	0.236	neutral
HOFI	-0.049	0.039	0.203	neutral	-0.080	0.060	0.180	neutral
LEGO	-0.013	0.074	0.864	neutral	0.011	0.095	0.970	neutral
LUWA	-0.177	0.099	0.073	positive	1.816	0.642	0.005	negative
MODO	0.001	0.049	0.980	neutral	0.017	0.038	0.653	neutral
NOCA	-0.004	0.011	0.702	neutral	0.051	0.053	0.338	neutral
SOSP	0.042	0.069	0.540	neutral	-0.230	0.094	0.014	positive
SUTA	0.095	0.043	0.028	negative	0.187	0.094	0.047	negative
VERD	0.084	0.072	0.246	neutral	-0.011	0.049	0.817	neutral
VEFL	-0.160	0.069	0.021	positive	-0.074	0.076	0.332	neutral
WWDO	-0.101	0.026	0.000	positive	-0.083	0.055	0.128	neutral
YWAR	-0.265	0.142	0.062	positive	-0.307	0.120	0.011	positive
YBCH	-0.148	0.057	0.009	positive	-0.192	0.228	0.398	neutral

Table 6. Observed edge response by species in open-forest edge type with mesquite matrix habitat based on linear regression of density as a function of distance from edge and site as a random effect from San Pedro River, Arizona for 1998-2001.

	Grassland / Mesquite				Desert Scrub / Mesquite			
Species	Coef	SE	P	Edge Resp	Coef	SE	P	Edge Resp
ABTO	-0.092	0.056	0.098	positive	-0.056	0.031	0.069	positive
ATFL	-0.091	0.038	0.017	positive	-0.125	0.056	0.026	positive
BEVI	-0.009	0.024	0.712	neutral	-0.018	0.014	0.184	neutral
BEWR	-0.050	0.033	0.142	neutral	0.003	0.046	0.956	neutral
BCHU	*insufficient observations*				-0.110	0.209	0.599	neutral
BTSP	-0.141	0.056	0.012	positive	0.005	0.101	0.961	neutral
BLGR	0.068	0.069	0.328	neutral	-0.048	0.033	0.147	neutral
BCFL	*insufficient observations*				-0.023	0.022	0.296	neutral
BHCO	-0.053	0.056	0.347	neutral	0.009	0.033	0.782	neutral
BUOR	-0.017	0.034	0.619	neutral	-0.114	0.048	0.017	positive
CAKI	-0.029	0.042	0.488	neutral	-0.017	0.013	0.184	neutral
COYE	0.006	0.022	0.777	neutral	-0.005	0.005	0.296	neutral
GIWO	-0.051	0.026	0.055	positive	-0.011	0.022	0.607	neutral
HOFI	-0.098	0.068	0.154	neutral	0.068	0.026	0.009	negative
LEGO	0.081	0.066	0.225	neutral	-0.026	0.025	0.302	neutral
LUWA	-0.310	0.176	0.007	positive	-0.177	0.084	0.036	positive
MODO	0.009	0.074	0.907	neutral	-0.012	0.021	0.559	neutral
NOCA	0.003	0.029	0.918	neutral	0.040	0.013	0.003	negative
SOSP	*insufficient observations*				*insufficient observations*			
SUTA	0.083	0.102	0.419	neutral	-0.062	0.046	0.174	neutral
VERD	0.022	0.048	0.643	neutral	0.026	0.034	0.434	neutral
VEFL	-0.050	0.133	0.710	neutral	-0.023	0.041	0.569	neutral
WWDO	-0.024	0.024	0.324	neutral	-0.010	0.011	0.360	neutral
YWAR	-0.040	0.085	0.642	neutral	-0.002	0.002	0.358	neutral
YBCH	-0.029	0.062	0.637	neutral	-0.067	0.032	0.038	positive

Table 7. Negative forest-open edge response predictions for 25 species

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	42	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.

Table 8. Negative open-forest edge response predictions for 25 species

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

Table 9. Positive forest-open edge response predictions for 25 species

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	42	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.

Table 10. Positive open-forest edge response predictions for 25 species

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.

Table 11. Percent correctly classified for negative and positive edge prediction models in forest-open and open-forest sub-edge types San Pedro River, Arizona.

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					
Cottonwood | Grassland	20	0	2	0	90.9
Cottonwood | Mesquite	21	0	3	0	87.5
Mesquite | Grassland	20	0	2	0	90.9
Mesquite | Desert scrub	20	0	5	0	80.0
Open-Forest					
Grassland | Cottonwood	20	3	1	0	83.3
Mesquite | Cottonwood	20	3	2	0	80.0
Grassland | Mesquite	20	2	0	0	90.9
Desert scrub | Mesquite	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	% correctly classified
Forest-Open					
Cottonwood | Grassland	14	5	0	3	77.3
Cottonwood | Mesquite	14	6	2	2	66.7
Mesquite | Grassland	13	7	1	1	63.6
Mesquite | Desert scrub	15	8	1	1	64.0
Open-Forest					
Grassland | Cottonwood	6	8	7	3	37.5
Mesquite | Cottonwood	11	11	3	0	44.0
Grassland | Mesquite	8	9	4	1	40.9
Desert scrub | Mesquite	9	10	4	1	41.7

Appendix 3. Prediction models, coefficients, codes for binary variables, cut points, and random effects for species and families.

Prediction Models:

Forest-Open Negative Edge Response Predictions

$$\text{log odds} = \ln\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 \cdot HU1 + \beta_2 \cdot IN + \beta_3 \cdot EP + \beta_4 \cdot MH + \beta_5 \cdot BM + \beta_6 \cdot LR + \alpha_i$$

Forest-Open Positive Edge Response Predictions

$$\text{log odds} = \ln\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 \cdot HU1 + \beta_2 \cdot DI1 + \beta_3 \cdot IN + \beta_4 \cdot NS + \beta_5 \cdot NT + \beta_6 \cdot LR + \beta_7 \cdot RE + \alpha_i$$

Open-Forest Negative Edge Response Predictions

$$\text{log odds} = \left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 \cdot HU2 + \beta_2 \cdot NH + \beta_3 \cdot CH + \beta_4 \cdot AG + \alpha_i$$

Open-Forest Positive Edge Response Predictions

$$\text{log odds} = \left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 \cdot HU2 + \beta_2 \cdot NH + \beta_3 \cdot LR + \beta_4 \cdot AG + \alpha_i$$

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	2.2737	HU1	2.2757	HU1	-2.6896	HU1	-1.9403
IN	0.1060	IN	0.1005	DI2	3.0974	DI2	1.3328
EP	-0.2110	EP	-0.1754	IN	-0.0946	IN	-0.0350
MH	0.8043	MH	0.8112	NS	1.2959	NS	0.9775
BM	-0.0112	BM	-0.0104	NT	0.9577	NT	0.7992
LR	0.0058	LR	0.0076	LR	0.0054	LR	0.0007
YINT	-3.5458	YINT	-3.7089	RE	-0.8370	RE	-0.4293
				YINT	2.2675	YINT	0.6921

Open-Forest Edge Response Coefficients

Negative Edge Response				Positive Edge Response			
Species		Family		Species		Family	
Variable	Coef.	Variable	Coef.	Variable	Coef.	Variable	Coef.
HU2	1.5357	HU2	1.5357	HU2	-1.1402	HU2	-1.1402
NH	-0.4286	NH	-0.4286	NH	0.1987	NH	0.1987
CH	0.8313	CH	0.8313	LR	0.0186	LR	0.0186
AG	3.6090	AG	3.6090	AG	-2.3465	AG	-2.3465
YINT	-3.1579	YINT	-3.1579	YINT	-1.1351	YINT	-1.1351

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 Prediction Models in Forest-Open

Family	Species	Negative	Positive
Aegithalidae		0.0000	0.0952
	Common Bushtit	0.2977	0.2848
Bombycillidae		0.0000	0.1462
	Cedar Waxwing	-0.0296	0.7406
Cardinalidae		0.0000	0.6149

	Blue Grosbeak	-0.0689	0.4419
	Indigo Bunting	-0.0784	0.8385
	Northern Cardinal	-0.1511	-1.5270
	Rose-breasted Grosbeak	-0.3299	2.4717
Certhiidae		0.0000	-0.1566
	Brown Creeper	0.3701	-0.5483
Columbidae		0.0000	0.2817
	Mourning Dove	-0.0404	0.5316
Corvidae		0.0000	-0.5815
	American Crow	-0.0098	0.8313
	Blue Jay	0.5714	-3.7725
	Common Raven	0.0000	-1.0151
	Fish Crow	-0.0183	0.2313
	Gray Jay	-0.2824	1.4568
	Scrub Jay	-0.0802	-1.3247
	Steller's Jay	-0.1252	0.9602
Cuculidae		0.0000	-0.4912
	Yellow-billed Cuckoo	0.2544	-1.7540
Emberizidae		0.0000	0.3461
	California Towhee	-0.0279	0.5279
	Chipping Sparrow	-0.0373	-0.7898
	Dark-eyed Junco	-0.1162	-0.0905
	Field Sparrow	-0.0601	1.0986
	Rufous-sided Towhee	0.2914	-0.7166
	Song Sparrow	-0.2117	1.1785
	White-throated Sparrow	-0.0291	1.0381
Fringillidae		0.0000	0.4853
	American Goldfinch	-0.0833	0.7061
	Cassin's Finch	0.0042	1.2858
	Pine Siskin	-0.3033	1.3006
	Purple Finch	-0.0442	-0.0626
Hirundinidae		0.0000	0.2675
	Violet-green Swallow	-0.0924	1.4860
Icteridae		0.0000	0.8974
	Brown-headed Cowbird	-0.1593	0.0000
	Common Grackle	-0.0510	0.3229
	Northern Bobwhite	-0.0270	1.0698
	Northern Oriole	-0.0233	0.9258
	Orchard Oriole	-0.0507	1.3595
	Red-winged Blackbird	-0.1130	0.9993
Laniidae		0.0000	0.1617
	Loggerhead Shrike	-0.0695	0.7764
Mimidae		0.0000	0.1086
	Brown Thrasher	-0.0174	0.0252
	California Thrasher	-0.0140	-1.4155
	Gray Catbird	-0.0685	0.5755
	Northern Mockingbird	-0.0571	0.6702
Odontophoridae		0.0000	0.0000
	California Quail	-0.0209	-0.0114

Paridae		0.0000	-0.6554
	Black-capped Chickadee	-0.1134	-1.7801
	Carolina Chickadee	-0.1432	-0.4631
	Mountain Chickadee	-0.2103	-0.2469
	Mountain Chickadee	-0.2103	-0.2469
	Plain Titmouse	-0.0798	-0.2010
	Tufted Titmouse	0.3922	-1.3468
Parulidae		0.0000	-0.0371
	American Redstart	0.0883	0.1458
	Black-and-white Warbler	-0.1403	-0.5409
	Black-throated Blue Warbler	-0.2993	-0.4741
	Black-throated Green Warbler	-0.0350	-1.2823
	Blue-winged Warbler	-0.0351	0.4405
	Canada Warbler	0.0592	0.3113
	Cerulean Warbler	0.1147	-0.5649
	Chestnut-sided Warbler	-0.5952	2.2256
	Common Yellowthroat	-0.2869	0.9451
	Hooded Warbler	0.2458	-2.1826
	Kentucky Warbler	0.5568	-1.5861
	Louisiana Waterthrush	0.1587	-0.6079
	Magnolia Warbler	-0.3947	2.0671
	Mourning Warbler	-0.3714	2.0189
	Northern Parula	-0.0056	0.8661
	Orange-crowned Warbler	0.3444	-1.6551
	Ovenbird	0.3772	-1.3361
	Pine Warbler	0.3791	-0.3211
	Prairie Warbler	-0.0148	0.2880
	Prothonotary Warbler	-0.1456	-0.5493
	Tennessee Warbler	-0.0662	0.6004
	Wilson's Warbler	-0.1825	-0.3992
	Worm-eating Warbler	0.3890	-1.2389
	Yellow-breasted Chat	-0.1581	0.4950
	Yellow-rumped Warbler	0.2117	-0.8946
Passeridae		0.0000	0.2053
	House Sparrow	-0.0332	0.8288
Phasianidae		0.0000	0.2147
	Ruffed Grouse	-0.0025	0.7207
Picidae		0.0000	0.1823
	Downy Woodpecker	0.2017	-0.8220
	Hairy Woodpecker	0.1901	-0.5615
	Northern Flicker	-0.2410	2.2930
	Pileated Woodpecker	0.2350	-0.3349
	Red-bellied Woodpecker	0.1380	-0.5687
	Red-cockaded Woodpecker	-0.3165	2.1959
	Red-headed Woodpecker	-0.0985	0.6794
	Yellow-bellied Sapsucker	-0.5127	-0.2247
Regulidae		0.0000	-0.0961
	Golden-crowned Kinglet	-0.2507	-0.1543
	Ruby-crowned Kinglet	0.1009	-0.3404

Sittidae		0.0000	0.2739
	Brown-headed Nuthatch	0.1257	-0.1940
	Red-breasted Nuthatch	0.3305	-0.3264
	White-breasted Nuthatch	-0.5899	1.3130
Sturnidae		0.0000	0.2708
	European Starling	-0.0844	0.7075
Sylviidae		0.0000	-0.8547
	Blue-gray Gnatcatcher	0.1873	-2.3215
Thraupidae		0.0000	0.1864
	Scarlet Tanager	0.1953	-1.7316
	Summer Tanager	-0.3030	2.7019
Timaliidae		0.0000	-0.0559
	Wrentit	-0.2313	-0.2617
Trochilidae		0.0000	-0.1325
	Allen's Hummingbird	0.2371	-0.5117
	Anna's Hummingbird	0.2074	-1.0242
	Ruby-throated Hummingbird	-0.1578	1.2708
Troglodytidae		0.0000	-0.2628
	Bewick's Wren	-0.0706	-1.0650
	Carolina Wren	0.2552	-1.2252
	House Wren	-0.0828	1.3720
	Winter Wren	0.1724	-0.4984
Turdidae		0.0000	-0.2224
	American Robin	-0.1696	0.0053
	Hermit Thrush	0.4446	-0.1527
	Swainson's Thrush	-0.0858	0.6351
	Varied Thrush	0.1640	-0.2704
	Veery	-0.1665	-1.1833
	Western Bluebird	-0.0798	-0.4658
	Wood Thrush	0.4614	-0.9422
Tyrannidae		0.0000	-0.4352
	Acadian Flycatcher	0.3273	-1.3738
	Eastern Kingbird	-0.0530	0.8573
	Eastern Phoebe	0.2231	-1.7928
	Eastern phoebe	0.2231	-1.7928
	Eastern Wood-pewee	-0.0635	0.4326
	Great Crested Flycatcher	0.3539	-0.8448
	Least Flycatcher	0.2336	-0.5394
	Pacific-slope Flycatcher	0.0929	-0.1333
	Western Wood-pewee	-0.1569	-0.4249
	Willow Flycatcher	-0.0673	0.3816
Vireo		0.0000	-0.7892
	Hutton's Vireo	-0.3866	1.3990
	Philadelphia Vireo	-0.1648	1.5805
	Red-eyed Vireo	0.8981	-2.2799
	Solitary Vireo	0.1674	-0.4308
	White-eyed Vireo	-0.1815	-1.2589
	Yellow-throated Vireo	-0.3306	-0.9218

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

Family	Species	Negative	Positive
Alaudidae		0.0000	0.0000
	Horned Lark	0.0000	-0.0438
Cardinalidae		0.0000	0.0000
	Blue Grosbeak	0.0000	-0.3044
	Indigo Bunting	0.0000	-0.0331
	Northern Cardinal	0.0000	0.2301
Charadriidae		0.0000	0.0000
	Killdeer	0.0000	-0.0905
Corvidae		0.0000	0.0000
	American Crow	0.0000	0.0023
	Blue Jay	0.0000	-0.1355
	Scrub Jay	0.0000	0.1206
Emberizidae		0.0000	0.0000
	Dark-eyed Junco	0.0000	-0.0117
	Field Sparrow	0.0000	-0.1025
	Rufous-sided Towhee	0.0000	0.3595
	Song Sparrow	0.0000	-0.1040
	White-crowned Sparrow	0.0000	0.0336
Fringillidae		0.0000	0.0000
	American Goldfinch	0.0000	-0.1272
Icteridae		0.0000	0.0000
	Brown-headed Cowbird	0.0000	-0.1386
	Common Grackle	0.0000	0.0319
	Northern Bobwhite	0.0000	0.2068
	Red-winged Blackbird	0.0000	-0.0713
Mimidae		0.0000	0.0000
	Brown Thrasher	0.0000	-0.0386
	California Thrasher	0.0000	-0.0293
	Gray Catbird	0.0000	0.0415
Paridae		0.0000	0.0000
	Carolina Chickadee	0.0000	0.2582
Parulidae		0.0000	0.0000
	Chestnut-sided Warbler	0.0000	0.1188
	Common Yellowthroat	0.0000	0.1166
	Prairie Warbler	0.0000	-0.1576
	Yellow-breasted Chat	0.0000	-0.1639
Passeridae		0.0000	0.0000
	House Sparrow	0.0000	0.0014
Picidae		0.0000	0.0000
	Red-headed Woodpecker	0.0000	0.0000
Thraupidae		0.0000	0.0000
	Scarlet Tanager	0.0000	0.0199

Troglodytidae		0.0000	0.0000
	Carolina Wren	0.0000	-0.0570
Turdidae		0.0000	0.0000
	American Robin	0.0000	0.0111
Tyrannidae		0.0000	0.0000
	Eastern Kingbird	0.0000	0.0103
	Eastern Wood-pewee	0.0000	0.0247
	Great Crested Flycatcher	0.0000	0.0010
Vireo		0.0000	0.0000
	Red-eyed Vireo	0.0000	0.0567
	White-eyed Vireo	0.0000	-0.0362

CHAPTER 3

PREDICTING ABUNDANCE OF DESERT RIPARIAN BIRDS: VALIDATION AND CALIBRATION OF THE EFFECTIVE AREA MODEL

Abstract

An ability to reliably predict the effects of landscape change on species abundance when there is insufficient time/resources to survey relevant locations is critical to land managers who must make frequent, short-term decisions with long-term consequences. However, due to the inherent temporal and spatial variability in ecological systems, previous attempts to predict species abundance in novel locations have been largely unsuccessful (Rotenberry 1986, Stauffer 2002, Wiens 2002). The Effective Area Model (EAM; Sisk et al. 1997) uses change in both habitat composition and geometry to predict change in species abundance with a model that can be parameterized with data collected from normal field surveys. In this chapter, I report on my attempts to validate and calibrate the Effective Area model in order to improve its ability to predict absolute abundance in novel landscapes. For model validation, I compared the EAM to a null model in terms of its ability to accurately predict observed species abundance. I found the EAM to outperform the null model for 83.3 % of species (n = 12) for which it was possible to discern a difference when considering all validation sites. Likewise, the EAM generally outperformed the null model when considering a subset of validation sites categorized on the basis of four variables (isolation, presence of water, region, and focal habitat). Additionally, I explored a framework for producing calibrated models to decrease prediction bias given inherent temporal and spatial variability in abundance. I calibrated the EAM to new locations using a linear regression between observed and predicted EAM abundance with and without additional habitat covariates. EAM abundance as the sole predictor explained a significant amount of variability in observed abundance for 11 of 20 species, with R^2 values > 23% for 8 species, and > 45% for 3 species. Site level variables improved prediction, and when considering all predictive models, I found that at least one of the models had $P < 0.05$ for 17 of the 20 species examined, with R^2 values > 10% for 5 species, > 25 % for 6 species, and > 48 % for 6 species. The calibration approach developed in this chapter improves the prediction of bird abundance in novel landscapes. Model adjustments for unexplained variability in time and space, as well as variability that can be explained by incorporating additional covariates, can be used to improve the EAM.

Introduction

Given the pace and extent of human-induced landscape change, conservation decisions often need to be made more rapidly than is possible to collect relevant data (Côté and Reynolds 2002). While there have been many studies that attempt to explain patterns of species occurrence or abundance in relation to habitat variables, few studies have attempted to predict abundance in novel locations (Stauffer 2002). An ability to predict species occurrence or abundance in previously unstudied locations is critical to the ability of land managers to make reliable, rapid decisions in the face of potential landscape alterations (Noon et al. 1980).

Predictions of species occurrence patterns have experienced modest success (Block et al. 1994, Stauffer 2002), but abundance has been much more difficult to predict (Rotenberry 1986, Morrison et al. 1987, Gutzwiller and Barrow 2001). However, accurate predictions of species abundance are much more useful than mere occurrence. Occurrence predictions enable managers to identify areas in which species are present, but cautions notwithstanding (see Van Horne 1983), abundance predictions enable managers to prioritize conservation areas, and to develop specific management objectives pertaining to population size and trends. Despite its importance to conservation planning, accurate abundance prediction remains a largely unachieved goal (Rotenberry 1986, Stauffer 2002, Wiens 2002).

One of the principal difficulties in predicting species abundance under novel conditions is the inherent variability in ecological systems (Rotenberry 1986, Stauffer 2002, Wiens 2002). Predictions are often hampered by random or unpredictable fluctuations in time and/or space due to weather, food, habitat, or disturbance processes (Gutzwiller and Barrow 2001). Given the inherent variability or "noise" in ecological systems, the ability to predict abundance in novel locations, or at different times at the same location, is commonly believed to be difficult or impossible (Rotenberry 1986, Stauffer 2002).

One of the principal ways to begin to understand this otherwise unexplained variability, and to evaluate the ability of models to accurately predict abundance, is to investigate prediction error (Starfield 1997, Wiens 2002). Prediction error may be caused by inability of models to predict under novel conditions due to environmental variability as well as inter-annual fluctuations in abundance (Gutzwiller and Barrow 2001). If the goal is to accurately predict abundance, prediction error is an important means to assess the utility of a given model (model validation). In addition, empirical estimation of prediction error, and adjustment for prediction error, may provide a means to effectively adjust predictions of absolute abundance to novel locations or to different time frames (model calibration).

The Effective Area Model (EAM; Sisk et al. 1997, 2002) utilizes both habitat composition and habitat geometry in a model structure that can be parameterized with data collected in traditional bird population surveys. In order to predict species abundance in novel landscapes or regions, the EAM utilizes edge response functions (e.g., change in density of a given bird species as a function of distance from edge) along with broad-scale vegetation (habitat) maps. Maps may be based on remotely sensed imagery or Global Positioning System coordinates. As used here, edge refers to a transition in vegetation structure and/or composition that has the potential to affect the distribution and abundance of bird species. The EAM operates in a GIS framework (ArcView 3.2) and was developed to be a "desk-top" management tool to predict population level responses to future landscape configurations at the landscape scale (Sisk et al. 2002).

In order to assess whether the EAM is an improvement to less complex, non-spatial models, I compared the ability of the EAM to predict abundance in novel locations relative to a null model. Models were assessed in terms of the difference between prediction and observation, referred to as prediction error. The null model provides a prediction of abundance based solely on habitat area without considering edge effects, and thus ignores the effects of within-habitat heterogeneity resulting from proximity to adjacent habitat types (Sisk et al. 1997, 2002). The null model provides a benchmark for comparison to assess whether the incorporation of edge response functions into the model structure decreases prediction error. The relative validity of the EAM model is compared to the null model in terms of magnitude of prediction error. Additionally, a robust model validation would include sites that are categorically different from those in which model predictions were made.

In addition to model validation, I also wanted to assess whether the EAM predictions of abundance in novel locations could be improved via model calibration. Calibration has been defined as "the estimation of model parameters from data" (Morrison and Hall 2002 as used in Rotenberry 1986). However, calibration is more often used in the general sciences as a means to improve measurement of a biased or imprecise parameter by adjusting its estimate with a highly accurate measurement process that is often more difficult or expensive (Denham and Brown 1993). For ecological applications, calibration has often been used to convert relatively easy to estimate population indices into estimates of absolute abundance for a variety of taxa (Eberhardt and Simmons 1987, Graham 2002, Hamm et al. 2002, Yoo et al. 2003).

Calibration may also be used to adjust for inherent spatial and temporal variability in ecological systems. It is in this sense that the term "calibration" is used in this paper. Currently, parameterization of the EAM is limited to edge response functions that remain constant in time and space. Here I propose a framework to improve the accuracy of abundance predictions and to extend usage of the EAM by adjusting the model parameterization to fit the unique attributes of new locations. Calibration of EAM predictions to new regions and inclusion of covariates describing site-level habitat characteristics may be an efficient way to further incorporate habitat models along with the EAM to improve prediction of absolute abundance.

The overall goals of this paper were to validate and calibrate the Effective Area model for the purpose of predicting species abundance in novel locations. For model validation, my primary objective was to compare the relative predictive ability of the EAM to null models, by species, in terms of prediction error. Comparisons were made for all validation sites, as well as subsets of validation sites from different regions, and varying degrees of isolation, presence of water, and different habitat types. My second objective was to assess whether some site-level factors consistently reduced EAM prediction error and would be candidate variables to include in a calibration. My final objective was to explore a framework for producing field calibrated models to improve the prediction of abundance in new locations.

Methods

Predicted Abundance

I predicted abundance for the 25 most common bird species in 50 validation sites for both the EAM and null models. In order to parameterize the EAM, I estimated edge response functions from data obtained on the San Pedro River, Arizona, USA along with habitat maps developed for each validation site. For the null model, parameter estimates were obtained as the average interior density of a given species in a given habitat type, along with the validation site maps, to predict abundance for each site. Data collection and analysis methods for model parameterization are discussed below.

Field Protocol

Data for model parameterization was collected on the upper and middle San Pedro River in Cochise county. Study sites extended from 2 km north of the U.S. / Mexico border to 145 km north of the international border to Cascabel. Elevation varied from 1300 m at the international boundary to 900 m in the most northern study site. Study sites included 16 areas within the San Pedro Riparian National Conservation Area (NCA) managed by the BLM as well as 7 sites on privately owned land north of the NCA. The study sites provided an excellent opportunity to study mostly natural edges between adjacent habitats. By surveying birds within distinct habitat types and across edge types, it was possible to develop edge response functions and to estimate average density within the interiors of specific habitat types for 25 species. This information allowed me to parameterize the EAM and null models.

The San Pedro River watershed has two primary zones of riparian vegetation extending perpendicular from the River thalweg upslope to expansive desert scrub communities. Adjacent to the river is a primary riparian zone that consisted of gallery forests dominated by Freemont cottonwood (*Populus fremontii*) and Gooding willow (*Salix gooddingii*). A secondary riparian zone consisted of mesquite (*Prosopis* spp.) interspersed with patches of Sacaton grass (*Sporobolus wrightii*). Distinct natural edges occurred 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 occurred at the primary to secondary riparian interface, including both sides of the edge where cottonwood was adjacent to mesquite, and both sides of the edge where cottonwood was adjacent to grassland. Two edge types occurred between the secondary riparian habitats at both sides of the mesquite / grassland edge. Two edge types occurred 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 289 point-count sampling locations were established on 23 sites in the upper and middle reaches of the San Pedro River. Each site 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 located at varying distances from habitat edges were used to construct edge response functions.

Each point represented the center of a variable circular plot extending to 60-m radius. Distance sampling was used at each survey point to estimate a detection function (Buckland et al. 2001). At each point, an observer mapped the location of each individual bird on field sheets representing a specific circular plot marked with cross-hairs at increments of 10 m. The distance 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. Point count locations were surveyed for 5 min after an initial 1 minute wait period. Additionally, in order to meet the Distance Sampling assumption of perfect detection at the point (i.e., $g(0) = 1$), and in order to reduce potential bias resulting from evasive movement in response to an observer, birds were also recorded as an observer approached a point. Movement of those birds detected at the point was then recorded during the subsequent wait period and survey period in order to avoid double counting. Surveys were conducted from 10 minutes before sunrise until 3 hrs after sunrise. The order in which transects were walked was varied systematically to avoid bias related to time of day.

A total of 2,720 point count surveys were conducted during the 1998-2001 field seasons. Each point was visited between 6-15 times, and survey effort was used to adjust density estimates in subsequent analyses by inclusion of a survey effort multiplier in the analysis. A total of 10 experienced observers conducted surveys during the 4 year study. At the beginning of each field season, a minimum of 2.5 wks of training on survey techniques, including identification of birds by sight and sound, was done prior to data collection. 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 distribution of horizontal sighting distances from the observer to individual birds was used to estimate a detection function separately for each species. Based on computational algorithms in program Distance 3.5 (Buckland et al. 2001, Thomas et al. 1998), the detection function provides an adjustment to the raw count and allows an estimate of the density of each species for each point location. 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 analysis. Between 5-15% of the distance data were truncated to eliminate heaping, depending on the pooled detection function observed for each species (Buckland et al. 2001).

AIC model selection (Burnham and Anderson 2002) was used to select the best detection function for each of the 25 species. Candidate detection functions included a habitat type covariate to test for this source of heterogeneity in detectability. In the most general model considered, the detection function for a given species was 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. I assumed it was appropriate to pool habitats for candidate detection functions when plant species composition differed but structure was similar. Candidate detection functions included pooling desert scrub with grassland, cottonwood with mesquite, and pooling grassland, desert scrub and mesquite separately from cottonwood. I considered inclusion of a detection function pooled across one or more habitats was justified when the structure of those habitats was relatively similar and thus was expected to be similar in terms of the detection function.

An additional difficulty in estimating the detection function is rarity of a given species in a given habitat. Even 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, in which they occur. When a species is rare in a habitat type, it may be necessary to pool data across habitats to estimate a global detection function. For example, detections in desert scrub may be pooled with those in grassland if a given species has low abundance in one of those habitats. The rule for pooling was that the habitat types were structurally similar, and thus assumed to be similar in terms of the detection function.

All candidate detection functions were compared via AIC model selection procedures to select the best detection function for each species. The best detection function was subsequently used to estimate density at all points where a species was detected. This analysis was done for the 25 most common species across all habitats.

Distances of point count locations to the closest edge were 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 18 to 42 locations per edge type ranging from 0 m to 330 m into interior habitat from the closest relevant edge. No overlapping "zero" points were used for the development of edge response functions in order to separate the edge response on opposite sides of the forest-open edge (Baker et al. 2002). Estimates of density as a function of distance from edge were used to estimate continuous edge response functions.

EAM and Null Model Parameterization

A total of 200 edge response functions were estimated for 25 species in 8 edge types using piecewise linear regression where possible, and linear regression otherwise, with density (dependent variable) regressed on distance from edge (independent variable). Piecewise linear regression was used since it has been found to accurately represent threshold patterns commonly observed with respect to distance from edges (Newmark 2001, Toms and Lesperance 2003) and provides the point estimates required for use of the EAM as currently parameterized (Sisk et al. 2002). All regression models were estimated with Stata 8.0 (StataCorp 2003).

Of the total species/edge type combinations, 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 (Figure 1).

The coefficients estimated via regression modeling were used as input parameters to the EAM. The three input parameters for the EAM are 1) density at the edge, 2) density in the interior (basal density), and 3) the breakpoint (D_{max}) represented the maximum distance of edge influence (Figure 2). The piecewise linear analyses provided these three basic inputs for the EAM (Figure 2). Using simple linear regression, D_{max} was taken as the maximum distance of the sampling effort (i.e., the maximum distance from edge sampled). Edge density was estimated by use of the intercept (density when distance = 0), and the basal (interior) density was calculated by using the linear regression equation = (edge density) + (slope parameter) x (maximum distance sampled; Figure 2).

Even though density estimates from point count locations may show spatial dependence, random effects were not included in the EAM parameterization. This was not considered a problem since least squares methods give unbiased estimates of parameter coefficients even with dependency in the data (Greene 2000). I concluded that use of estimates pooled across sites does not greatly affect the parameterization of the EAM and null models.

In order to parameterize the null model, I estimated the interior density for each of the 200 species/edge type combinations as described above for the EAM parameterization. Interior density was then considered to be constant across an entire habitat patch regardless of distance from adjacent habitats.

Validation Study Sites

A total of 50 sites located between <1 km to >200 km from the San Pedro River were used to evaluate the predictive performance of the EAM. Validation sites were established in 4 general areas: sites on the San Pedro River not used to estimate the edge response functions, sites within the east and west ranges of Fort Huachuca, Sonoita Creek managed by The Nature Conservancy, and Empire Cienega National Riparian Conservation Area managed by the BLM. Study sites were located in Cochise, Pima, and Santa Cruz counties and ranged in elevation from 900 m to 1200 m and in latitude from 31°30' N to 32°20' N. Seven of these sites had been set up in 2000 for pilot validation work, and 47 additional sites were set up in 2001. Four sites that had been used in 2000 were no longer accessible, and were dropped for the work in 2001.

Validation sites varied by 4 site-level factors: region, focal habitat, degree of isolation, and presence / absence of surface water. First, sites varied by region as described above, and were classified as within (18 sites), or beyond (32 sites), the San Pedro River riparian corridor. Of the validation sites, 34 sites were dominated by cottonwood focal habitat, and 16 sites by mesquite. Cottonwood habitat was adjacent to mesquite, grassland or both. Mesquite habitat was adjacent to desert scrub, or both cottonwood and desert scrub. Cottonwood sites were classified as isolated if they were >100 m from the primary riparian corridor of the San Pedro River, Sonoita River, or the Cienega River. All Cottonwood sites on Fort Huachuca were considered isolated, since they were all narrow drainages eventually discharging into the San Pedro River.

Mesquite sites were classified as isolated if they were narrow strips vegetation occurring in washes (< 50 m wide), and non-isolated if they were part of the much wider secondary riparian corridor immediately adjacent to the primary riparian corridor. Sites were also classified as surface water absent if surface water was not present at any of the visits to the site, and present otherwise.

To develop habitat maps for use in the EAM and null models, I used a Trimble GPS unit to record UTM coordinates along edges between habitat types within validation sites. Classification of habitat types within sites was done by field reconnaissance. The perimeter of habitat types within validation sites was grouped and differentially corrected in Pathfinder Office to obtain accuracy of 2-5 m. Location data were 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, point count locations were established and each point location was buffered to 60 m. To standardize the area of estimation between the predicted and observed abundance, the buffered polygon was used as the outer limit of predicted abundance for both the EAM and null models.

Observed Abundance

The number of point count locations established at each location depended 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 remaining 44 sites contained 3 point count locations. There were 95 plots in 34 cottonwood sites, and 47 plots in 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. The order in which sites were visited was varied systematically in order to avoid bias related to time of day.

Distance sampling, as described above for the development of edge response functions, was used to obtain an abundance estimate for each species in each of the 50 sites. The area of each validation site, calculated within Arc View 3.2 as described above, was used to obtain abundance estimates per site. To obtain a per-site abundance 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 (Buckland et al. 2001). Two different observers conducted surveys during the 2 years, with a single observer (L.A.B.) doing approximately 92% of the 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 (Buckland et al. 2002). Sufficient detections were obtained to enable estimation of abundance of 20 species by validation site. All data were analyzed in program Distance 3.5 (Thomas et al. 1998).

AIC model selection (Burnham and Anderson 2002) was used to select the best detection function to estimate per site abundance for each of the 20 species. Eight candidate detection functions were assessed, including detection functions allowed to vary by habitat type, riparian corridor width, adjacent habitat type. In addition, a global detection function was estimated based on pooling across sites. I selected the best model via AIC with a minimum of 50 detections. All candidate detection functions were assessed by species (Buckland et al. 2001). Due to relatively small sample sizes for the species-specific analyses, only 2 detection functions were used across the 20 species: focal habitat (separate detections for cottonwood vs mesquite) or global (pooling across all sites).

Comparison of Observed and Predicted

Model Validation -- Comparison of Relative Predictive Performance of EAM vs. NULL

I evaluated the relative predictive performance of the EAM and null models for 20 species that were sufficiently common on both the model parameterization and validation study sites. In order to assess the relative performance of the models, I compared prediction error between observed and predicted abundance using both models for each of the 20 species. Prediction error was estimated as the absolute value of the mean difference between the observed and predicted and was used to compare model performance. Mean absolute prediction error (called prediction error) was calculated separately for each species for each of the two models (EAM and null) as:

$$\text{Prediction Error}_{\text{species x / model A}} = \frac{\sum_{i=1}^{50} \left| (E(observed_i) - (E(predicted_i) \right|}{50} \qquad \text{(eqn.1)}$$

where i indexes validation site.

To estimate the expected value of the observed abundance for each validation site, I regressed observed abundance (dependent variable) onto predicted abundance (independent variable) for each species in each validation site separately for each model. The fitted line from the linear regression model represents the expected value of observed abundance for different levels of the predicted (i.e., different validation sites) for both models. I call these lines the regression of observed vs. predicted (illustrated without x-marks, Figure 3). The rationale for this approach is that the regression estimates the expected value of observed abundance, at a given predicted abundance, and smoothes the inherent variability in the observed data. Much of this variability is believed to be related to sampling variation and should not be attributed to prediction error.

To represent predicted abundance, I graphed predicted abundance vs. predicted abundance for both the EAM and null models. The predicted lines have y-intercept = 0 and slope = 1, or a 45 degree angle (illustrated with x-mark lines; Figure 3). The predicted lines, distinguished from the regression of observed vs. predicted lines discussed above, represented the benchmark for a 1:1 relationship that would indicate a "perfect" predictive relationship.

Comparing the absolute difference between the observed vs. predicted line, versus the predicted vs. predicted line, for each validation site, provides a means to compare the prediction error of the EAM vs. prediction error of the null model. The data structure for this comparison was appropriate for a paired t-test—however, the independence and equal variance assumptions were not met. Therefore, model comparisons were based on 10,000 bootstrap replicates of the 50 validation sites with replacement to estimate the distribution of prediction error for the EAM and the null model, and the difference in prediction error between the models. The first step of the bootstrap process computed the absolute value of the difference between the fitted observed abundance and predicted abundance lines (analogous to the residuals), for each validation site. Next, I calculated the mean of the absolute difference between the fitted observed vs. predicted abundances by species, and used bootstrap replicates to obtain 95% bootstrap percentile confidence intervals and P-values to test the hypothesis that the prediction error of the EAM < prediction error of the null model (Efron and Tibshirani 1993). The upper and lower 95%

percentile confidence intervals were calculated for each statistic, and two, one sided P-values 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; Efron and Tibshirani 1993). It was necessary to use one-sided P-values because the bootstrap distribution is asymmetric, so I reported P-values appropriate to the sign of the difference between the mean absolute bias of the EAM and null models. Using $\alpha = 0.05$ for the 1-sided case is analogous to $\alpha = 0.10$ for the two-sided case, which was used to minimize the probability of Type II error.

Model Calibration -- Prediction of abundance in novel locations

In addition to model validation, I also wanted to assess whether abundance prediction by the EAM might be improved by model calibration. A model with no prediction error would provide an unbiased prediction of abundance, and, in a regression sense, would have the y-intercept parameter = 0 and the slope parameter = 1 as follows:

$$avg(y) = 0 + (1) \cdot EAMabund \qquad \text{(eqn. 2)}$$

where y = observed abundance, and $EAMabund$ = predicted EAM abundance.

However, when attempting to predict abundance in locations (validation sites) different from those used to parameterize the model (San Pedro River), substantial prediction error may occur between the average of the observed and predicted. Deviation of the slope and y-intercept parameters from 0 and 1 respectively represent an overall shift due to unexplained sources of spatial or temporal variability.

To assess whether calibration is needed to more reliably predict abundance in novel locations, I calculated EAM prediction error across all validation sites for each species. Additionally, because I was interested in whether incorporation of site level variables improved prediction, I subset the 50 validation sites to investigate EAM prediction error as a function of four site-level variables: focal habitat, isolation, presence of water, and region. In comparing the performance of the EAM separately for each subset of the site-level covariates, it was possible to ascertain whether these covariates affect the ability of the EAM to predict abundance in validation sites that are different from those in which the models were parameterized. If the prediction error was higher in isolated sites, for example, then an additional site-level covariate (such as isolated vs. not isolation) may improve predictions.

Calibration of EAM predictions utilizes empirical estimation of the slope and intercept parameters to adjust or correct abundance predictions for novel locations. Use of the regression of observed vs. predicted for each model represents the calibrated relationship between observed and predicted. Calibration can be achieved by regressing the predicted abundance on the observed abundance using a basic regression model:

$$avg(y) = \beta_0 + \beta_1 \cdot EAMabund \qquad \text{(eqn.3)}$$

where y = observed abundance, and $EAMabund$ = predicted EAM abundance. Additionally, I wanted to evaluate whether prediction of absolute abundance could be improved by incorporating site-level covariates, such as the 4 site level variables discussed above. In addition to the EAM predictions, I used augmented calibration models to incorporate each of the 4 site-level variables by themselves, as well as all together. These models shifted the intercept but did not change the slope. While different structure of additional covariates (e.g., continuous covariates such as canopy height) could be used, in the augmented calibration approach used here EAM predictions were augmented with binary site-level factors in an ANCOVA model:

$$avg(y) = \beta_0 + \beta_1 \cdot EAMabund + \beta_2 \cdot region \qquad \text{(eqn.4)}$$

where y = observed abundance, and $EAMabund$ = predicted EAM abundance. To evaluate improvement in prediction by the EAM by using augmented calibration models in terms of the percent of the variation in abundance explained, I calculated the coefficient of determination (R^2 values) and model P-values by species as a function of EAM predictions alone, EAM predictions separately by site-level variable, and EAM predictions with all 4 site-level variables.

Results

Model Validation

Comparing the relative performance of the EAM and null models based on all validation sites, I found a difference ($P < 0.05$) in mean absolute prediction error for 12 of 20 species (Figure 4, Table 1). For example, for the Yellow-breasted Chat the EAM outperformed the null model, as seen by the smaller mean absolute prediction error between the observed vs. predicted regression line, and the predicted vs. predicted line for the EAM (Figure 4). In contrast, for the Black-throated Sparrow the null model outperformed the EAM (Figure 4). Of the 12 species for which it was possible to discern a significant difference between models, the EAM performed better than the null for 10 species, and the null performed better than the EAM for 2 species. As such, 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).

When comparing the performance of the models 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 affected the relative performance of the 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 region in terms of the % of species for which the EAM outperformed the null (Table 2). The EAM most out-performed the null model in isolated validation patches and in validation patches without water—91% of the species were better predicted by the EAM when it was possible to discern a difference between the two approaches (Table 2). It was not possible to discern a different in mean absolute prediction error between the two models for 8 of 20 species when considering all validation sites, and between 9-15 of 20 species when considering subsets of validation sites (Tables 1,2).

Model Calibration

Each of the 20 species examined showed significant EAM model bias when considering all 50 validation sites. The 95% percentile confidence interval of mean EAM bias did not overlap zero for any of the species (Figure 5). In particular, 5 species: Cassin's Kingbird, Lucy's Warbler, Brown-crested Flycatcher, Song Sparrow and Yellow Warbler showed substantial prediction bias (Figure 5). These results indicate that across all 50 validation sites, calibration may be needed to improve the ability to predict abundance for common desert riparian bird species in novel locations (validation sites).

When I subset validation sites by site-level variables, 9 of 20 species showed a difference ($P < 0.05$) in EAM bias as a function of one or more of the four site-level covariates (focal habitat, isolation, presence of water, and region). These results indicate that it may be possible decrease the bias of the EAM by incorporating additional site-level variables to enhance abundance prediction in novel locations.

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. Similar results were observed with isolation and presence of water. All five species showed higher bias in both contiguous patches and in sites where water was present (Common Yellowthroat, Song Sparrow, Summer Tanager, Yellow-breasted Chat, and Yellow Warbler; Figure 6). Type of 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; Figure 6) 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. Region (San Pedro River vs. off- San Pedro River) was a significant predictor of EAM bias only for the Song Sparrow, which showed significantly increased bias outside the San Pedro corridor (Figure 6). This result indicates that the EAM predictions are robust across regions for the majority of species.

Of the 6 models examined for improvement in prediction by the inclusion of covariates, I found that at least one model with $P < 0.05$ for 17 of the 20 species examined, with R^2 values > 10% for 5 species, > 25 % for 6 species, and > 48 % for 6 species (Table 3). The EAM as a predictor by itself explained a significant amount of variability in observed abundance for 11 of 20 species, with R^2 values > 23% for 8 species, and greater than 45% for 3 species (Table 3). At least one of the additional site-level variables significantly improved predictions for the majority of species examined (Table 3).

Calibration and augmented calibration models (eqns. 3 and 4) can be used to predict abundance in sites different from those in which data were collected, if the population of sites to which one would like to statistically infer is sampled in some probabilistic way. As a framework for calibration, the method used here may be applied more broadly if care is taken to identify a target population of interest and then conduct a random calibration sample. The subsequent calibration equations can then be used to predict absolute abundance, adjusted for known site-level factors as well as for unknown variation due to year-to-year variability, regional differences, or other unmeasured sources of variation.

Discussion

Distance from habitat edge is strongly related with abundance response for many bird species resulting from putative abiotic and biotic mechanisms occurring at edges (Chapter 1). Given the strong relationships between abundance, habitat type, and distance from edge, it is essential to incorporate these factors into predictive models (Sisk et al. 1997, 2002). Despite the large amount of effort given to the study of the response of birds to habitat edges (Chapter 1), the EAM is the only tool currently available that projects information from edge response studies in a given set of focal/matrix habitats to population level responses at the landscape scale.

Comparison of the predictive performance of the EAM and null models is a means to assess the importance of edge response and patch context for predicting avian abundance. I found that when comparing the relative predictive performance of the EAM to a null model that ignores edge effects, the EAM had lower mean absolute prediction error and thus was better able to predict absolute abundance than the null model. I found this to be true for all validation sites as well as subsets of validation sites. Overall, it appears that including information on the response of bird to habitat edges, as well as to habitat composition, provides more accurate predictions of abundance in novel locations.

The EAM performed better overall, but it was not consistently better than the null model. For example, abundance of Black-throated Sparrow and Summer Tanager were predicted more accurately by the null model than the EAM when considering all validation sites. The reason for this does not appear to be due to neutral edge responses, since both species showed a significant edge response in 3 of the 8 edge types sampled in the validation sites (Chapter 2). One possible explanation for instances in which the null model outperforms the EAM, is that some species may not consistently demonstrate edge responses across sites. Currently it is unknown why, and to what extent, edge responses change for a given species from on region to another in the same habitat types. Additionally, situations in which the models don't predict well may be due to bias and lack of precision in model parameterization and also possibly due to poor model form.

That it was not possible to discern a difference between the predictive performance of the two models for certain species could be due to lack of importance of edge effect for those species. For the eight species for which it was not possible to discern a difference when considering all validation sites, 2 had neutral edge responses in 7 of the 8 edge types (Bewick's Wren, Song Sparrow), 3 had neutral edge responses in 6 of the 8 edge types (Gila Woodpecker, Lesser Goldfinch, and Mourning Dove), 2 had neutral edge responses in 5 of 8 edge types (Common Yellowthroat, Ash-throated

Flycatcher), and 1 species (Abert's Towhee) had 4 of 8 neutral edge responses (Chapter 2). For common species such as Abert's Towhee with fewer neutral edge responses, the inability to discern a difference between the EAM and null models may also be related with inconsistency in edge response across sites as discussed above. Given the increased number of species for which it was not possible to discern a difference between the models for subsets of validation sites, it is also likely that lack of power became more of a problem as the sample size was fragmented.

Additionally, EAM predictive capability compared with the null model was also improved with the inclusion of site-level variables for certain species. While the EAM performed better overall, it did not perform as well when compared with the null model for certain subsets of validation sites. For example, the relative performance of the EAM versus null was best in isolated, dry sites compared with contiguous, wet sites (91% versus 60% EAM better prediction than the null model). As such, edge response appears to be affected by these site level variables. The significance of local covariates provides additional evidence that edge response may change due to different characteristics of habitats, even if habitat composition remains constant. Even though there are clearly some cases where incorporation of a species' edge response functions does not increase prediction success, overall it appears to improve model prediction.

Even though the EAM provided less biased abundance predictions in novel locations when compared with the null model, substantial prediction error was observed. EAM predictions showed substantial and significant bias for all 20 species examined. There are many sources of variability that likely increase bias due to fundamental differences between San Pedro sites (used to parameterize the model) and validation sites. Inter-annual variability may have been a source of bias in that parameterization and validation sampling occurred during different years (1998-2001 and 2000-01 field seasons, respectively). Year to year variation in regional abundance has been found to occur in many other breeding bird studies (Noon et al. 1985, Villard et al. 1995, Wesolowski and Tomialojc 1997, Gutzwiller and Barrow 2001) and is likely to have affected prediction errors. Regional differences between model parameterization and validation sites included differences in the landscape surrounding the riparian corridor, with the San Pedro riparian corridor surrounded by Chihuahuan or Sonoran desert and validation sites on the Sonoita Creek preserve, Fort Huachuca, and Empire cienega surrounded by high desert grassland. Inter-annual or regional differences may have affected the regional species pool, which in turn, could affect environmental factors such as food abundance or biotic interactions such as competition or predation. In summary, there were many sources of potential variability that likely affected the magnitude of bias between observed and predicted abundance.

Others have attempted, but largely failed to predict absolute abundance in novel locations or at different time periods (Rotenberry 1986, Morrison et al. 1987, Wiens 2002, Whittingham et al. 2003), probably in large part due to inherent variability between time frames or locations. For example, Morrison et al. (1987) found that attempts to predict abundances at the same locations at a different time underestimated observed abundances by 25-50%. Rotenberry (1986) and Wiens (2002) attempted to use habitat models that explained up to 70% of the variation in observed abundance to predict abundance in new locations and time frames, and found these models did not predict well. Whittingham et al. (2003) applied predictive habitat models to new locations, and found that models developed in one region performed poorly when applied in other regions. However, Whittingham et al. (2003) also noted that observed skylark territories were significantly correlated with predicted skylark territories, even if they did not predict a 1: 1 relationship. From this result, they cautioned that models developed in one place cannot be used to make absolute abundance predictions in other regions. However, they may have been overly pessimistic because they failed to recognize that estimating fitted observed values (estimated from a regression between observed vs. predicted abundances) enables empirical estimation and adjustment for bias that can be used to calibrate models to new locations.

Given the possibility of strong causal relationships between abundance and a large number of habitat factors, (Rotenberry 1986, Lowe and Bolger 2002), it is unlikely that a model such as the EAM based on habitat composition and edge responses alone can be used to reliably predict abundance for all species. The use of additional categorical variables as site-level covariates proved useful as a means to explain components of variability in bird abundance and reduce EAM prediction bias. By subsetting validation sites by meaningful ecological factors, it was possible to assess additional factors that influenced EAM bias. Five species showed higher bias in contiguous patches and in sites where water was present. Three of the five species (Song Sparrow, Yellow-breasted Chat, and Yellow Warbler) are species that require mesic conditions (Ehrlich et al. 1988). Of the six species that showed higher EAM bias in cottonwood sites, three 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 habitat structure and other environmental factors related with degree of isolation and/or presence of water. A number of the validation sites on the Empire Cienega and Sonoita Creek appeared to be in extremely good hydrologic condition, even compared to the San Pedro River where the models were parameterized (*personal observation*). The three other species that showed higher bias in cottonwood focal habitat (Brown-crested Flycatcher, Cassin's Kingbird, and Lesser Goldfinch) may have been responding to unmeasured factors that varied between the cottonwood sites other than degree of isolation and presence of water (e.g., understory cover, dominant tree basal area, or canopy height). Differences in environmental factors that affect bird abundance between parameterization and validation sites likely contributed to the observed bias for many of these species.

In addition to helping to explain EAM bias, the four site-level covariates provided a means to improve predictions of abundance after model calibration. The calibrated models with and without site-level factors explained observed abundance with R^2 values > 25 % for 6 species, and > 48 % for 6 species. Compared with other studies (Morrison et al. 1987), the predictive power of these models was quite good. Use of the site-level habitat covariates, along with calibrated EAM predictions, significantly improved prediction success.

Increased accuracy of abundance predictions using the methods outlined in this chapter requires close attention to model parameterization and calibration. To predict abundance in novel locations using the EAM requires it to be parameterized in terms of absolute (not relative) abundance and to account for the effect of edge on density. Given the large amount of theoretical development of abundance estimation methods, edge response functions can and should be parameterized using distance sampling (Buckland et al. 2001) or mark-recapture methods (Seber 1982, White et al. 1982) that enable abundance estimation by adjusting for detection probabilities that are heterogeneous and <1.0. Additionally, in order to calibrate predictive models to local site conditions, the target population, such as the breeding bird community in cottonwood/willow riparian corridors in southern Arizona, needs to be clearly identified. If a calibration sample is drawn randomly (or according to some probabilistic scheme) from the target population, then the calibration equations can be applied to make statistically valid absolute abundance predictions to sites within that target population other than those which were sampled.

Literature Cited

Baker, J., K. French, and R. J. Whelan. 2002. The edge effect and ecotonal species: Bird communities across a natural edge in Southeastern Australia. Ecology 83: 3048-3059.

Block, W. M., M. L. Morrison, J. Verner, and P. N. Manley. 1994. Assessing wildlife-habitat-relationships models: A case study with California oak woodlands. Wildlife Society Bulletin 22: 549-561.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. J. Thomas. 2001. An Introduction to Distance Sampling: Estimating Abundance of Biological Populations. Oxford University Press, Oxford, UK. 432 pp.

Burnham, K. P., and D. A. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach, 2nd edition. Springer-Verlag, Inc. New York. 488 pp.

Côté, I. S., and J. D. Reynolds. 2002. Predictive ecology to the rescue? Science: 1230-1231.

Denham, M. C., and P. J. Brown. 1993. Calibration with Many Variables. Applied Statistics, Vol. 42: 515-528.

Eberhardt, L. L., and M. A. Simmons. 1987. Calibrating population indices by double sampling. Journal of Wildlife Management 51: 665-675.

Efron, B., and R. J. Tibshirani. 1993. An introduction to the bootstrap. Chapman & Hall, New York.

Ehrlich, P. R., D. S. Dobkin, and D. Wheye. 1988. The Birder's Handbook: A field guide to the natural history of North American Birds. Simon and Schuster Inc.

Graham, I. M. 2002. Estimating weasel Mustela nivalis abundance from tunnel tracking indices at fluctuating field vole Microtus agrestis density. Wildlife Biology 8: 279-287.

Greene, W. H. 2000. Econometric analysis, 4th edition. Prentice Hall, New Jersey.

Gutzwiller, K. J., and W. C. Barrow, Jr. 2001. Bird-landscape relations in the Chihuahuan desert: Coping with uncertainties about predictive models. Ecological Applications 11: 1517-1532.

Hamm, K. A., L. V. Diller, and D. W. Kitchen. 2002. Comparison of indices to estimate abundance of dusky-footed woodrats. Wildlife Society Bulletin 30: 64-70.

Lowe, W. H., and D. T. Bolger. 2002. Local and landscape-scale predictors of salamander abundance in New Hampshire headwater streams. Conservation Biology 16:183-193.

Morrison, M. L., and L. S. Hall. 2002. Standard terminology: Toward a common language to advance ecological understanding and application. Pp. 43-52 418 *in* J. M. Scott, P. J. Heglund, and M. L. Morrison (editors). Predicting species occurrences: Issues of accuracy and scale. Island Press, Washington. 868 pp.

Morrison, M. L., I. C. Timossi, and K. A. With. 1987. Development and testing of linear regression predictive bird-habitat relationships. Journal of Wildlife Management 51:247-253.

Newmark, W. D. 2001. Tanzanian Forest Edge Microclimatic Gradients: Dynamic Patterns. Biotropica 33: 2-11.

Noon, B. R., D. K. Dawson, D. B. Inkley, C. S. Robbins, and S. H. Anderson. 1980. Consistency in habitat preference of forest bird species. Transactions of the North American Wildlife and Natural Resources Conference 45:226-244.

Noon, B. R., D. K. Dawson, and J. P. Kelly. 1985. A search for stability gradients in North American breeding bird communities. Auk 102: 64-81.

Robertsen, M. J., S. A. Temple, and J. Coleman. 2002. Predicting the distributions of songbirds in forests of central Wisconsin. Pp. 399-418 *in* J. M. Scott, P. J. Heglund, and M. L. Morrison (editors). Predicting species occurrences: Issues of accuracy and scale. Island Press, Washington. 868 pp.

Rotenberry, J. T. 1986. Habitat relationships of shrubsteppe birds: even "good" models cannot predict the future. Pp. 217-222 *in* J. Verner, M. L. Morrison, and C. J. Ralph (editors). Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison, Wisconsin. 470 pp.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters, 2nd ed. Macmillan, New York, NY.

Sisk, T. D., N. M. Haddad, and P. R. Ehrlich. 1997. Bird assemblages in patchy woodlands: modeling the effects of edge and matrix habitats. Ecological Applications 7(4): 1170-1180

Sisk, T. D., B. R. Noon, and H. M. Hampton. 2002. Estimating the effective area of habitat patches in heterogeneous landscapes. Pp. 713-725 *in* J. M. Scott, P. J. Heglund, and M. L. Morrison (editors). Predicting species occurrences: Issues of accuracy and scale. Island Press, Washington. 868 pp.

Starfield, A. M. 1997. A pragmatic approach to modeling for wildlife management. Journal of Wildlife Management 61:261-270.

StataCorp. 2003. Stata Statistical Software: Release 8.0. College Station, TX: Stata Corporation.

Stauffer, D. F. 2002. Linking populations and habitats: Where have we been? Where are we going? Pages 53-61 *in* J. M. Scott, P. J. Heglund, and M. L. Morrison (editors). Predicting species occurrences: Issues of accuracy and scale. Island Press, Washington. 868 pp.

Thomas, L., J. L. Laake, J. F. Derry, S. T. Buckland, D. L. Borchers, D. R. Anderson, K. P. Burnham, S. Strindberg, S. L. Hedley, M. L. Burt, F. F. C. Marques, J. H. Pollard, and R. M. Fewster. 1998. Distance 3.5. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK. Available: http://www.ruwpa.st-and.ac.uk/distance/

Toms, J. D., and M. L. Lesperance. 2003. Piecewise regression: A tool for identifying ecological thresholds. Ecology 84: 2034-2041.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47: 893-901.

Villard, M-A, G. Merriam, and B. A. Maurer. 1995. Dynamics in subdivided populations of neotropical migratory birds in a fragmented temperate forest. Ecology 76:27-40.

Watts, J. 1996. San Pedro River Vegetation Mapping Project. U. S. Army Engineer Research and Development Center, Topographic Engineering Center.

Wesolowski, T., and L. Tomialojc. 1997. Breeding bird dynamics in a primaeval temperate forest: Long-term trends in Bialowieza National Park (Poland). Ecography 20: 432-453.

White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory Report LA-8787-NERP, Los Alamos, NM. 235pp.

Whittingham, M. J., J. D. Wilson, and P. F. Donald. 2003. Do habitat association models have any generality? Predicting skylark *Alauda arvensis* abundance in different regions of southern England. Ecography 26:521-531.

Wiens, J. A. 2002. Predicting species occurrences: Progress, problems, and prospects. Pp. 739-749 *in* J. M. Scott, P. J. Heglund, and M. L. Morrison (editors). Predicting species occurrences: Issues of accuracy and scale. Island Press, Washington. 868 pp.

Yoo, H. J., A. Stewart-Oaten, and W. W. Murdoch. 2003. Converting visual census data into absolute abundance estimates: a method for calibrating timed counts of a sedentary insect population. Ecological Entomology 28: 490-499.

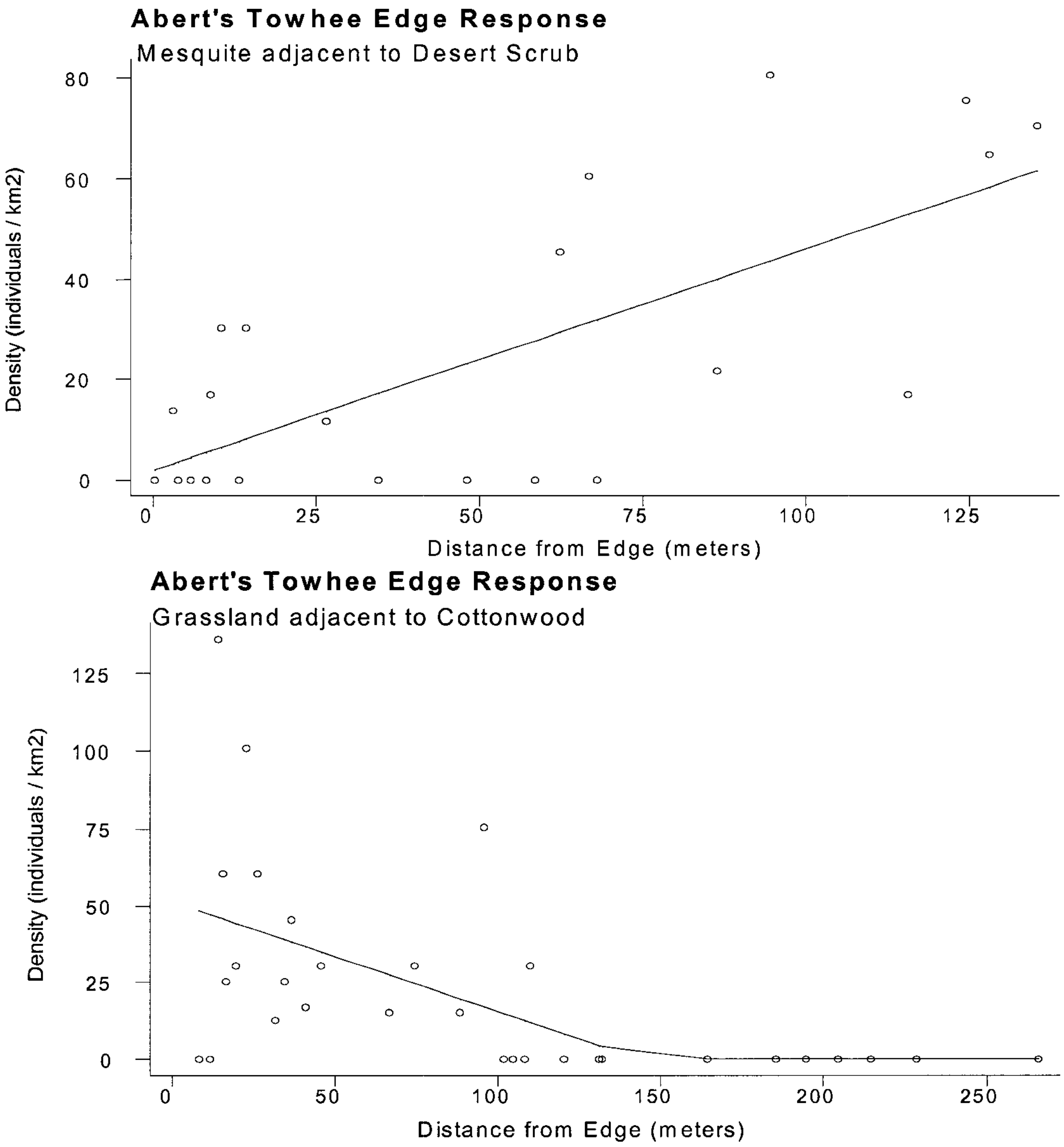


Figure 1. Edge response function for Abert's Towhee in mesquite adjacent to desert scrub using simple linear regression, and in grassland adjacent to cottonwood using piecewise linear regression.

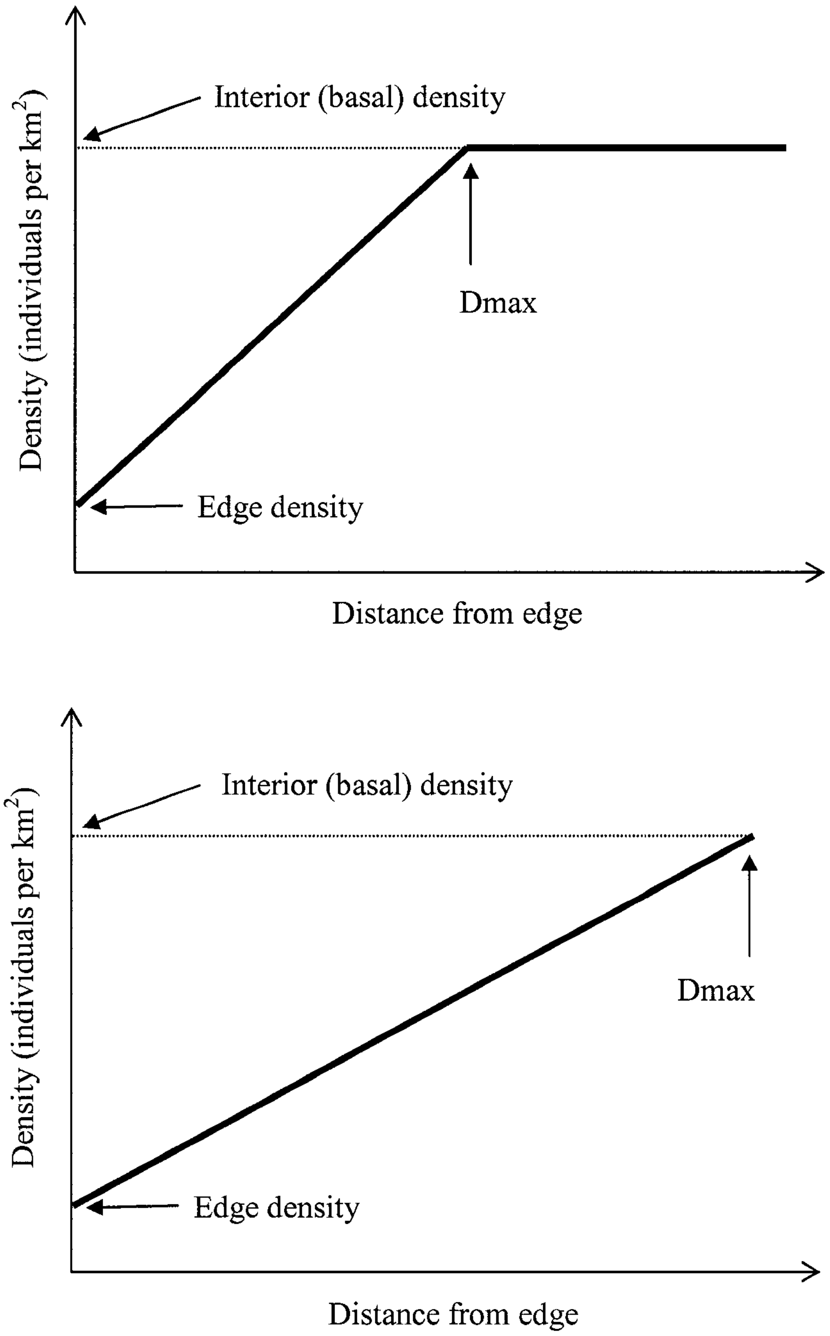


Figure 2. Three EAM input parameters when using piecewise linear and linear regression.

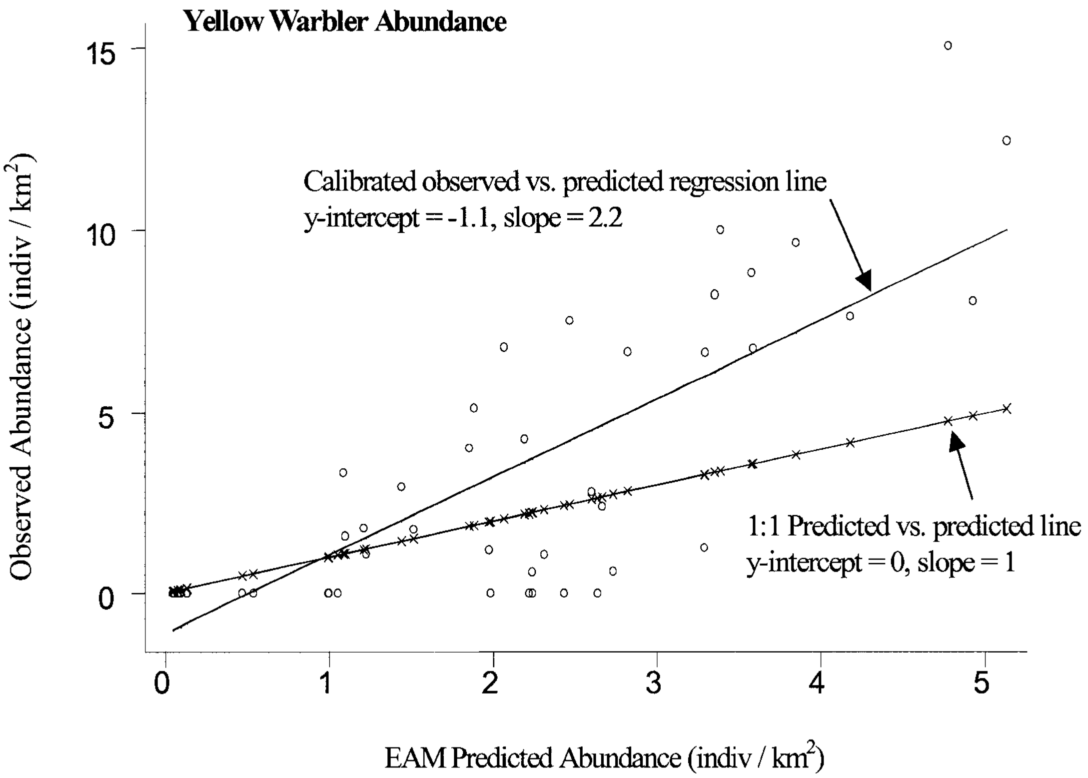
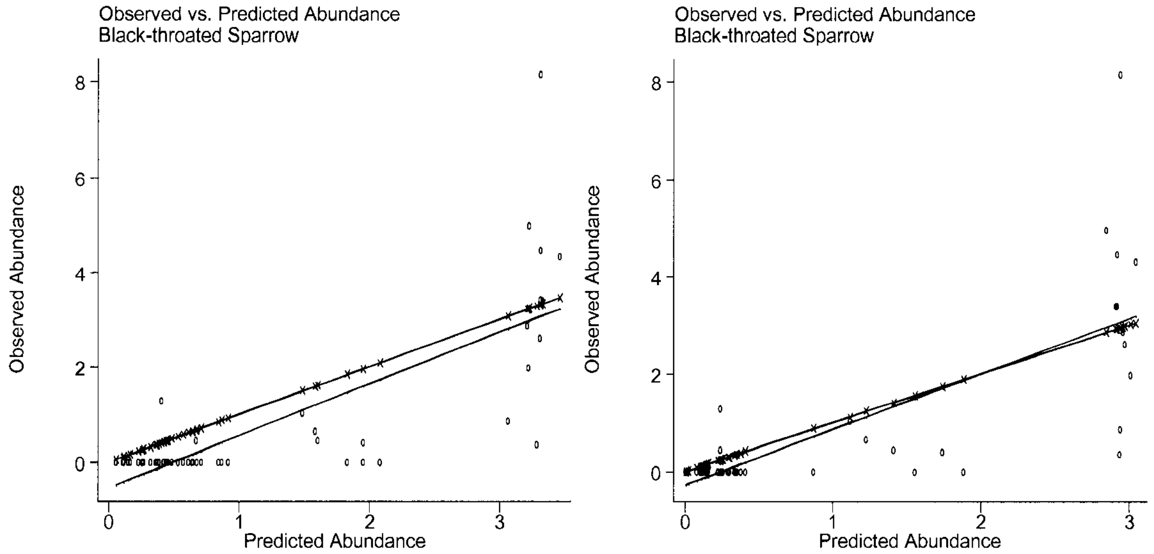


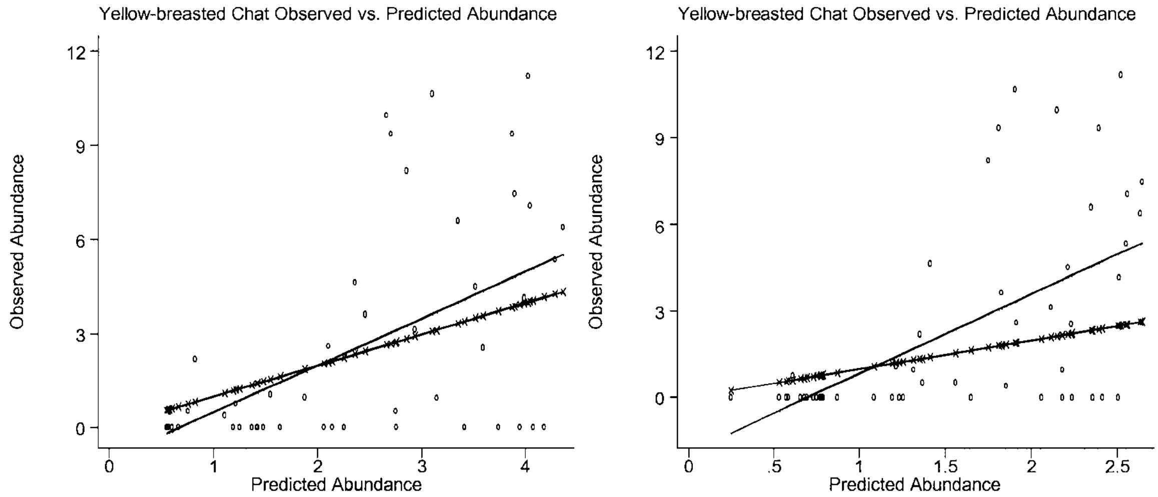
Figure 3. Yellow warbler observed vs. EAM predicted abundance showing the calibrated observed vs. predicted regression line, and the 1:1 predicted vs. predicted line.


Observed vs. Predicted Abundance Black-throated Sparrow

Observed vs. Predicted Abundance Black-throated Sparrow

EFFECTIVE AREA MODEL

NULL MODEL


Yellow-breasted Chat Observed vs. Predicted Abundance

Yellow-breasted Chat Observed vs. Predicted Abundance

EFFECTIVE AREA MODEL

NULL MODEL

Figure 4. Black-throated Sparrow and Yellow-breasted Chat predicted line at 45 degree angle with x marks, fitted observed line without x marks.

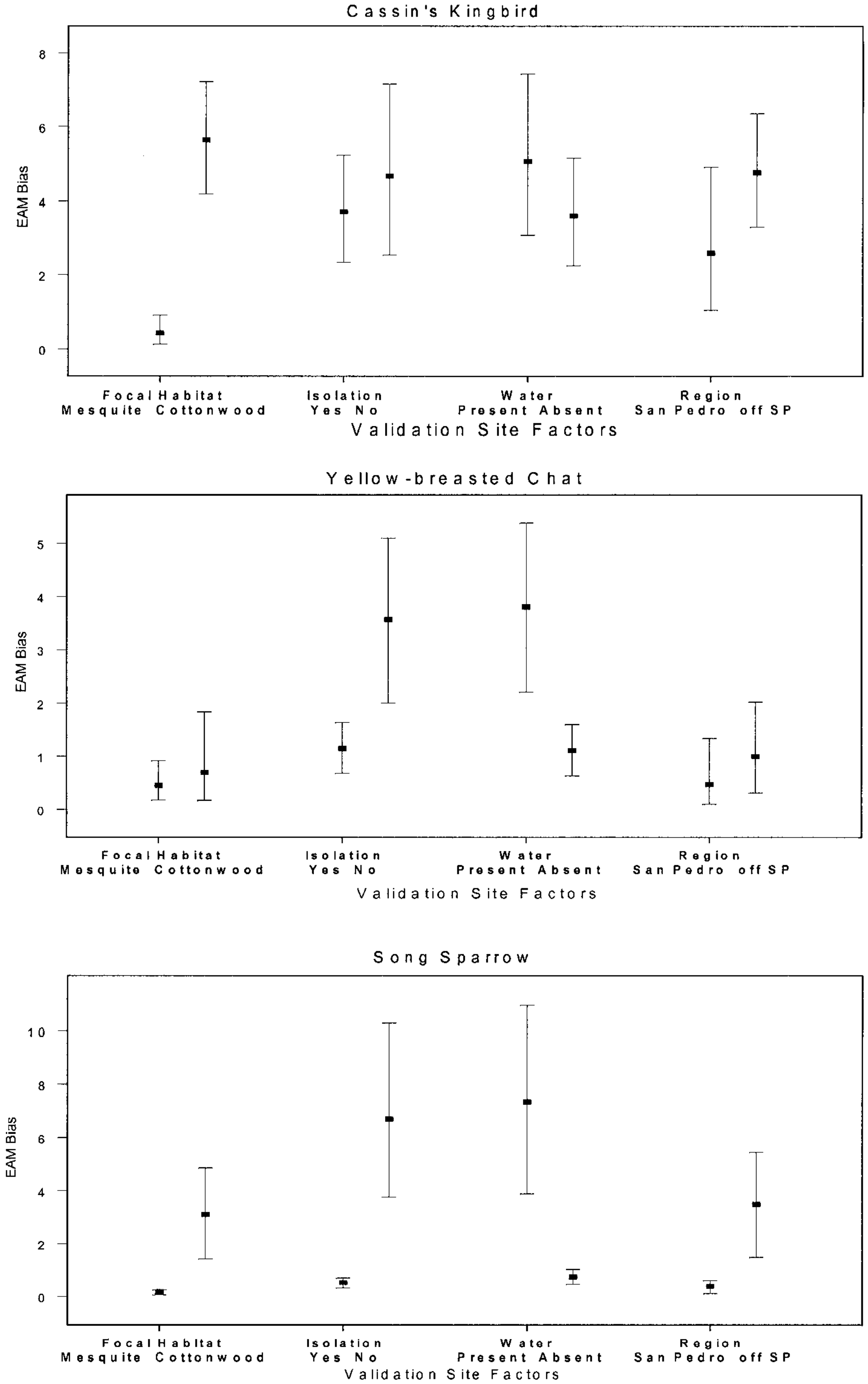


Figure 6. Mean absolute EAM bias with 95% percentile confidence interval for Cassin's Kingbird, Yellow-breasted Chat, and Song Sparrow as a function of four site level variables: focal habitat, isolation, presence of water, and region.

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	Best Model
ABTO	0.457	0.463	-0.005	-0.466	0.266	0.456	either
ATFL	0.404	0.462	-0.058	-0.214	0.086	0.187	either
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	either
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	either
GIWO	0.759	0.743	0.016	-0.127	0.159	0.385	either
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	either
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	either
SOSP	2.397	2.480	-0.083	-0.409	0.291	0.299	either
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

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

Table 3. Coefficient of determination (r^2•100) representing percent of variability explained in observed abundance as a function of EAM prediction alone and EAM prediction plus site-level variables for calibrated models by species.

Species	EAM [1]	EAM+ focal [1]	EAM + isolation[1]	EAM + region [1]	EAM+ water [1]	EAM+ all [1]
ABTO	0.7	6.5	2.9	** 20.2	1.0	* 25.6
ATFL	3.2	3.9	* 15.1	4.7	10.9	16.4
BCFL	1.0	*14.1	4.5	4.2	4.1	16.8
BEWR	*** 23.3	*** 27.2	*** 27.1	** 24.4	** 25.4	** 34.7
BHCO	1.0	3.0	1.4	1.4	2.4	10.3
BLGR	* 9.8	9.8	10.3	9.8	10.7	13.8
BTSP	*** 58.3	*** 61.4	*** 58.5	*** 59.3	*** 58.3	*** 61.7
BUOR	0.0	4.3	8.0	0.1	1.0	13.7
CAKI	*** 26.1	*** 35.4	*** 26.1	*** 26.3	*** 26.1	*** 37.0
COYE	5.7	9.9	*** 32.2	8.5	*** 40.8	*** 48.5
GIWO	*** 28.1	*** 28.1	*** 28.2	*** 28.2	*** 28.5	** 29.1
HOFI	0.4	3.7	0.6	8.4	4.5	10.9
LEGO	*** 27.5	*** 31.2	*** 28.1	*** 28.2	*** 27.8	** 32.4
LUWA	* 7.2	** 25.4	7.3	* 13.9	9.4	** 28.8
MODO	* 9.8	9.8	11.3	* 11.9	* 13.8	16.2
SOSP	*** 45.9	*** 52.0	*** 59.6	*** 46.2	*** 61.2	*** 67.5
SUTA	0.0	*** 36.8	*** 33.4	11.1	*** 34.3	*** 49.5
WWDO	5.0	5.1	5.4	7.6	* 12.5	19.4
YBCH	*** 29.9	*** 30.0	*** 64.7	*** 31.5	*** 67.8	*** 77.6
YWAR	*** 63.6	*** 66.4	*** 72.0	*** 63.6	*** 68.2	*** 73.1

[1] Coefficient of determination with model significance ($p < 0.05$) marked with single asterisk (*), $p < 0.01$ marked with double asterisk (**), and $p < 0.001$ marked with triple asterisk (***).