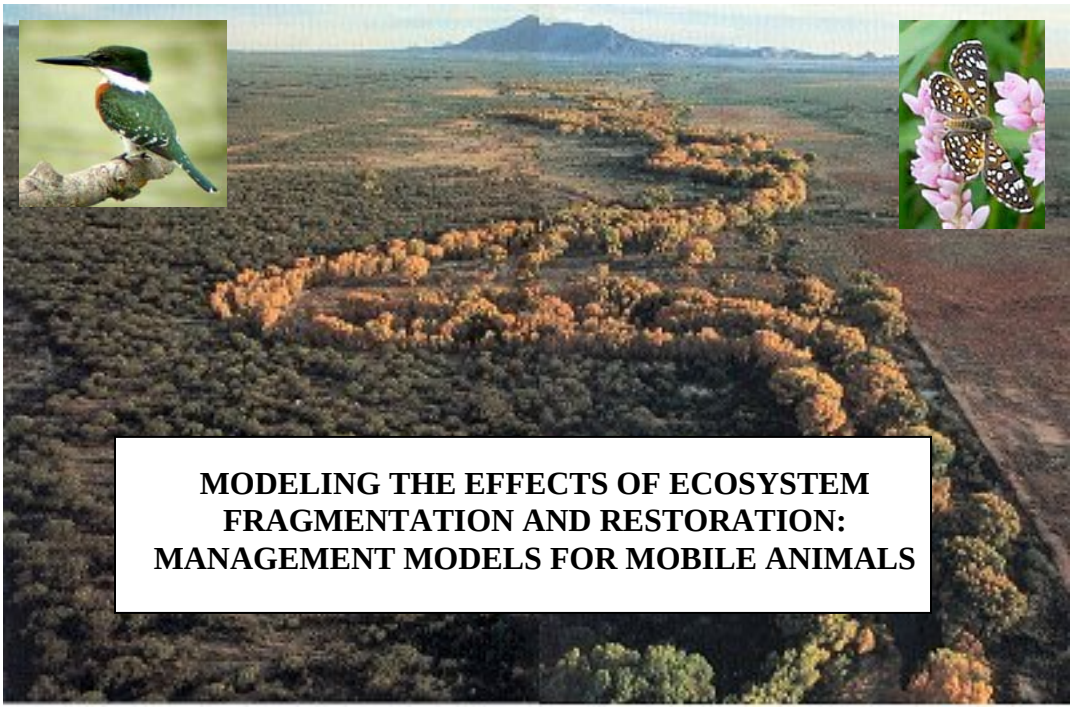
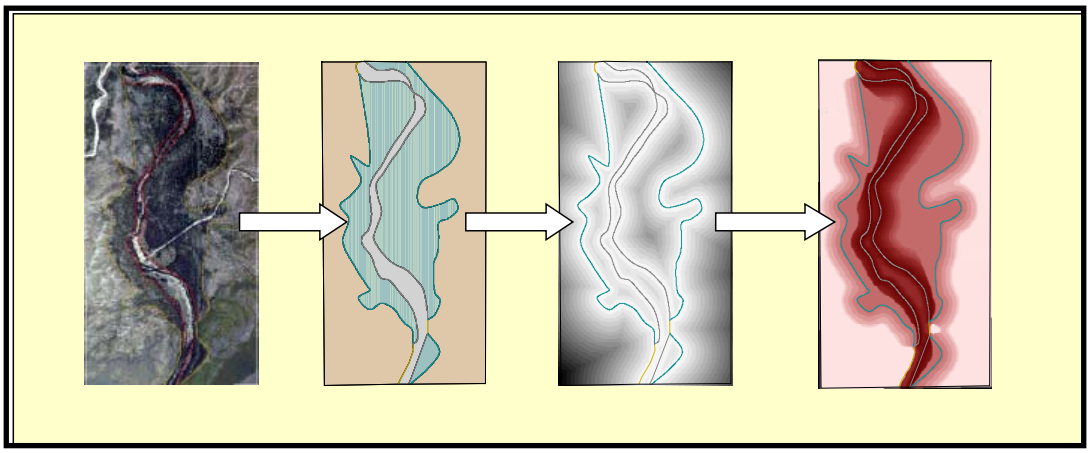
FINAL REPORT

SERDP PROJECT CS-1100



MODELING THE EFFECTS OF ECOSYSTEM FRAGMENTATION AND RESTORATION: MANAGEMENT MODELS FOR MOBILE ANIMALS



1 DECEMBER 2003

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INTRODUCTION: A PREDICTIVE FRAMEWORK FOR UNDERSTANDING EDGE EFFECTS

The detrimental effects of habitat fragmentation on animal populations are widely documented (Whitcomb et al. 1981, Robinson et al. 1995). However, the development of practical tools to predict the effects of fragmentation and design appropriate mitigation efforts has progressed slowly (Saunders et al. 1991, Wiens 1995). A predictive approach to assess the effects of habitat fragmentation is needed because sufficient time and/or resources are lacking to study each species in each habitat for which conservation decisions need to be made (Côté and Reynolds 2002, Lens et al. 2002). Current models typically apply average animal density values to thematic maps of vegetation or habitat. However, it is known that many animals avoid or exploit boundaries or "edges" between habitats. That is, the habitat adjacent to a focal habitat patch can influence its quality, which is sometimes referred to as the matrix effect (Forman and Godron 1988).

Despite hundreds of published articles documenting the effects of patch size and distance from edges on different taxa in various locations, no general relationship has emerged that will allow *a priori* predictions of a given species' expected abundance response. In order to be useful, fragmentation research needs to move beyond the simple description of the effects of fragmentation in each new landscape, toward a predictive capability that is applicable in many situations. The development of models that enable species-specific predictions should be parameterized with data that are relatively easy to obtain, so that the species most likely to be sensitive to fragmentation can be identified, predictions can be tested and evaluated quantitatively. Managers can then apply modeling tools in novel locations with reasonable confidence, and with an understanding of uncertainties in the modeling process. It is also critical for conservation planning to be able to extrapolate from specific edge responses to population parameters that describe the status of focal species at the landscape scale.

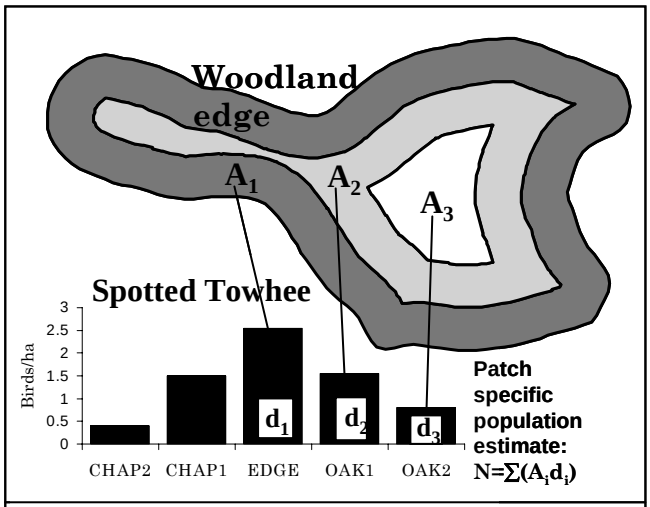


Figure 1. The Effective Area Model uses information about density responses at different distances from each unique edge type to estimate densities for each patch that are weighted by the influence of the surrounding habitat.

Until recently, the only method for including edges into landscape-level considerations was through "core-area" models (Laurence and Yensen 1991), which effectively removed edge zones from landscape maps and allowed the consideration only of so-called "core" areas that were assumed to be free of edge influence. However, these models are deficient because they are only applicable to extreme habitat specialists that avoid all habitat edges. In reality, most species show a variety of edge responses, including many that show higher abundances near some edges. In order to consider the full range of responses that a species may show to

the great variety of edges that exists in virtually all real landscapes, managers need a tool flexible enough to consider specific responses or each species of management interest.

The Effective Area Model (Sisk et al. 1997) offers a new, more comprehensive approach, based on the assumption that the quality of habitat within each patch may be influenced by the response that each species shows to bordering habitat (Fig. 1). Over the course of this project, we developed three successful modeling techniques and several new empirical approaches that, together, provide an integrated, predictive framework for evaluating landscape-level consequences of ecosystem fragmentation on mobile animal species. The centerpiece of this effort is the Effective Area Model (EAM), which uses empirically measured or modeled edge responses to predict animal abundances in complex landscapes. In this report, we summarize the various components of this edge effects "toolbox" that, together, provide a management-relevant ecological modeling capability for assessing the consequences of habitat fragmentation or landscape-scale changes resulting from alternative land management scenarios.

PROJECT OBJECTIVE: DEVELOPMENT OF A PRACTICAL TOOL FOR SUPPORTING MANAGERS OF FRAGMENTED ECOSYSTEMS

Our objective for this project was to develop the Effective Area Model into a practical tool that could be implemented tractably within real landscapes. We did this by developing the software necessary to implement the EAM using spatial data in the form of landscape maps. We also carried out an extensive field effort to develop the best ways of deriving rigorous ecological data for use in the EAM, as well as tested the predictions of the model. In this final report, we provide conceptual models, protocols for implementation, and statistical approaches for identifying the complex edge responses of diverse animal species in a manner that feeds into the EAM. We present several field validation tests of this modeling approach. Finally, we describe several applications of our modeling approach in real-world management situations. Our work provides the only tool currently available that can extrapolate edge responses to larger landscapes, and it provides managers with one approach for considering how different landscape structures, resulting from alternative decisions, can impact animal populations and ecological function in managed landscapes. The development and tests of our modeling approach were carried out in two distinct ecosystems on two taxa of conservation interest, birds and butterflies.

MODEL SYSTEMS

In order to ensure that our modeling approach is generally applicable, we developed and tested the EAM in two distinct systems, desert riparian habitat and higher elevation ponderosa pine forests undergoing restoration. While the EAM can be applied to virtually any taxonomic group or ecological variable of interest, our model parameterization efforts focused on birds and butterflies because these taxa represent diverse life histories and ecologies. Both taxa are highly mobile and, thus, able to respond rapidly to changes in habitat quality. Their vagility allows them to select habitats based on behavioral cues, rather than on limitations imposed by dispersal ability. Both groups are rich in species and easy to identify and survey in the field, and there is

abundant natural history information available to permit analysis of the links between habitat selection and life history traits (Sisk et al. 1997; Haddad and Baum 1999; Sisk and Haddad, 2002). Below, we describe in detail each of our model systems that were used to develop and test the EAM.

Birds and Butterflies on the San Pedro River

Riparian areas are a major reservoir of both plant and animal diversity in arid ecosystems (Naiman et al. 1993). The San Pedro is the last major, free-flowing river in Arizona and supports a diverse plant and animal community compared to the surrounding desert. It also supports one of the most diverse bird and butterfly communities in North America. The San Pedro originates in Sonora, Mexico and flows north into southeast Arizona (Fig. 2). It is located within a transition zone between Sonoran and Chihuahuan deserts and supports vegetation communities found in both ecotypes. The Nature Conservancy has declared the San Pedro riparian corridor one of the twelve "last great places of the western hemisphere" in terms of ecological diversity, and much of its course lies in a National Riparian Conservation Area. American Rivers, a non-profit group, listed the San Pedro fourth on its 1999 list of the top ten endangered American rivers. The main threats to the San Pedro River are groundwater pumping and urban sprawl (Stromberg et al. 1996), both of which are associated with the operation of Ft. Huachuca. This lead to protracted litigation and cross-boundary management initiatives involving the U.S. Army (1999 May 4, NY Times). In 1999, a bi-national initiative to preserve the San Pedro was announced by the then U.S. Secretary of the Interior.

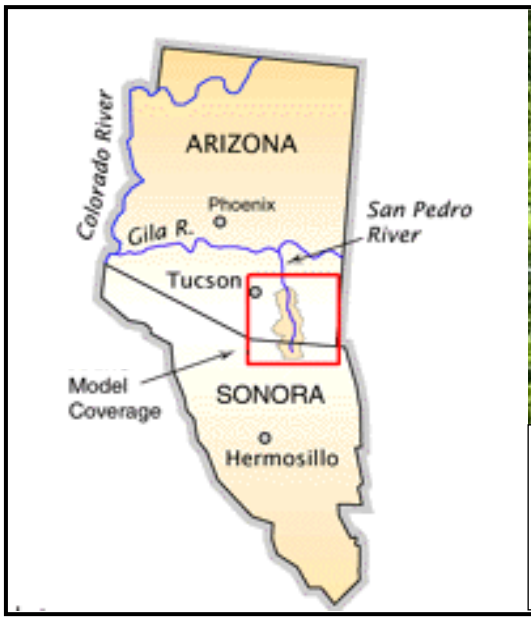


Figure 2. The San Pedro River in southeastern Arizona is an oasis of trees and grassland surrounded by desert.

The San Pedro River has undergone dramatic transformation since European settlement in the mid-1800s. At that time, the river was marshy, sinuous, and supported only scattered trees with some forested reaches (Stromberg 1998). Grazing and cultivation had become common by the early 1900s, and a combination of events at the turn of the century, including tree-removal and drought followed by a series of floods,

caused major stream incision and subsequent channelization (Stromberg et al. 1996). This created a two-tiered flood plain with primary and secondary zones dominated by different vegetation communities. Since the turn of the century, the vegetation structure has changed dramatically from a primarily open marsh/grassland to a highly heterogeneous landscape increasingly dominated by edges between wooded areas, scrub, and the remaining open habitat.

The primary flood plain is now characterized by gallery forests dominated by Fremont cottonwood (*Populus fremontii*), Gooding willow (*Salix goodingii*) and, in the middle reaches, exotic salt cedar (*Tamarix chinensis*). These gallery forests are highly variable in their degree of canopy closure, ranging from almost completely closed to primarily open habitat with a few, scattered trees. Between the primary floodplain and the surrounding desert scrub, there is an upland riparian zone that also exhibits a great deal of structural variation. This area ranges from completely open habitat to areas with mixed grass and mesquite (*Prosopis velutina*) to areas dominated by mesquite "bosques" (forests) with a closed canopy and tree heights of up to 5 m. These bosques often have large openings in the canopy, below which a more developed herbaceous layer is likely to develop. Surrounding these two zones of riparian vegetation is an expansive area dominated by desert scrub. It was the edges between these three habitat zones (Fig. 3) that were the focus of our modeling efforts. Water diversions, the major threat to riparian habitat in this region, tend to cause riparian habitat to become narrower and more fragmented. Both of these changes increase the amount of edge in the landscape, making it an appropriate system for development of the EAM.

Figure 3. Basic habitat structure of the San Pedro River. The riparian habitat is composed of a primary riparian zone dominated by cottonwood and willow, and an upland riparian zone dominated by grassland and mesquite. The riparian habitat is surrounded by expansive desert scrub.

Birds in a Post-Restoration Ponderosa Pine Forest

The Mt. Trumbull Resource Conservation Area in the Grand Canyon/Parashant National Monument served as our second model system (Fig. 4). Located just north of the Grand Canyon, approximately 120 miles northwest of Flagstaff, Arizona, the Mt. Trumbull area represents the first large-scale application of ecosystem restoration treatments in the ponderosa pine forest type (Friederici 2003a). Approximately 1,200 hectares of ponderosa pine (*Pinus ponderosa*) and ponderosa pine-Gambel oak (*Quercus gambeli*) forest, ranging from about 2050 to 2200 m in elevation, are slated for restoration at Mt. Trumbull (Friederici 2003b). Restoration treatments in dense forest stands are intended to return this fire-adapted ecosystem to conditions that will support frequent, low intensity ground fires, rather than the large, destructive crown fires that characterize recent burns in stands that have been subjected to a century of logging, overgrazing, and fire suppression. The tree thinning and prescribed burning used in restoration treatments creates a forest mosaic composed of dense stands of untreated forest and more open stands of restored forest, creating a high density of edges between the two stand types. Restoration treatments influence animal distributions and reproductive success in complex ways, and the goal of conserving sensitive, management-indicator species may conflict with ecosystem restoration goals, including the reduction of the threat of catastrophic wildfire. Because of the social imperative of reducing fire risk, and of protecting sensitive species in landscapes undergoing restoration treatments, the Mt. Trumbull area presents unique opportunities for addressing the linked issues of habitat fragmentation and ecosystem restoration, and their effects on bird species. Preliminary work at Camp Navajo, U. S. Army National Guard, focused on birds, butterflies, and microclimatic studies (see Appendix II), and set the stage for more involved experimental work. However, recurring delays in implementing planned forest restoration treatments at this installation in northern Arizona necessitated a shift of focus to Mt. Trumbull for the second half of the project period.

Figure 4. Photographs of untreated forest (left) and treated forest approximately 150 m away (right). Restoration treatment, including thinning and burning, was completed less than two years prior to the date on which the photograph was taken. Note the more open canopy and greater understory development that results from restoration treatment.

UNTREATED

TREATED

TECHNICAL APPROACH

Our project consisted of four distinct elements that are described in detail below. First, we developed the EAM from a conceptual model (Fig. 1) into a practical tool by creating an Arc View extension that allows users to implement the EAM within a GIS environment (Fig. 5). Then, we developed robust methods to parameterize the EAM both for situations where empirical data are available, and for situations where local field data are lacking. Next, we carried out three independent field tests of model predictions that evaluated the accuracy and applicability of the EAM in different ecosystems and for different taxa. Finally, we applied the EAM and associated modeling tools in real-world management situations on military installations and, in an expansion of this project, two spin-off efforts in our San Pedro River and ponderosa pine model systems.

PART 1: DEVELOPMENT OF THE EFFECTIVE AREA MODEL

The Effective Area Model (EAM) is a straightforward concept that combines field-based or modeled measures of species' responses to habitat edges with habitat maps derived from remotely sensed data. We developed this concept into a software package that is integrated into the ArcView GIS package and allows species-specific data on edge responses to be combined with habitat maps to project animal distributions across heterogeneous landscapes (Fig. 5). The integration of these different sources of information allows us to predict variations in animal abundance (or other relevant response variables) across heterogeneous landscapes, and to explicitly account for the spatial context of habitat patches. This method incorporates variability in response to landscape boundaries by relating multiple species' responses to a common, classified habitat map. The EAM can model a variety of ecological responses (e.g., density, reproductive success) that often vary with landscape heterogeneity. The association of the edge response functions with a detailed habitat map combines a simplified biological response, described in the response function, with the detailed spatial information available from remotely sensed data and GIS technology. Although complex habitat and animal responses are necessarily simplified to provide an avenue for practical use of this approach, we believe the EAM achieves the proper balance between model complexity and management utility. In order to demonstrate the structure of the EAM program and how it is used, we show how the model is implemented for one bird species in one section of the San Pedro River.

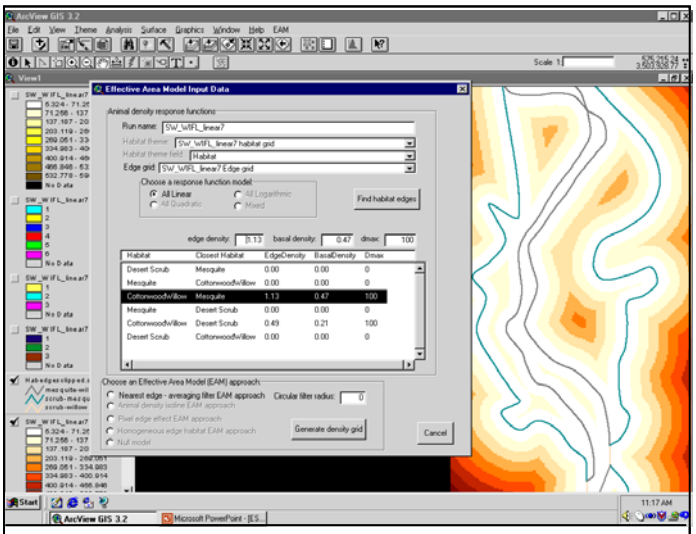
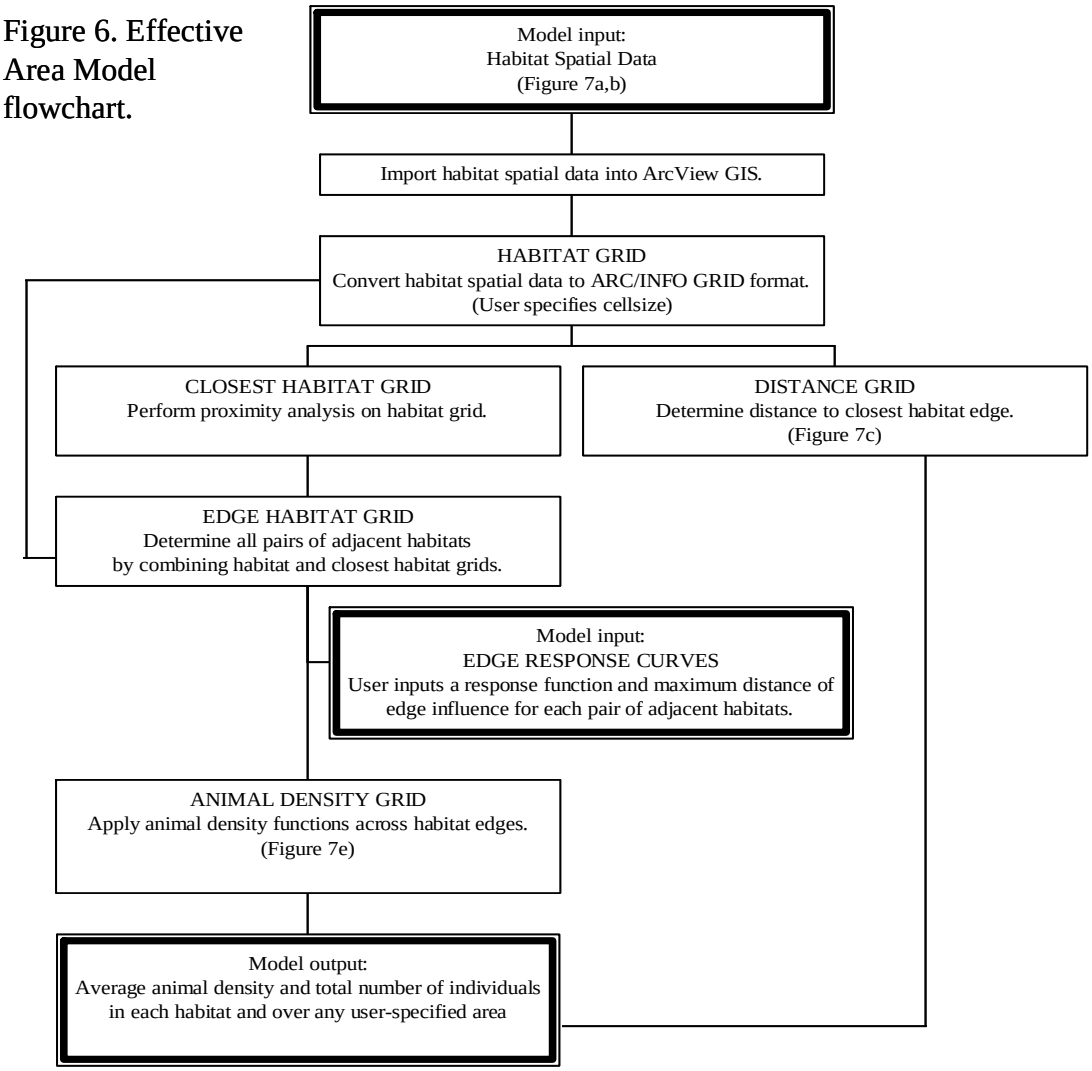


Figure 5. The Effective Area Model (EAM) in an ARC/View GIS framework

Model Structure and Implementation

The Effective Area Model is a raster-based spatial model. It creates a species-specific density grid by evaluating a species' response, relative to the nearest edge, for each pixel in the habitat map. The number of individuals in any region or habitat type can then be calculated by summing across cells in a particular habitat patch, or across the entire landscape. The model was developed for ArcView GIS (ESRI, Redlands, California) using the Spatial Analyst extension and Avenue scripting language. The current developmental version has been tested under ArcView 3.2 (Windows 95/98/NT). Rapid evolution of the ArcGIS environment has forestalled efforts to translate the developmental version of the key EAM software to the most recent GIS modeling platforms. Such efforts, which will necessitate structural changes and recoding to accommodate changing formats and handling procedures for spatial data, may be advisable in the future, following robust testing and evaluation of the EAM in applied management contexts.

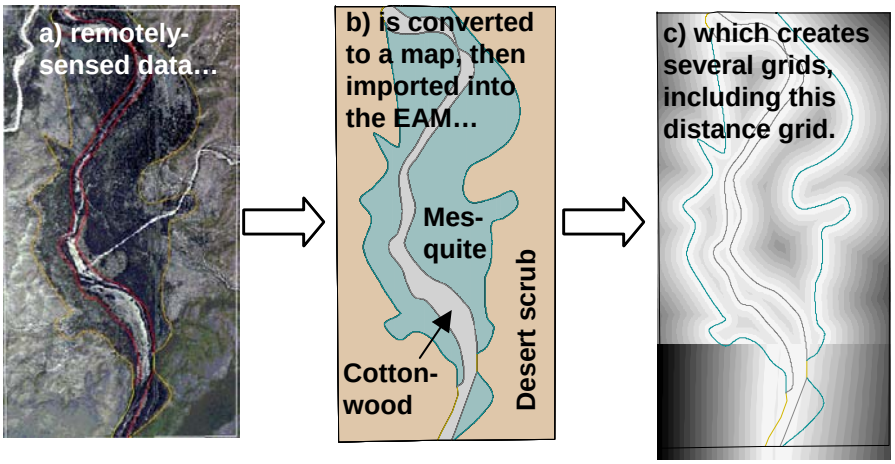
Figure 6. Effective Area Model flowchart.



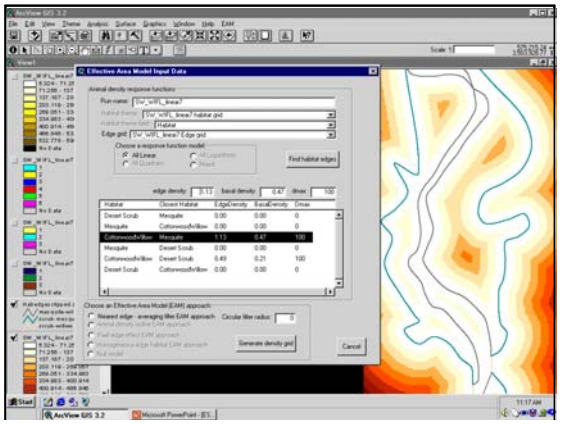
The EAM requires two classes of model input: a classified habitat map (the habitat spatial data must be an Arc/Info coverage, ArcView shapefile or Arc/Info GRID) and a characterization of each species' density response to habitat types and edges. The step-down process used for implementing the EAM is summarized in Figure 6. Running the EAM is a two-step process (due to the two types of input required for model implementation). These two steps are illustrated for one section of the San Pedro River in Figure 7. In the first step, the user imports a habitat map derived from remotely-sensed or field data (Fig. 7a,b). Two decisions are made at this point: (1) the resolution of the map in terms of the number of habitat types to recognize; and (2) the grid cell size of the map. In practice, these decisions are often constrained by data availability and the management objectives. It is important, however, that the resolution and minimum-

RUNNING THE EAM

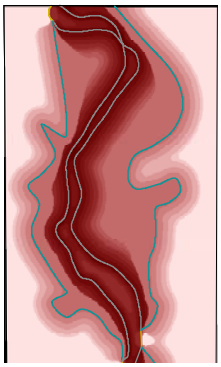
STEP 1: IMPORT SPATIAL DATA



STEP 2: ENTER MODEL PARAMETERS



d) The EAM identifies all unique edge types and the user enters species-specific values for each.



e) The EAM then creates an animal density grid and allows the user to summarize by patch or for the whole landscape.

Figure 7. An illustration of a single run of the EAM for a section of the San Pedro River. The process is described in more detail in the flowchart illustrated in Figure 6.

mapping unit be appropriate for the focal species with the finest-grained response to edge and matrix effects. After the map is imported, the EAM renders it into a series of three grid coverages (the distance grid is illustrated in Fig. 7c). In the second step, the EAM identifies every unique edge type in the landscape and prompts the user to enter parameters for a single species at all unique edge types (Fig. 7d).

In our example, there are four different edge types for which edge response data are necessary: 1) cottonwood adjacent to mesquite, 2) mesquite adjacent to cottonwood, 3) mesquite adjacent to desert scrub, and 4) desert scrub adjacent to mesquite. Methods to develop parameters used to enter into the model are described in detail in the next section of this report. The EAM takes these parameters and develops an animal density grid (Fig. 7e). The user can then output average animal densities and total number of individuals in each habitat patch or over any user-specified area. Our user's manual (Appendix I) contains a complete description of the EAM and how it is used.

Other features of the EAM

Including error in model predictions

Although many sources of error influence EAM output, we believe that the most important potential source of prediction error is in the empirical estimation of edge response functions. The EAM is currently programmed to incorporate estimates of error assuming that the dependent variable (e.g., animal density) is normally and independently distributed given any value of the explanatory variable (i.e. distance to the habitat edge) and calculates expected error based on several parameters entered by the user (see Appendix I). Another potential source of error comes from uncertainty in the habitat maps. However, using a modeling technique developed by A. King and colleagues (pers. comm.), we found that errors in spatial data had a relatively minor influence on model predictions. This approach employs Monte Carlo methods to sample from the digital habitat map, introducing alternative maps with known levels of mapping error. Our results suggested that empirical errors associated with the estimation of edge responses were much more important.

Dealing with multiple, converging habitat types

When three or more habitat types converge, there is a potential for multiple edge effects where a single point may be influenced by two or more edge types. The EAM allows the user to employ an averaging filter so that the influence of both edge types can be taken into account. If this filter is not employed, the EAM simply uses the closest edge to predict the density for each individual pixel. This issue of multiple converging edge types has received little theoretical attention, and no studies have measured the influences of multiple edges. Despite this paucity of data, multiple edges are a common feature of most landscapes. The EAM allows the user to use either of these two simple approaches to modeling the effects of multiple edges; greater sophistication will require additional basic research on this topic.

Removing noise from habitat maps

The EAM has the ability to smooth grid-based habitat maps by allowing the user to enter a minimum mapping unit. Any patches smaller than this mapping unit are effectively absorbed into the surrounding patch. This smoothing feature allows the user to ignore heterogeneity that occurs on a scale that their organism of interest may not respond to.

PART 2: PARAMETERIZING THE EFFECTIVE AREA MODEL

In order to predict distributional patterns across a landscape, the EAM requires values for a minimum of three parameters for each species at each unique edge type: animal densities at the edge, densities in the interior of the habitat, and the distance into the habitat that edge responses extend (henceforth referred to as D_{max}). This approach captures the threshold effect that is associated with edge-related functions (Toms and Lesperence 2003). The EAM also permits more complex approaches by allowing the use of non-linear functions that can describe complex mathematical relationships between the distance to the closest edge and the density of each species. However, most edge patterns described in the literature can be captured by the three fundamental parameters (edge density, interior density, D_{max}) so that most applications of the model would likely not require using the option to enter a non-linear formula. In all applications of the EAM carried out for this project, we used this basic linear approach because none of our extensive non-linear modeling efforts suggested that more complicated patterns were evident. However, the determination of D_{max}, as well as the magnitude of the difference between the edge and interior densities, is most rigorously determined through non-linear modeling, while the spatial structure incorporated into the design of most edge studies requires either random effects or repeated measures analysis. In this section, we describe our work to deal with both of these statistical issues. We also describe models that we developed to enable the parameterization of the EAM when local field data are unavailable.

Rigorous Methods to Derive Edge Response Functions

Although there is a vast literature describing the responses of a wide array of organisms to habitat edges, little work has been done on developing a rigorous method to describe those functions. Most studies report qualitative results, such as whether a species shows a positive or negative response to edges, and only rarely are magnitudes reported. Some studies report the distance that responses penetrate into habitat interiors, but these values are often based on visual inspection of the data and have little statistical support.

One possible reason that there has been little progress towards developing methods to rigorously describe edge response functions is that many studies have been focused solely on describing simply whether variables near the edge either increase or decrease. There are almost no examples in the literature of edge responses being used in a predictive modeling framework. Therefore, there may have been little reason for others to tackle this issue. However, most studies that have attempted to describe densities as a function of distance from the edge have used regression techniques. Regressions describe the relationship between a response variable (in this case, animal densities),

based on one or several predictor variables (in this case, distance from edge). In most cases, linear models are used for response functions because the regression methods are simple and there are several well-developed software packages that will perform very complex linear regressions that can include multiple variables.

Despite their widespread use, linear models are restrictive in that the functions are very inflexible and can take only a limited number of shapes. For edge responses, it is generally assumed that, at some distance from the edge, densities will level off, at which point some "interior" density has been reached. Most linear models do not allow a function to level off after reaching a maximum (or minimum) value. Non-linear models, on the other hand, can take a variety of shapes, and can be very flexible, allowing a researcher to describe a wide range of shapes with a single underlying model. However, non-linear regression is more difficult to implement, with fewer software options. In addition, parameter estimation in non-linear regression is much less straightforward, mathematically, than for linear models. Parameter estimates in linear regression are unbiased and always converge to the correct value. In contrast, parameter estimation in non-linear regression is biased and may converge on a local minimum, which will yield the wrong value. In order to deal with this problem, there has been a great deal of work done to identify non-linear models whose parameters exhibit "close-to-linear" behavior (Ratkowsky 1990). These models are generally "well behaved" but make the choice of appropriate non-linear models more complicated. Throughout the course of this project, we explored several different classes of non-linear models that seemed to be appropriate candidates, and found that piece-wise linear regression (a non-linear model despite its name) was the optimal approach because it allowed a clear identification of all three values that are needed to parameterize the EAM: edge density, interior density, and D_{max} (Fig. 8). A recent article in Ecology provided strong support for this approach by suggesting that piece-wise linear regression was an appropriate statistical method for determining the depth of edge influence (Toms and Lesperence 2003).

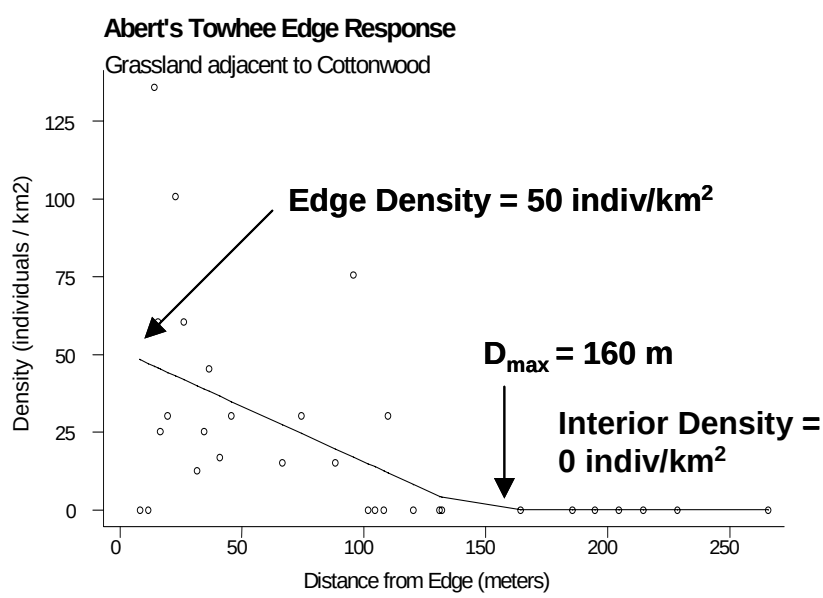


Figure 8. An example of how piece-wise linear regression is used to identify the three values needed to parameterize the EAM: edge density, interior density and D_{max}. This example presents results for one bird species at one edge type on the San Pedro River.

Another major statistical issue that we tackled while developing the best methods for EAM parameterization was dealing with the spatial structure of our data sets. Because edge response data are most commonly collected within plots along transects, which represent repeated measures along a non-independent sampling unit, most data sets violate a critical assumption of ordinary regression techniques, that of independence among data points (Diggle et al. 1994). Despite this, transects are still the optimal design for most edge studies because they reduce variability due to differences in habitat quality between sites, which can be substantial in ecological systems. In fact, another drawback of using ordinary regression is that there is no ability to partition the effect of site-to-site variability from variability due to the main effect of interest (in this case, distance from edge). Therefore, ordinary regression is not able to take advantage of the design of transect-based edge studies. In order to deal with these issues, it was necessary to use a statistical approach that not only did not assume spatial independence, but was able to take full advantage of our transect-based field designs and use the information on spatial structure to increase power to detect edge responses. This method, random-effects mixed models, proved to be a powerful tool for our data, and it should prove generally useful for the most commonly used design for edge studies. However, statistical tools that combine non-linear and random-effects mixed models are only beginning to become available. Therefore, we used non-linear modeling for some of our data (birds on the San Pedro River) and random-effects modeling for other data sets (butterflies on the San Pedro and birds in Ponderosa Pine). Although the tools needed to combine both statistical methods (non-linear and mixed models) were not readily available when we were developing our statistical approaches, we suspect that a combination of these two approaches will soon become the standard for edge response modeling, and it is a technique that we continue to pursue in our applications.

Predicting Edge Responses When Data are Lacking

In the face of rapid loss and fragmentation of habitat and limited research funding, there is not sufficient time or adequate resources to study each species in each habitat for which conservation decisions must be made. Often, managers are faced with complicated land management decisions, informed by little or no data. We therefore developed two separate approaches for using the EAM when field data are unavailable or limited. Both of these approaches utilize information that is widely available in the published literature to make predictions about which species are most likely to show positive, negative or neutral edge responses in specific landscapes. This information can be used by managers to explore whether edge responses are likely to play an important role in how individual species respond to different management decisions, and it can be used to focus future field efforts. Our first approach uses information on general habitat associations and resource distribution to predict likely edge responses for any species in any landscape. The second approach is more specific and capitalizes on the wealth of published data on bird responses to forest edges. It identifies specific life-history characteristics that are predictably associated with avian edge responses. For both approaches, we tested the predictive power of the model both by using results reported in the literature and carrying out intensive field efforts to test model predictions for birds and butterflies along the San Pedro River. The results of both model tests indicate that these approaches can provide

reasonable predictions of the most likely edge responses and can be used to make preliminary explorations of landscape-level changes and help guide managers in targeting scarce research dollars.

A General Habitat-Based Model

Edge responses that show the most consistency within the literature are often tied to species with strong habitat associations. For instance, two species that show very consistent edge responses are brown-headed cowbirds (*Moluthrus ater*) and ovenbirds (*Seiurus aurocapillus*). Ovenbirds are dependent on forest habitat, and they consistently show negative responses near the edge of non-preferred habitat. Brown-headed cowbirds forage in open habitat, but nest in forests. In this case, the resources in the open habitat complement resources in the forest habitat. Therefore, being near the boundary between these two habitats offers convenient access to both critical resources. In contrast, if two bordering habitats are both used by a species, but resources are equally available in both (so the resources in one habitat supplement the resources in the other), then an edge response isn't expected because being near the edge doesn't offer an advantage. Finally, in some cases, resources are known to be concentrated along the edge and increases have been shown for species dependent on those resources. An example is shrub dependent birds being found near forest edges that develop a shrub layer absent or rare in either bordering habitat. These four situations are illustrated in Figure 9. When nothing is known about a species' edge response at a particular edge type, this model can be used to identify species that are most likely to show a particular type of response. To apply this model, the only information needed is the species' habitat associations in each bordering habitat type, as well as information about the distribution of their principal resources.

We performed two tests of this model. The first used the model to make predictions for 60 species of birds at forest edges, and then tested those predictions based on observed edge responses in three published studies (see Appendix VIIg for a full description of the model and test). The model performed well, with 83% of the observed edge responses in the predicted direction ($p < 0.0001$). A much more detailed test of the model was performed on 15 butterfly species at 12 edge types on the San Pedro River (see Appendix VIIh for a full description of this field test). The model performed well in this test also, with 70% of the observed edge responses in the predicted direction ($p = 0.01$), although model performance varied by habitat type and species. For both the bird and butterfly tests, the vast majority of unexplained variation was derived from the observation of unpredicted neutral responses, suggesting that greater understanding of responses will require more detailed knowledge of conditions under which predicted edge responses are weak or not operative.

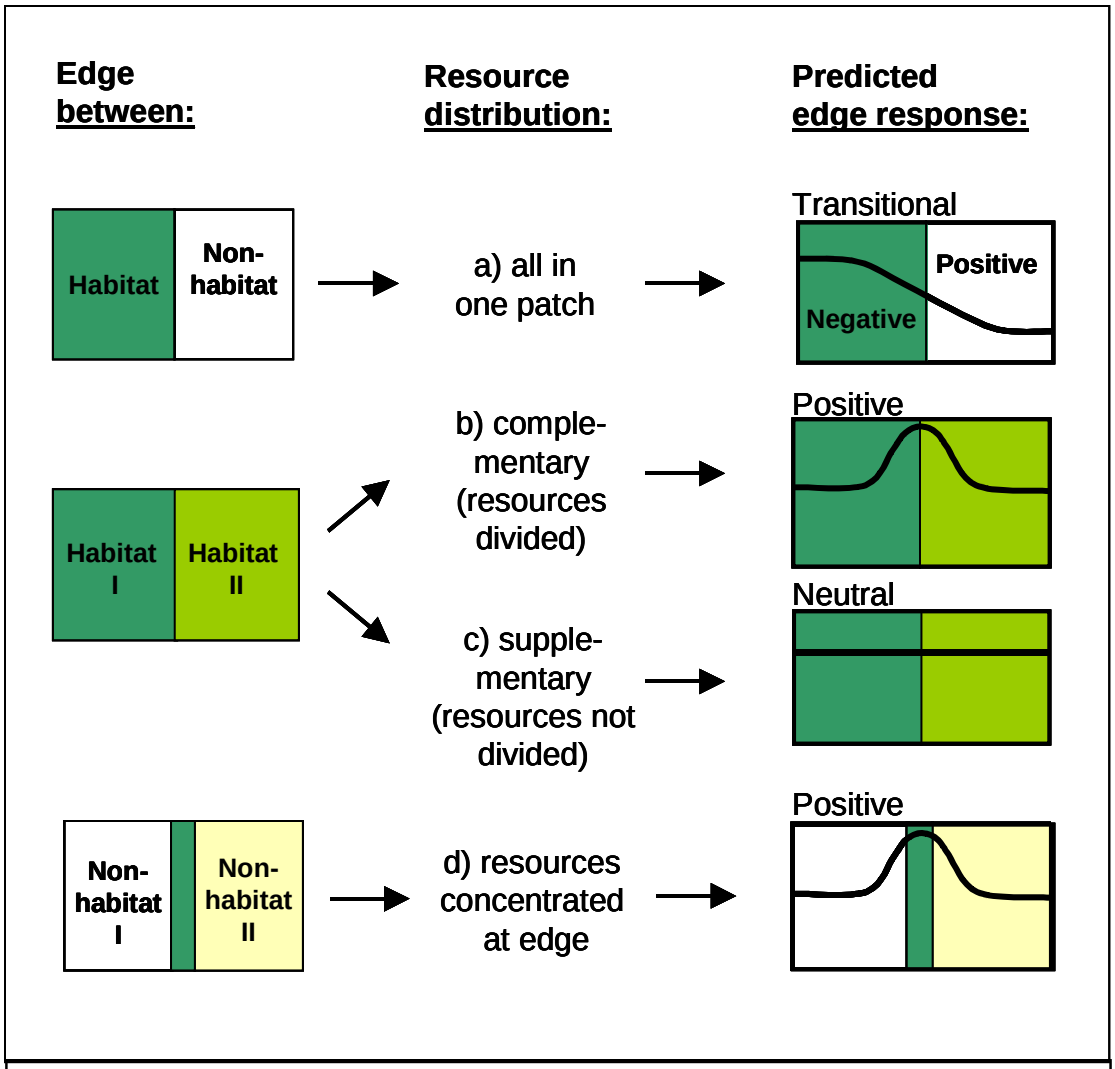


Figure 9. A general model of edge effects for any species at any edge type based on habitat associations and resource distribution.

A Life-History Model for Birds

In order to take advantage of the decades of published studies on avian responses to habitat edges in forested landscapes, we conducted a literature review and performed a meta-analysis to identify species-specific ecological and life-history traits that may allow *a priori* predictions of edge responses. From the published literature, a database was developed for avian edge responses 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 using Akaike's Information Criterion adjusted for small sample sizes (AICc), and the best

model in each set was used to predict whether birds should show increases or decreases near forest edges. 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 the prediction of the edge responses of previously unstudied species in a wide range of habitat types and regions. To internally validate the predictive edge models, an analysis was used to compare observed versus predicted edge responses by calculating the percentage correctly classified. Development of these predictive models is detailed in Appendix VIId.

The predictive models for negative edge responses at forest-open edges indicated that species were significantly more likely to have a negative edge response if they utilized mesic forest habitat, had longer incubation and nesting periods, had lower ecological plasticity, and had smaller body mass ($p < 0.05$). Species were significantly more likely to have a positive edge response if they utilized open habitat or both forest and open habitat, were shrub-nesters, had shorter nesting and incubation period, and were omnivorous ($p < 0.05$). In open-forest edge types, a negative edge response was significantly more likely for lower-nesting birds and for birds that utilized primarily open habitats in non-agricultural landscapes. A positive edge response was significantly more likely for birds that nested higher on average, had larger lifetime reproductive output, and utilized forest habitat or both forest and open habitats in agricultural landscapes ($p < 0.05$). Analyses showed that the percent of observations correctly classified by positive and negative edge predictive models ranged from 74-78% for the forest-open models and between 82-89% for the open-forest models. These results indicate that the models were highly successful in predicting edge responses (see Appendix VIId for detailed results). An independent field test of this model was carried out using bird responses to edges along the San Pedro River (results are detailed in Appendix VIIe). Of the 16 edge response/edge type combinations, this predictive model performed very well in 7 cases (80-96% correct classification), well in 4 cases (64-76% correct classification) and poorly in five cases (29-55% correct classification).

PART 3: TESTS OF THE EFFECTIVE AREA MODEL

As part of this extensive effort to develop new tools for examining edge effects and their role in habitat fragmentation, we devised a series of field tests of the predictions of the EAM. In each of three tests, described in detail below, we followed the same general procedure, we: 1) located several independent test sites, 2) created maps of those test sites that could be imported into the EAM, 3) parameterized the EAM using our measured edge response functions from our model systems (San Pedro River and Mt. Trumbull), 4) generated predictions from the EAM for each independent test site, 5) generated predictions from a null model that ignored edge effects and patch context, 6) measured actual animal densities at each test site, and 7) compared measured densities to those predicted by the EAM and null models to determine which model made better predictions. This null model is analogous to many traditional habitat models that ignore spatial context and assume a uniform distribution within each patch based on habitat type alone. Cases where the EAM outperforms the null model indicate situations where including information on edge responses will be valuable for ecological understanding and management decisions.

Testing the EAM with Birds on the San Pedro River

A complete description of the design, results, and conclusions of this test are found in Appendix VIIf. A total of 50 sites located from within 1 km of the San Pedro River to over 50 km away were used to evaluate the predictive performance of the EAM relative to the null model. Test sites consisted of cottonwood surrounded by mesquite or mesquite surrounded by desert scrub. The predicted abundances of 25 species of birds in 50 validation sites were estimated for both the EAM and null models by utilizing habitat maps developed for each validation site and edge response functions developed in the model parameterization phase for birds on the San Pedro River. Distance sampling was used to estimate abundances for each species in each of the 50 sites. Relative performance of the EAM and null models was assessed by comparing the relative bias between observed and predicted densities, using a bootstrap methodology to test the hypothesis that mean absolute bias for the null is greater than the EAM (i.e. the EAM performs better). Sites were also subsetted by focal habitat, isolation, presence of water, and region to ascertain whether these site-level variables may be affecting the ability of the EAM or null model to predict relative abundance in validation sites that are different from those in which the models were parameterized. The EAM bias was investigated by itself (not in reference to the null model) as a function of the four site-level variables. If the bias was higher in one focal habitat than another, then an additional offset pertaining to site-level variables (such as isolated vs. not isolated) may improve predictions in future refinement of the EAM.

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

Species	Null Bias	EAM Bias	Δ Bias (Null-EAM)	Δ Bias 95% LCL	Δ Bias 95% UCL	P-value	Best Model
ABTO	0.457	0.463	-0.005	-0.466	0.266	0.456	neither
ATFL	0.404	0.462	-0.058	-0.214	0.086	0.187	neither
BCFL	1.776	1.646	0.130	0.105	0.151	0.001	**EAM**
BEWR	0.738	0.591	0.147	-0.103	0.224	0.103	neither
BHCO	1.021	0.852	0.169	0.079	0.257	0.005	**EAM**
BLGR	0.586	0.459	0.126	0.085	0.163	0.000	**EAM**
BTSP	0.197	0.425	-0.228	-0.321	-0.002	0.022	**NULL**
BUOR	0.757	0.529	0.228	0.072	0.272	0.007	**EAM**
CAKI	4.134	3.979	0.155	0.100	0.221	0.000	**EAM**
COYE	1.188	1.123	0.064	-0.029	0.164	0.089	neither
GIWO	0.759	0.743	0.016	-0.127	0.159	0.385	neither
HOFI	0.777	0.568	0.210	0.158	0.252	0.000	**EAM**
LEGO	1.127	1.146	-0.019	-0.098	0.059	0.309	neither
LUWA	3.490	2.152	1.339	1.013	1.693	0.000	**EAM**
MODO	0.622	0.614	0.008	-0.013	0.030	0.234	neither
SOSP	2.397	2.480	-0.083	-0.409	0.291	0.299	neither
SUTA	0.177	0.650	-0.473	-0.530	-0.134	0.005	**NULL**
WWDO	0.566	0.467	0.099	0.069	0.131	0.000	**EAM**

YBCH	1.312	0.568	0.743	-0.068	0.989	0.030	**EAM**
YWAR	1.752	1.601	0.151	-0.031	0.379	0.053	**EAM**

It was possible to discern a significant difference ($p < 0.05$) in terms of the relative performance of the EAM and null models for 12 of 20 species. Of the 12 species, the EAM performed better than the null for 10 species, and the null performed better than the EAM for 2 species. As an overall assessment, the EAM outperformed the null for 83.3 % of species for which it was possible to discern a difference when considering all validation sites (Table 1). When comparing the performance of the EAM and null model separately for subsets of the site-level variables, the EAM still generally outperformed the null model across species and validation sites. When evaluating the site-level variables, the EAM showed better predictions, relative to the null model, in cottonwood focal habitat versus mesquite focal habitat (79% versus 67%), isolated versus non-isolated patches (91% versus 60%), and in sites where water was absent versus present (91% versus 60%) (Table 2).

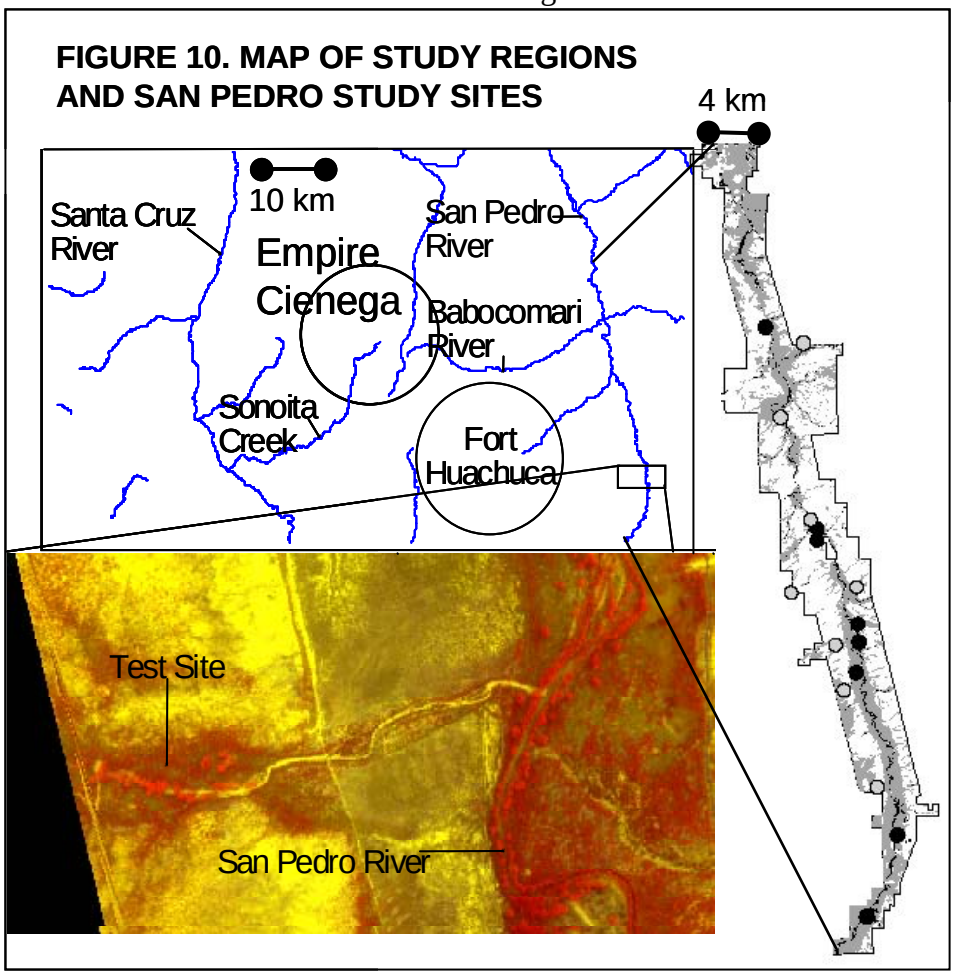
Table 2. Comparison of EAM and null model relative performance by site-level variables

Subsetting Factors	Number of Sites	EAM better prediction	NULL better prediction	% EAM better prediction
Isolation				
Contiguous	36	6	4	60.0
Isolated	14	10	1	90.9
Water				
Present	13	6	4	60.0
Absent	37	10	1	90.9
Focal habitat				
Cottonwood/deciduous	34	11	3	78.6
Mesquite	16	4	2	66.7
Region				
San Pedro	18	4	1	80.0
Off -San Pedro	32	8	2	80.0
All Sites				
	50	10	2	83.3

There was no difference based on regions in terms of the percentage of species for which the EAM outperformed the null. To assess whether it may be possible to decrease the bias of the EAM by incorporating additional site-level variables, we found that 9 of the 20 species showed a significant difference in the EAM bias as a function of one or more of the four site-level variables (focal habitat, isolation, presence of water, and region). These results indicate that bias was higher for certain species based on one or more site-level variables, so that an additional offsets pertaining to these site-level variables may improve predictions for certain species in future refinements of the EAM.

Testing the Model with Butterflies on the San Pedro River

A complete description of the design, results, and conclusions for this model test are found in Appendix VIIi. We established three types of test patches in order to assess the general ability of the EAM to predict distributions across landscapes. The three patch types were: cottonwood surrounded by mesquite (CW), mesquite surrounded by desert scrub (MES-DS), and mesquite with one side bordered by cottonwood and one side bordered by desert scrub (MES-CW/DS). Multiple patches were set up in three regions that were increasingly distant from the San Pedro, the source of the data used for parameterization of the models. The three regions were 1) On or near the San Pedro, 2) Ft. Huachuca, a military base approximately 14 km from the San Pedro, and 3) Empire Cienega, a National Conservation Area approximately 40 km from the San Pedro. The location of the three regions, the location of study sites along the San Pedro, and an aerial image of one of the test sites are illustrated in Figure 10.



A total of 14 test sites were established in 2000 and 38 in 2001. Parameters were developed for 8 butterfly species for the 2000 field season 11 butterfly species for the 2001 field season, and these were used to generate predictions using the EAM (Table 3). Due to the fact that a linear approach was used (see Part 2), we were unable to designate D_{max} based on our data and, instead, used 50 m as D_{max} for all species at all edge types. Although not ideal, the fact that all of our 38 test patches were less than 100 m in width

meant that, in practice, D_{max} was never reached. In addition, because our transects were at least 50 m in length, we never extrapolated past the extent of our field data. We used the EAM to generate predictions separately for 2000 and 2001 based on the parameters in Table 3. We then compared measured densities to the predictions of the EAM, as well as the densities predicted if edge responses were not taken into account (the null model). For each comparison, we classified the outcome in one of four ways: 1) the EAM's prediction was closer (EAM), 2) the null model was closer (NULL), 3) the models were indistinguishable (TIE), or 4) neither model was close in its predictions (NEITHER). Details on how these designations were made are provided in Appendix VIIi.

In evaluating the performance of the EAM, we looked at each butterfly species in each patch in each year separately. Based on the number of observed edge responses, we had 253 separate opportunities to compare the predictions of the EAM and null models across all species and in all model-testing sites, over two years.

Table 3. Parameter values for the EAM based on edge response functions calculated from field data collected along the San Pedro River. Significant edge responses were identified with regressions (Reg) and T-tests. Parameters are described for cottonwood sites, and mesquite sites near desert scrub (DS) and cottonwood (CW). The null model parameters are also shown and are the same as the interior values for the EAM.

		Cottonwood sites			Mesquite sites							
		Test	Parameters		Tests			Parameters				
Species	Year	Reg	Edge	Interior (Null)	Reg (CW)	Reg (DS)	T-test	Edge (CW)	Interior (CW)	Interior (DS)	Edge (DS)	Null
Battus philenor	2001				*			0.15	0.05	0.05	0.05	0.05
Brephidium exilis	2001				**			0	0.46	0.46	0.46	0.46
Chlosyne lacinia	2001	*	0	0.17								
Colias cesonia	2000	**	0	0.08		**		0	0	0	0.09	0
Colias eurytheme	2001	*	0.04	0.56			**	0.19	0.19	0.02	0.02	0.1
Euptoieta claudia	2000				*			0	0.1	0.1	0.1	0.1
Eurema mexicanum	2000				*			0	0.1	0.1	0.1	0.1
	2001				*			0.1	0.03	0.03	0.03	0.03
Eurema proterpia	2000				**			0.15	2.56	2.56	2.56	2.56
	2001	*	0.08	0	**			0.22	0.07	0.07	0.07	0.07
Libytheana carinenta	2000				*	*		0.02	0.21	0	0.27	0.11
	2001					*		0	0	0	0.08	0
Liminitis archippus	2000	**	0	0.1								
	2001	*	0.06	0								
Phoebis sennae	2000	**	0	0.59	*			0.63	0.34	0.34	0.34	0.34
	2001				**		*	0.37	0.14	0	0	0.07
Pholisorus catullus	2001				*			0.22	0.08	0.08	0.08	0.08
Pieris protodice	2001	*	0.25	0.75	***		*	0.55	4.01	9.34	9.34	6.68
Pyrgus communis	2000				**	*		0	0.14	0.26	0	0.2

In general, the predictions of the EAM and null models were distinguishable, with TIES being called in only 48 cases (19%). Neither model was able to predict the outcome in 19 cases, leaving 186 opportunities to directly compare the predictions of the EAM and null models with values observed in the field. In 2001, the EAM outperformed

Table 4. Comparisons of EAM and null model predictions with field data. Values reflect, for 14 butterfly species at three types of test sites, the number of times each model predicted values that were closest to observed values. There were two types of mesquite test sites, one surrounded solely by desert scrub (MES-DS) and one with desert scrub on one border and cottonwood on the other (MES-CW/DS).

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

the null in the primary riparian habitats dominated by cottonwood and willow ($p < 0.001$). There were no significant differences in the other test site types, although the EAM performed marginally better in MES-CW/DS patch types in 2000, while the null model performed marginally better in MES-DS patch types in 2000. The number of times that predictions of the EAM or NULL models were closer to the actual values for each butterfly species, in each of the 3 patch types in 2000 and 2001, is detailed in Table 4. There was no indication that model performance was better in sites closer to locations where data were collected to parameterize the models. The EAM performed equally or marginally better in all three regions (San Pedro sites, Ft. Huachuca, and Empire Cienega), with the best proportional performance occurring at the most distant test region (Empire Cienega).

For butterflies in desert riparian habitat, the inclusion of edge responses in predictions of landscape-level densities resulted in improved predictions only in

cottonwood patches. The model also clearly performed better for some species than for others (see Table 4). Based on our results, we believe that there were three factors that led to variability in model performance. The first was site-to-site variability, which is substantial for butterflies. For future applications of the model in this context, it may be useful to include variables related to overall habitat quality in each of the patches. This would allow the user to adjust predictions up or down, and may allow some of the natural ecological variability to be filtered out. The second factor was the variable expression of edge responses. Although known to be variable, the results of our modeling work suggest that edge responses of the same species to different instances of the same edge type rarely show both positive and negative responses. Instead, edge responses are stronger (and more likely to be detected) in some situations than in others. Determining the factors that underlie this type of variability is a key challenge to improved understanding of edge responses. However, because edge responses that are expressed are usually in a consistent direction, when integrated over large areas or time frames, the impacts of fragmentation are likely to be predictable. Finally, when extrapolating edge responses to complex landscapes, it is necessary to consider the influence of the complex geometry of the patch, including convergent and multiple edge responses. Although the EAM, as currently coded, allows for an averaging filter that can take into account multiple, converging edge types, the linear structure of the habitat in this landscape was such that habitats rarely converged (although they were in close proximity), so this function could not be fully utilized. A species-by-species examination of these factors (detailed in Appendix VIIi), suggests that different species may respond consistently to these factors, so they may be tractably included in future versions of the EAM, pending sufficient advances in empirical work on this subject. Overall, the results of this study suggest that extrapolating edge responses to the landscape level, for mobile invertebrates such as butterflies, worked best in the simpler landscapes. This suggests that additional research on responses to complex landscape geometry will likely lead to improvements over the current model. However, the consistent and predictable direction of edge responses, when they are observed, indicates that over large spatial and temporal scales, the EAM is likely a valuable improvement over current approaches that ignore these factors.

Testing the Model with Birds in Ponderosa Pine Forests

A complete description of the design, results, and conclusions for this model test are found in Appendix VIIc. We tested the predictions of the EAM against a null model that did not include edge effects in areas undergoing restoration-like forestry treatments. We measured edge effects on the abundances of the eleven most frequently observed bird species at the Mt. Trumbull Resource Conservation Area, where forest restoration treatments are currently being implemented. We used the edge responses measured at Mount Trumbull to parameterize the EAM (Table 5).

We tested the model at two sites: the Kaibab Plateau and the Fort Valley Experimental Forest. To test the model, we measured the abundances of our eleven target species in seedtree cuts (Kaibab) and restoration areas (Fort Valley) and compared observed bird densities to those predicted by the model. In general, both the EAM and the null models fared poorly at predicting animal abundances at our model test sites.

There was considerable between-site variation in model performance. The EAM and the null model performed equally poorly at the Fort Valley site. At the Kaibab site, both models fit the observed data better than at Fort Valley, but it was unclear which model performed better. In 2000, the EAM was marginally better than the null, but in 2001, the opposite was true. Between-year variability in model fit was greater than between-model variation within a year.

Table 5. Relative abundances of each bird species used in model tests at edge and interior. These are the values that were used as model parameters for the test of the Effective Area Model.

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

We conclude that, due to a lack of suitable model test sites, we were unable to develop a robust test of the EAM for ponderosa pine forest restoration. We chose the best sites available for model testing, but large difference between Mt. Trumbull (our model development site) and our two model test sites in habitat type, treatment type and age, and/or local bird community structure caused site-specific factors to overwhelm the possible benefits of including edge effects in our model. We continue to believe that the inclusion of edge effects is likely to improve our predictions of bird community responses to restoration and suggest that, because birds appear to show a stronger response to habitat edges in untreated areas, a greater emphasis should be placed on modeling edge effects in this habitat type.

A Summary of the Tests

The results of our three tests are summarized in Table 6. Although it was often not possible to distinguish the predictions of the EAM and NULL models, when there was a difference, the EAM always outperformed the null (Table 6). One overarching comment bears on the difficulty of appropriate testing. The EAM is intended to help managers assess the effects of alternative management decisions, and thus it is designed to predict the effects of management actions on multiple species in a particular landscape.

Table 6. Summary of outcomes for three tests of the EAM	
	Outcome
Birds on the San Pedro	
Cottonwood	EAM
Mesquite	EAM
Butterflies on the San Pedro	
Cottonwood	EAM
Mesquite (DS)	TIE
Mesquite (CW/DS)	TIE
Birds in Ponderosa Pine	
Kaibab forest	NEITHER
Ft. Valley	TIE

However, testing of this model could not await the completion of the management decision process, implementation of the resulting plan, and monitoring of the actual results of management actions. Instead, we substituted space for time in conducting these tests, by generating model predictions, and then collecting field data, at numerous *independent* sites previously influenced by different land uses. This approach provided the opportunity to test the EAM against the appropriate null models; however, it also introduced significant site-to-site variation that is not incorporated into the EAM modeling process. While we did our best to select test sites that resembled areas where models were developed, we nevertheless introduced considerable "noise" into the predictive process, and the results of the tests should, therefore, be considered very conservative assessments of model performance. When one model consistently outperformed the other, this should be considered strong support for that approach. In cases where the models are indistinguishable, this is more likely indicative of problems caused by the inherent variability of ecological systems, rather than failure of the model, *per se*. While the EAM was an improvement over the null model in a subset of our tests, the null model was never a clear improvement over the EAM.

In the case of birds in desert riparian habitats, the EAM did very well. For butterflies in the same habitat types, results were ambiguous in all but the primary riparian habitats dominated by cottonwoods and willows. These differences may be attributed, in part, to the overall superior understanding of avian habitat relations, due to decades of concentrated field research. The vagility and fine-grained habitat specificity of butterflies may also make this taxon more difficult to model with spatial data derived from remotely sensed sources (for example, herbaceous host plants may vary at scales not captured in the available imagery). Finally, we were unable to identify appropriate sites to test predictions for birds in fragmented ponderosa pine habitats. This case illustrates the difficulty in assessing the accuracy of landscape-scale models with data from plots distant in space and different in many subtle ways from the model-building sites.

In summary, when the predictions of the EAM and null models were clearly distinguishable, the EAM always outperformed the null model. Site-to-site variation and even species-specific differences suggest specific areas where the EAM could be improved. The EAM performed best in those cases where test sites corresponded most closely to model-building sites, and for taxa that are well studied. Ultimately, the most meaningful tests of the EAM will occur in cases where specific focal habitats are altered by management actions, and monitoring data can be used to assess before-and-after effects and compare them to model predictions. Such robust evaluations are possible at sites where the EAM has been used to assess real-world management scenarios, such as in efforts currently underway at Ft. Hood and Ft. Benning, and along the course of the San Pedro River, near Ft. Huachuca.

Decades of study support the importance of edge responses in understanding fragmentation impacts. Our efforts to predict edge responses show that, when edge responses are observed, they are consistent. This suggests that over large spatial and time scales, the landscape-level impacts of edge responses are likely to occur in a predictable manner. Currently, the EAM is the only tool available to extrapolate known edge responses to predict landscape-level effects. Although the results of our tests indicate that continued development of the model would be valuable, in its current form it offers a valuable improvement over traditional models that ignore edge effects. Although applications to poorly studied regions or taxa should be undertaken with caution, our results suggest that real-world applications are justified for well studied species in landscapes where fragmentation is pronounced and the resulting habitat mosaic is composed of relatively discrete habitat patches separated by relatively abrupt edges.

PART 4: MANAGEMENT APPLICATIONS OF THE EFFECTIVE AREA MODEL

This section describes real-world applications of the EAM in management situations. In all of these examples, we take an approach that models several alternative management decisions. Maps are developed that reflect landscape structures that are expected to result from different management or land-use plans. We then parameterize the EAM using data from a variety of different sources and use the EAM as a tool to explore the potential ecological consequences of different management decisions. Our first major use of the EAM was for a demonstration project requested by SERDP to show how the model could be applied to assess the impacts of training exercises on military lands. We are also currently engaged in two collaborative projects that are direct spin-offs of our SERDP-supported efforts, one focused on the San Pedro River, and the other on forest restoration efforts in Ponderosa Pine ecosystems in Arizona and New Mexico.

EAM Demonstration for Military Land Management

In order to demonstrate the utility of the EAM for military land management, we carried out collaborative applications of our approach on two military bases, Ft. Hood in central Texas and Ft. Benning in Georgia. On both bases, we explored how the EAM could be used to inform two types of management issues. The first explored how military activity, specifically tank maneuver exercises, could be balanced with conservation. The second explored how targeting specific areas for restoration to meet endangered species management goals could be carried out in a way that maximizes benefits for the larger ecological community. For both questions on both bases, we developed maps that reflected how landscapes might look in the future, based on different management scenarios. We then used the EAM to explore the ecological consequences of those decisions. Here, we briefly summarize our progress to date on each base. Results for each modeling exercise on each base will be detailed in a separate report for this extension of the larger SERDP project, to be submitted once these efforts are complete.

Ft. Benning Project

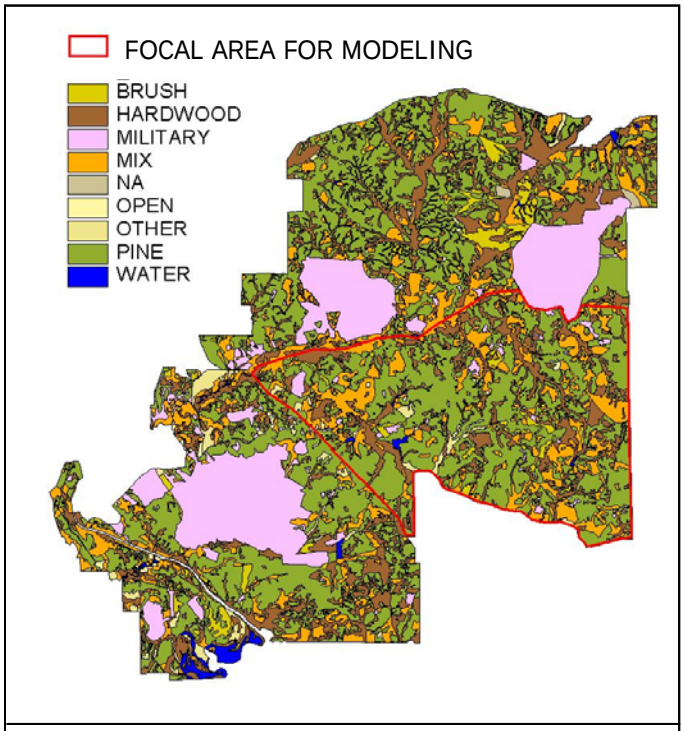


Figure 11. Ft. Benning habitat classifications. The focal area for modeling efforts is outlined in red.

Ft. Benning is a 75,000 ha installation that supports both piedmont and sand hills vegetation. As part of SERDP's Ecosystem Monitoring Program (SEMP), there has been an ongoing effort to understand the impacts of military activities on the natural community. Ft. Benning lies at the intersection of the sand hills and upper loam hills ecoregions, and supports highly diverse pine and hardwood communities that have been subjected to various intensities of forest management. This has resulted in a complex of forest stands that shows a wide diversity of dominant species (Fig. 11). We targeted a 21,000 ha portion of the landscape (outlined in red) for modeling purposes. For this planning region, we created a series of alternative maps that reflect different management decisions. Because no data were available from Ft. Benning that could be used to directly parameterize the EAM, we developed parameters using our general habitat model (described in Part 2) to identify the most likely edge responses. This model requires information on habitat associations (which we obtained from Land Condition Trend Analysis survey data) and information on resource distribution, which we took from the literature.

In order to explore the potential ecological consequences of allowing different levels of tank maneuver exercises on the larger landscape, we developed 13 maps that reflected different densities of tank trails. We began with the current distribution of tank trails in our study area (approximately 400 km), then "removed" trails in 50 km increments until no trails remained, and "added" trails in 50 km increments until there were approximately 50% more than the current level. Then, using the EAM, we explored the impacts on several species, some of which were likely to avoid trails, some of which are expected to be attracted to trails, and some of which are unlikely to respond at all. Our preliminary results indicate that the EAM predicts that densities in patches will increase, decrease, or remain the same depending on whether each species is expected to be attracted to, avoid, or ignore tank trails. However, in some cases those responses appear to be relatively linear (Fig. 12a) while in other cases, there appears to be a threshold effect (Fig. 12b). This threshold effect is potentially important because it suggests that there is a range of activity levels that may cause little impact until that

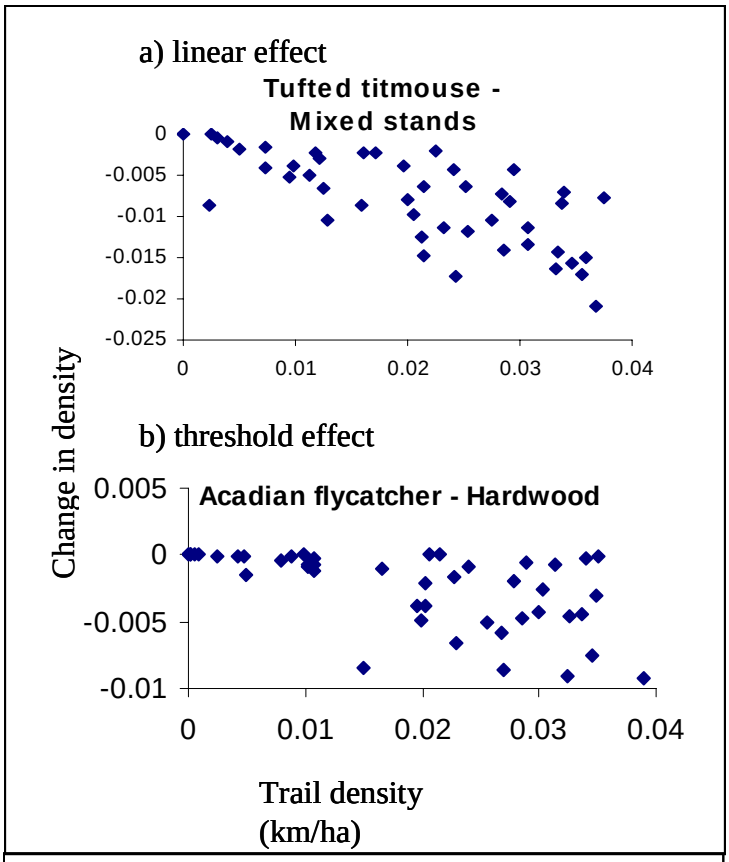


Figure 12. The impact of tank trails on patch density for two species in their preferred habitats. Both species avoid trails, so decreases with increased road density are expected. However, the top example (a) shows a linear response to roads, while the bottom example (b) indicates that there is a threshold effect where a range of low road densities have little impact.

threshold is crossed. Determining the factors that influence such threshold points may provide science-based guidelines that allow mangers to set a range of sustainable activity levels that would minimize ecological impacts. In all cases, there was a great deal of variability in the response to trail density (Fig. 12), meaning that some other landscape factors either mitigated or exacerbated the impacts of the tank trails. Further exploration of the landscape factors that influenced these responses could be useful in identifying training areas that are able to withstand higher activity levels and areas that are particularly sensitive.

To explore the consequences of different landscape restoration scenarios, we imagined two ways of targeting stands for restoration for one of the main species of management concern on Ft. Benning, the red-cockaded woodpecker (*Picoides borealis*). Using data made available from Ft. Benning, we determined the habitat preferences for this species, for habitats other than its preferred habitat type (old-growth, long-leaf pine), which has only limited distribution across the landscape. Using these preferences, we targeted habitat for restoration in one way that reduced habitat fragmentation, and one way that did not. Once again, responses of individual species within the bird community were varied and complicated. However, our EAM "toolkit" provides new capabilities for assessing the effects on multiple species in a robust, straightforward manner. We are continuing to analyze these results to determine how they could best be used to help managers balance single-species management goals while protecting the integrity of the larger ecosystem.

Ft. Hood Project

Ft. Hood is an 88,500 ha active military installation located on the Edwards Plateau in central Texas. The habitat consists mainly of a mixture of grassland meadows and oak-juniper woodlands. The natural interspersion of these habitat types creates distinct habitat edges that may exert significant influence on local animal populations. Similarly to the Ft. Benning project, we created a series of alternative maps of Ft. Hood that reflected different potential management decisions relating to allowed levels of tank maneuver exercises and habitat management for the two principal endangered species on the base, the golden-cheeked warbler (GCWA) and the black-capped vireo (BCVI). Unlike Ft. Benning, there is a great deal of data available to parameterize the EAM. We have created a series of 12 maps that reflect different allowed levels of tank maneuver exercises within GCWA habitat. Similar to the approach used for Ft. Benning, we incrementally "removed" tracks from the landscape, until there were none left. Subsequently, we "added" tracks until the density was similar to the most heavily used GCWA habitat on the base. For the habitat management scenarios, we allowed GCWA habitat that had been designated as non-core areas to be converted into BCVI habitat through military activity, (all of which tends to convert older-successional GCWA habitat into mid-successional BCVI habitat). Then we targeted BCVI habitat in protected areas that could be managed in a way that would allow them to succeed naturally to GCWA habitat. As in the Ft. Benning work, we did this in two ways: one scenario reduced fragmentation while the second ignored spatial context and resulted in a more fragmented landscape. The bird data made available from Ft. Hood suggest that individual species in the bird community respond to different fragmentation pressures in complex ways, but that this complexity can be tracked using the EAM as a management tool. We are still in the process of running the EAM using Ft. Hood bird data. However, our preliminary results indicate that there are some similarities in responses with Ft. Benning, suggesting that some general principles may emerge that can help guide management on military bases with heavy training missions. Results will be detailed in our upcoming report on this demonstration project.

Sustainability of Semi-Arid Hydrology and Riparian Areas (SAHRA)

The main threat facing the San Pedro River and associated riparian habitats is water diversion, mainly through groundwater pumping. These activities cause the water table to drop and impact the composition and structure of the vegetation in the riparian corridor. These changes in vegetation, as well as changes in surface-water availability, will have strong impacts on the ecological community. One ongoing collaborative project (SAHRA) is bringing together an interdisciplinary team, including economists, political scientists, hydrologists, plant physiologists, and animal ecologists to determine how continued population growth and water use will impact the San Pedro River System.

Arriana Brand, one of the main researchers on our SERDP project, has joined this group as a post-doctoral researcher. The primary goal of her portion of this work is to develop the avian component within a larger effort linking hydrologic, vegetation, avian, and economic components into an integrated modeling framework. Projections of

changes in riparian vegetation, combined with bird habitat models, will be used to predict the effects of hydrologic changes on songbird populations along the San Pedro River.

The Effective Area Model will be used to model avian population change within a spatially explicit modeling framework incorporating avian edge response functions along with habitat maps to assess the potential impacts of variation in vegetation composition, structure, and spatial arrangement resulting from different ground-water draw-down scenarios. In order to implement the Effective Area Model, Arriana will use the maps generated by the hydrologists and plant physiologists that reflect how the San Pedro may look in the future under different development and water-use scenarios. She will link these maps with data that she collected as part of our SERDP project and use the EAM to predict the ecological consequences of those different scenarios on the bird populations. Efforts to link those maps with butterfly data are also planned. This project represents a major opportunity to take advantage of a multi-disciplinary approach to conservation that is occurring within one of our main study systems. This work, a direct spin-off of Project CS-1100, continues a collaborative relationship that began with the Semi-Arid Land Surface Atmosphere (SALSA) research program of the USDA Agricultural Research Service.

Forest Ecosystem Restoration Analysis (ForestERA)

The ForestERA project is a major initiative, funded by Congressional action through the Bureau of Land Management, to develop landscape planning tools to support forest restoration in fire-prone ponderosa pine ecosystems of the arid Southwest. The goal of ForestERA is to provide a framework for assessing the impacts and implications of ponderosa pine restoration treatments at landscape and regional scales. This framework will provide a data-based means for analyzing cumulative effects of multiple restoration treatments, and a means of integrating consideration of fire and forest ecology with consideration of wildlife and biodiversity issues. The ForestERA project will provide a landscape ecology framework to help guide the location and timing of restoration treatments in ponderosa pine forests across northern Arizona and in contiguous areas of adjacent states.

Much of the landscape modeling and wildlife effort is a continuation of work initiated through Project CS-1100, particularly the work carried out at Camp Navajo and Mt. Trumbull. Direct application of the EAM is being used in limited areas, where planning is occurring at the appropriate spatial scales. Future applications of edge effects modeling are likely as the ForestERA toolbox is used to address the scaling issues that typically divide regional planning efforts from project-level planning of management activities. This effort will provide a series of real-world applications of landscape-level planning in the context of forest restoration and fire and fuels management.

SUMMARY AND CONCLUSION: A PRACTICAL TOOL SET FOR MODELING EDGE EFFECTS IN FRAGMENTED LANDSCAPES

As terrestrial landscapes become increasingly fragmented by human activities, a predictive approach for estimating animal abundance that accounts for spatial heterogeneity is needed to guide habitat management and conservation. The Effective Area Model provides a spatial approach, developed as an ArcView GIS extension that incorporates empirical or modeled data on animal responses to habitat edges and predicts abundances under various land management scenarios. Inputs to the model include habitat maps and animal density response functions. The latter describe animal density along a habitat gradient between adjacent habitat types, allowing us to generate maps of predicted animal abundances.

The ultimate product of these modeling efforts is a new toolbox for assessing the effects of fragmentation – and its inverse, ecosystem restoration – on animal populations and other ecological variables of interest (e.g., microclimate near edges.) The EAM can be used to explore the consequences of different habitat configurations that result from different approaches for managing a large landscape. Our results suggest that the EAM provides a useful approach for integrating landscape-scale considerations into management decisions. We are continuing to build on the results of Project CS-1100, implementing the EAM in novel situations from Arizona to Georgia. These exercises will show how the EAM can help set management goals, as well as balance the training needs of the military, endangered species management, and associated impacts on the larger ecological community.

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The relationship between habitat selection and habitat quality for the plumbeous vireo in a changing landscape, by James Battin

Testing the Effective Area Model for ponderosa pine forest birds, by James Battin

Ecological and life-history traits predict avian edge response: a meta-analysis, by Arriana Brand

Empirical validation of a method for predicting species-specific edge response for birds in forested landscapes, by Arriana Brand

Using the Effective Area Model to predict abundance at the landscape scale, by Arriana Brand

A predictive model of edge effects, by Leslie Ries

Butterfly edge effects are predicted by a simple model in a complex landscape, by Leslie Ries

Extrapolating edge responses to landscape patterns: lessons learned from an empirical test of the Effective Area Model, by Leslie Ries

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TRANSITION PLAN AND RECOMMENDATIONS

Transitioning this new capability will require incentives for constructive engagement in cross-boundary habitat planning on military installations and neighboring lands. Our experience suggests that military and DOE lands face complex and rapidly changing management objectives, and that multi-habitat, multi-species planning is difficult. Many installations are expected to manage for wildlife and other environmental objectives without compromising training and mission readiness. In this demanding decision environment, planning for complex habitat needs of multiple species may seem overly ambitious, too complex, or less pressing than other management objectives. While the ecological modeling tools described here are effective in making these tasks much more manageable, they nevertheless require significant training and start-up efforts. Investment in these efforts is essential if a busy land management team is to identify planning objectives, develop requisite habitat maps and ecological data, and engage in

practical modeling of outcomes of alternative management scenarios. Because of the challenges encountered among collaborators throughout the course of this project, we recommend the following steps to assure that appropriate installations develop the capacity to use these tools:

1) Identify installations most in need. Some installations are experiencing greater levels of habitat fragmentation than others, and some of these face significant challenges in planning for rare and sensitive species. These installations should be identified and this report and other materials and documentation should be made available to planners and environmental offices.
2) Several appropriate installations should be supported in training and implementation of the EAM and associated tools. In some cases, ancillary support in the development of overall land management planning may be necessary, for example, when the installation has not developed a capacity for assessing alternative management scenarios.
3) Once modeling capabilities have been implemented and management decisions made, participating installations should monitor the effects of the selected management approach, both for the purposes of tracking key species and for assessing the accuracy of model predictions.
4) Utility of the EAM tool box at selected installations should be assessed, and experienced practitioners (installation land managers) should develop an agency-wide plan for adoption of this management support technology. In this manner, practical experience will guide the final transition of this capability to the most appropriate installations.

We have pursued steps 1-2 throughout the duration of this project. Interaction with Ft. Huachuca and Camp Navajo, during the early stages of the project, provided initial insight into management paradigms within the military, while work with the Bureau of Land Management and USDA Forest Service gave similar access to other federal agency approaches. We found that, although both Huachuca and Navajo were actively addressing issues of habitat fragmentation and restoration, neither installation was at that time, engaged in integrated habitat management at the landscape scale, and their interests in furthering this capability shifted with changing management priorities. Adoption of the EAM as a management tool has yet to occur at these installations. In contrast, BLM and Forest Service have begun to pursue more focused applications of the EAM toolbox and its spin-off, the ForestERA Project.

More recently, SERDP provided continuing support for our project so that we could develop applications at Ft. Hood, Texas, and Ft. Benning, Georgia. In our view, these installations provide good opportunities for project transitioning. In both cases, we have worked with land managers to develop existing data, model edge responses, and develop management scenarios needed for application of the Effective Area Model. Progress has been good, however, land management planning has taken longer than expected and, thus, we find ourselves mid-stream in our collaborative efforts at both bases as our project funding expires. We believe that as alternative management scenarios are articulated at each installation, our modeling tools will provide valuable and unique insight into the implications of each management scenario under consideration. In the case of Ft. Hood, this could help resolve the competing interests of two federally

listed endangered species. For Ft. Benning, it could provide an integrated perspective on how training exercises impact numerous species of management interest.

Therefore, our final recommendation regarding transitioning of the capabilities developed through Project CS-1100 is that these initial transition efforts at Ft. Hood and Ft. Benning be supported in some way so that the Effective Area Model and related modeling tools can be fully implemented, tested and evaluated (step 3, above) enabling the development of a fully informed agency-wide transition strategy (step 4).

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