Measuring Edge Responses to Capture Complex Effects (adapted from our final technical report to SERDP, July 2010)

The best approach to measuring edge responses has been a topic that has received a great deal of attention in the edge literature (Ries et al. 2004) and has been something that our group has grappled with in the past. The most common topic of debate has been the best way to capture the non-linear dynamics that result from the threshold nature of edge effects. By this we mean that edge effects are expected to extend only a limited distance into habitat, thereafter leveling off at a characteristic distance that is associated with the "core" of the habitat patch. Several approaches have been proposed (Fraver 1994, Cadenasso et al. 1997, Laurance et al. 1998, Mancke and Gavin 2000, Brand and George 2001, Harper and MacDonald 2001, Toms and Lesperance 2003, Ewers and Didham 2006), although none has become commonly used. Further, none of these models address the critical assumption of most edge studies - that the best metric for describing edge effects is the distance to the closest edge. This assumption allows researchers to ignore both complex edge geometry (Fig. 9a,b) and the presence of multiple adjoining habitat types (Fig. 9c). In some cases, researchers studying edges attempt to set up transects along the straightest, most "ideal" edges (Fig. 10a), far from converging edge types. More commonly, nothing about edge geometry is noted in the study design, so we assume that the issue is entirely ignored. In either case, both force an assumption of "ideal" edge geometry. This critical assumption is problematic, however, when seeking to extrapolate edges over landscapes, which typically have complex geometries and multiple, converging edge types (Fig. 10b,c).

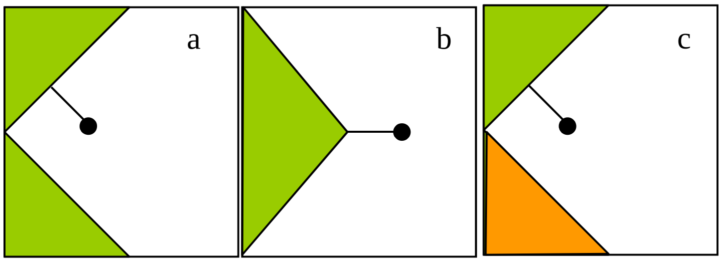


Figure 9. Complex and multiple edge effects. Edge influence may be strengthened (a) or lessened (b) depending on edge geometry. How responses interact when three habitat types intersect (c) is unknown.

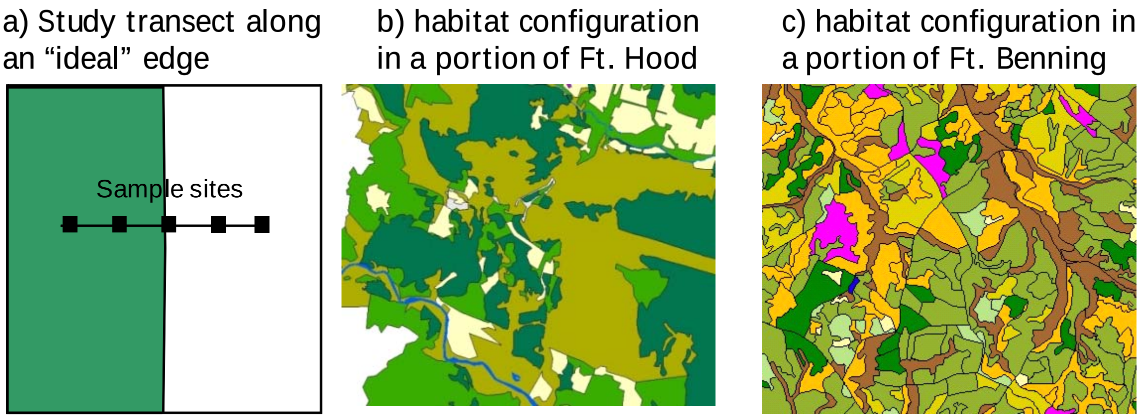


Figure 10. Most edge studies seek out simple landscapes in which to measure edge effects (a), but then may not reasonably be used to extrapolate responses over real landscapes such as those found at Ft. Hood (b) and Ft. Benning (c).

There have been very few studies that have explored the implications of complex edge geometry. The most thorough to date have shown that edge effects are intensified in corners (Fletcher 2005) and corridors (Harper et al. 2007) and incorporating complex geometries into landscape-level extrapolations has minor, but measurable impacts (Fletcher 2005). Surprisingly, of the hundreds of edge studies published in the past several decades, none have empirically measured the influence of the convergence of multiple habitat types, although one study showed how these effects could be approached mathematically (Fernandez et al. 2002). This, despite the fact that a recent study showed up to 60% of a landscape is within 120m of a convergence point between three or more habitat types (Li et al. 2007). Despite this dearth of knowledge, we must confront these implications because our model takes local edge responses and extrapolates them over entire landscapes potentially multiplying errors of overly simplistic assumptions regarding landscape structure. Real landscapes are invariably filled with complex shapes and the convergence of multiple habitat types (Fig. 10b,c). Currently, the EAM uses the distance to the closest edge as the key measure of edge effects. However, we have begun to explore the best approach to considering complex geometry, the impact it may have on our predictions, and determining how these calculations could or should be incorporated into future versions of the EAM.

Malcolm's Model of Complex Geometry

Malcolm (1994) developed a model that we believe offers the best framework both for determining the distance of maximum edge influence and dealing with the issue of complex edge geometry. Malcolm's model has been cited numerous times (139 as of Jan 2010), but we found no evidence that it has ever been implemented (beyond the original publication). The model's solution was useful in that it can incorporate actual patch geometry and also results in a non-linear solution with the exact type of threshold effect that has been sought by many in the past. Further, this modeling approach allows complex geometry to be factored in either when measuring edge effects in the field or when predicting edge influence throughout a landscape. Ultimately, Malcolm's solution is useful because it returns parameters that are of interest to most researchers: estimates in the habitat core (k), the maximum distance of edge influence (Dmax), and a parameter describing the effect of the edge (e0). We can only speculate as to why such a useful model has never been applied (beyond the original paper) over a 15 year period, but we suspect that at least part is due to the mathematical complexity of applying the model in real landscapes.

The basic model considers that every point along an edge can exert an ecological influence (say on animal density or plant height) on any point in space, up to some maximum distance (Fig. 11). In Malcolm's original model this point edge effect was assumed to be linear from the edge to the maximum distance of edge influence (Dmax), at which point it was assumed to level off (Fig. 11a). We have extended this model to allow plateaus at both the edge and the interior (Fig. 11b) by adding an additional parameter, Do. Point effects are integrated across the entire edge at all distances less than Dmax to arrive at a predicted density (or plant height, etc.) at any point in space, as long as the configuration of all edges within the specified distance are known. In the original paper, the only solution presented was for a point along an "ideal" edge that is perfectly straight, divides two habitats only, and extends to infinity in both directions (Fig. 12a). However, the model was intended to be used in more complex patch shapes, and Malcolm (1994) noted that the model could be used on patches of *any* shape. To do this, Malcolm

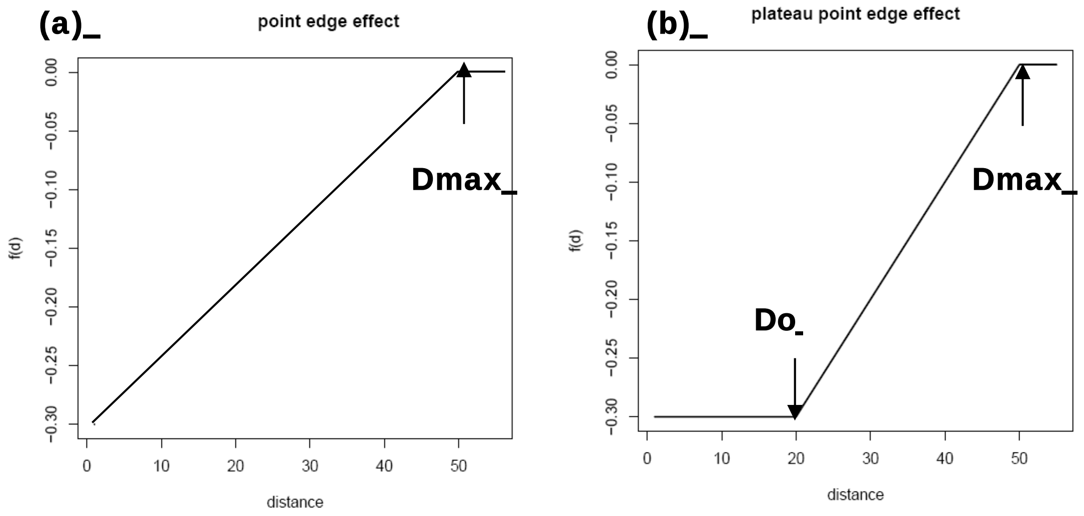


Figure 11. Malcolm's model uses a point edge effect that is a function of distance. The original model allowed a plateau only at Dmax (a), but has now been extended to allow a plateau at the edge via the parameter Do.

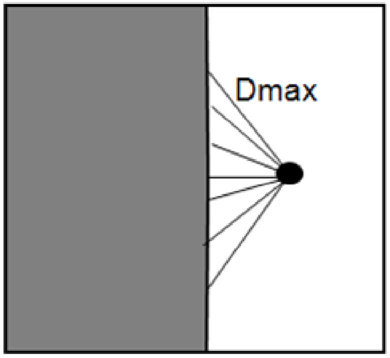
suggested dividing the patch into straight- line segments, and then adjusting the limits of integration accordingly. We did this for a simple, "ideal" corner (meaning that it is exactly 90^o and extends past Dmax in both directions). The solution is shown in Fig. 12b and gives an indication of why this model has never been implemented in real landscapes. This solution is only applicable to a perfect corner and even a corner of slightly different geometry (e.g., 89^o) would require a different solution. In reality, a unique solution is required for every patch in a typical landscape (except, perhaps, experimental landscapes). Obviously, the task of individually finding a unique solution to every patch on the landscape is intractable. This presented us with the dual challenges of applying this model on our real landscapes and also developing a method that makes it approachable for others to do so.

To tackle both challenges, we developed an R package ("edgefx") that, given a simple map of all edges within Dmax, calculates the solution and allows parameterization of and predictions generated from Malcolm's model. Further, we implemented our four-parameter version of Malcolm's original equation along "ideal" edges within the package. This function is useful because many edge studies establish transects along these types of edges (or simply assume they are "ideal"). The "edgefx" package also implements a simplified version of the EAM on a binary landscape to determine the effects of extrapolating edge effects where the complex geometry of the landscape is incorporated into the predictions, rather than considering only the distance to the closest edge (as the EAM currently implemented in ArcGIS does). We used the extensive bird survey network on Ft. Hood to determine how using Malcolm's model influenced the measurement and prediction of edge responses.

Testing Malcolm's Model at Ft. Hood

Our two main goals in testing Malcolm's model were to 1) determine its current usefulness in developing parameters for the EAM and 2) determine whether EAM

(a) “ideal” edge

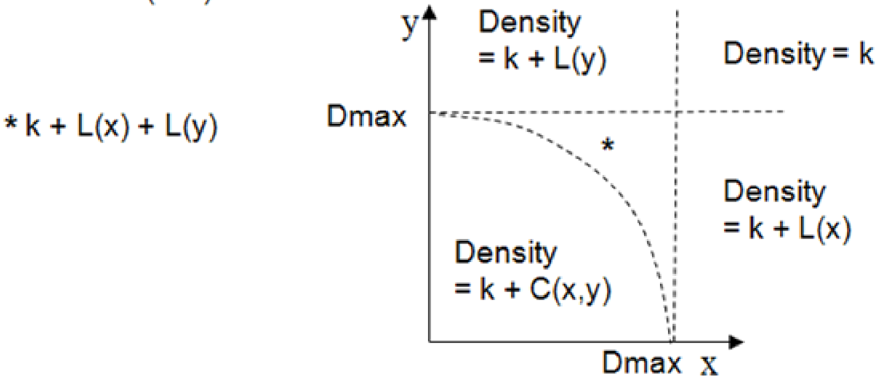


$$Density = k + L(D)$$

$$Where\ D < Dmax\ ,\ else\ k$$

$$L(D) = e_0[\sqrt{D\max - D^2} + \frac{D^2}{2D\max}\ln(\frac{D\max - \sqrt{D\max - D^2}}{D\max + \sqrt{D\max - D^2}})]$$

(b) “ideal” corner (90°)



Where:

$$\begin{aligned} C(x,y) &= \int_0^{x+\sqrt{D_{max}^2-y^2}} e_0\left(1-\frac{\sqrt{y^2+(t_x-x)^2}}{D_{max}}\right)dt_x + \int_0^{y+\sqrt{D_{max}^2-x^2}} e_0\left(1-\frac{\sqrt{x^2+(t_y-y)^2}}{D_{max}}\right)dt_y \\ &= e_0\left[\frac{1}{2}\sqrt{D_{max}^2-x^2}+\frac{1}{2}\sqrt{D_{max}^2-y^2}+(x+y)\left(1-\frac{\sqrt{x^2+y^2}}{2D_{max}}\right)\right. \\ &\quad \left. +\frac{x^2}{2D_{max}}\ln\left(\frac{\sqrt{x^2+y^2}-y}{D_{max}+\sqrt{D_{max}^2-x^2}}\right)+\frac{y^2}{2D_{max}}\ln\left(\frac{\sqrt{x^2+y^2}-x}{D_{max}+\sqrt{D_{max}^2-y^2}}\right)\right] \end{aligned}$$

Figure 12. The solution to Malcolm’s model for the two simplest geometries within a landscape: along a perfectly straight (“ideal”) edge that extends past Dmax in both directions (a) and a perfect (“ideal”) 90° corner that extends past Dmax in both directions (b).

implementation incorporating complex geometry could improve predictions of edge effects across complex landscapes. To do this, we compared four models: Malcolm’s complex edge model (COMPLEX), a simplification of Malcolm’s model assuming an “ideal” edge (IDEAL), a traditional model that uses only distance to the nearest edge (DNE) and a null model that ignored edge influences entirely (NULL). The value of implementing the IDEAL simplification of Malcolm’s model lies in its assumption of “ideal” geometry, thus it requires only information on distance to the closest edge (rather than detailed patch geometry maps), yet it still returns the critical parameters Dmax, k, e0 and, now, Do (Fig. 11b), parameters that are of interest to most managers and researchers. Further, these parallel the parameters currently used for the EAM.

We built the four models from data drawn from the 638 points in Ft. Hood's bird survey network (Fig. 4a) that are along the straightest (in other words, most "ideal") edges. We then used the parameters derived from these points to predict densities near edges with the most complex geometries. We were then able to compare densities observed near those complex edges with predictions from the four models to see which model's predictions were closest to the observed values. This is the first test of Malcolm's model that we are aware of in a complex landscape (Malcolm's original 1994 paper tested the model in square patches).

It should be noted that the bird survey program at Ft. Hood was in no way designed to measure edge responses. However, because of the large number of survey points in Ft. Hood's network, points coincidentally occur at various distances from many different edge types, but are scattered haphazardly across the base. Obviously, we could not formally control for any aspect of edge geometry. Ideally, points would be set up along transects at varying distances from each edge of interest (as in Fig. 10a), reducing variability due to local effects. Further, Ft. Hood surveys are conducted so that birds are counted up to 50m from each point, meaning that we were unable to use data from any point closer than 50m from an edge. This eliminated surveys in the closest edge zones where edge effects are strongest (see Fig. 11). Data from 2002-2005 were used because all survey routes had been set up by 2002, but methodology was radically changed in 2006 in SCRUB habitat, making comparisons after 2005 impossible. Analyses were performed on each year (2002 through 2005) as well as on mean densities from all four years combined.

We used data from nine bird species, including those that prefer WOOD habitat (the GCWA's main habitat type), SCRUB habitat (the BCVI's main habitat type), and also a set of species that are found in both (Fig. 13). We focused on four edge types: WOOD|OPEN, WOOD|SCRUB, WOOD|SCTREES AND SCRUB|WOOD. We also used Malcolm's model to fit responses at road edges, but because roads were largely straight, there was not an opportunity to test the model on roads with complex geometries, so we omit those results here. However, we present them in the section 5.5 on parameterizing edge responses for the EAM at Ft. Hood. As always, we began the analytical process by developing predictions for edge responses we

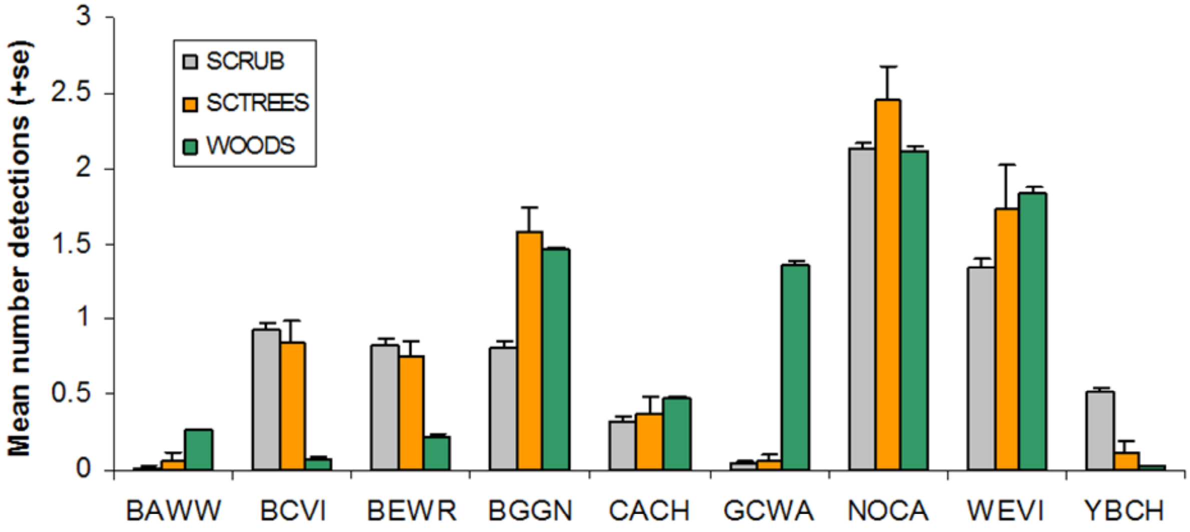


Figure 13. The habitat associations of nine common species on Ft. Hood relative to three main habitat types. Full species names are shown in the acronym list (page iv of this report).

expected to see for each species based on our edge response model (Fig. 1c). This approach allows us to make better sense of the results and to continue to refine our model. We did not use published results from other studies to make our predictions, but it is worth noting that several of the species have been shown to show edge responses in other studies. For instance, the GCWA has been shown to have lower fecundity at edges (Peak 2007) and are also known to be area sensitive (Ladd and Gass 1999). In general, species associated with scrub are thought to prefer edges, but recent reanalysis shows that this is only in reference to forest interiors and if compared to the interiors of their preferred habitat, these species often avoid edges (Schlossberg and King 2008).

For all species, there is a great deal of scatter in the data, as was expected due to the distribution of points throughout the landscape. Of the nine species, four showed the most consistent edge responses, and always in the predicted direction (Table 1). Because our main goal here is to test Malcolm's model, we restrict the presentation and discussion of results to four species: golden-cheeked warblers (GCWA), black-capped vireos (BCVI), black-and-white warbler (BAWW), and bewick's wrens (BEWR). GCWA and BAWW are associated primarily with the oldest WOOD habitat and BCVI and BEWR are associated with SCRUB and SCTREE habitat (Fig. 13).

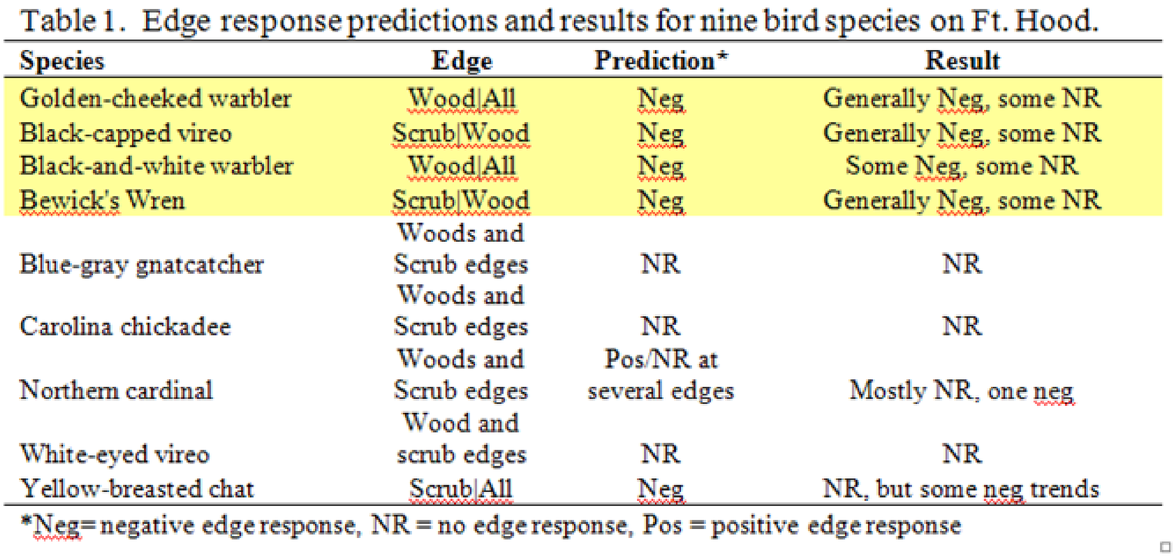
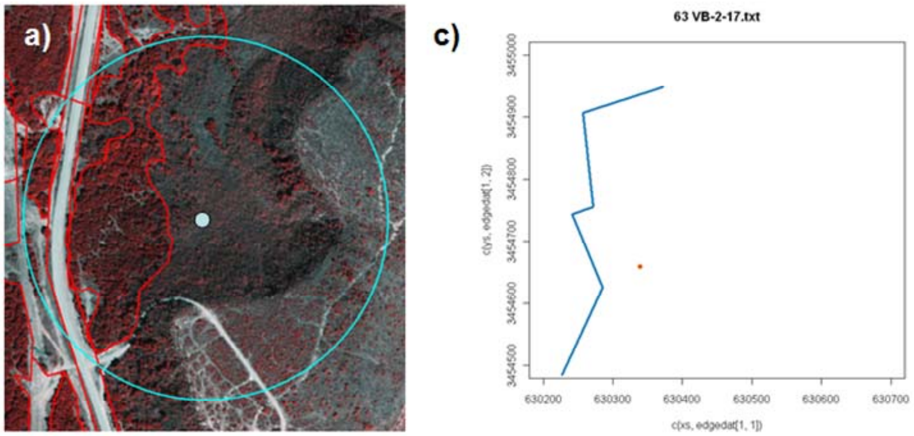


Table 1. Edge response predictions and results for nine bird species on Ft. Hood.

Species	Edge	Prediction*	Result
Golden-cheeked warbler	Wood|All	Neg	Generally Neg, some NR
Black-capped vireo	Scrub|Wood	Neg	Generally Neg, some NR
Black-and-white warbler	Wood|All	Neg	Some Neg, some NR
Bewick's Wren	Scrub|Wood	Neg	Generally Neg, some NR
Blue-gray gnatcatcher	Woods and Scrub edges	NR	NR
Carolina chickadee	Woods and Scrub edges	NR	NR
Northern cardinal	Woods and Scrub edges	Pos/NR at several edges	Mostly NR, one neg
White-eyed vireo	Wood and scrub edges	NR	NR
Yellow-breasted chat	Scrub|All	Neg	NR, but some neg trends

*Neg= negative edge response, NR = no edge response, Pos = positive edge response

In order to develop parameters for our four competing models (NULL, DNE, IDEAL, COMPLEX), we went through several steps that allowed us to classify each point among Ft. Hood's network of 638 point count stations. All classifications were made using false-color remotely-sensed satellite imagery with 1 m resolution (Fig. 14a). Our model allowed us to deal with complex geometry, but not converging edges of multiple habitat types, so we were constrained to look for points with only one edge type within a specified distance. First, we arbitrarily set a preliminary tolerance of 500m to allow initial exploration of basic patterns. This is a very conservative distance since most reported bird Dmaxes are on the order of 100-200m (Laurance 2008). Based on this, we found a small number of points with relatively straight edges and no multiple edges within that large radius. Based on this small number of points, we did some preliminary analyses (not shown) that suggested edge responses were generally occurring on the scale of 200-300m. Therefore, we reset our cut-off and identified points among Ft. Hood's bird survey network along the four edge types with each focal edge type only within



b)

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630339,3454659, , ,#Point VB-2-17
630372.647,3454948.064,630256.760,3454906.789,ScrubVI|WoodsWA
630256.760,3454906.789,630271.120,3454754.802,ScrubVI|WoodsWA
630271.120,3454754.802,630240.885,3454743.276,ScrubVI|WoodsWA
630240.885,3454743.276,630284.936,3454625.554,ScrubVI|WoodsWA
630284.936,3454625.554,630226.301,3454485.160,ScrubVI|WoodsWA
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Figure 14. Geometry from satellite imagery of a survey point in SCRUB bordering WOODS (a) is converted into line segments and input into R via text files (b). The segments visualized in R output (c).

300m. Necessity forced us to allow similar edges between 200-300m (otherwise we would not have been able to find a sufficient number of points for analysis). Beyond 300m, we ignored multiple edges and complex edge geometry but still recorded the distance to and type of the closest edge. Only points within 500m of a focal edge were used.

We then separated all points into two groups: model building points (which we used to develop parameters for our four models) and model testing points (which we used to test the predictions of each model). The model-building points were along edges that were the straightest (when the nearest point was within 200m) or any points were the nearest edge was beyond 200m. Model testing points were those with the most convoluted edges within 200m. The following list shows the final number of points designated for each edge type.

WOODS|OPEN:	38 (BUILD), 15 (TEST)
WOODS|SCRUB:	26 (BUILD), 8 (TEST)
WOODS|SCTREES:	41 (BUILD), 15 (TEST)
SCRUB|WOODS:	22 (BUILD), 13 (TEST)

We developed parameters for the four models as follows. For the DNE model, we used ordinary linear regression. Although some DNE methods have been developed to detect plateaus (i.e., Toms and Lesperence 2003), in reality they are rarely implemented, so this approach represents what is likely the most common analytical approach to measure edge effects. For the IDEAL model, we used a custom function (infinite.edge.effect) in our “edgefx” R-package. This model assumes that all edges are straight and extend to infinity in both directions. For the COMPLEX model, we used a custom function (edge.nls) in our “edgefx” R-package which optimizes the four (or, optionally, only Malcolm’s original three) parameters by considering actual edge geometry. Edge geometry is supplied for each point via a text file that has the x,y coordinates of the survey point and the start and stop point of each edge segment within our pre-determined cutoff of 300m radius (Fig. 14). An example of imagery of a survey point, the text file, and the resulting edge map that R uses as input are provided in Fig. 14. Finally, we use interior densities (k) predicted by Malcolm’s model for the NULL model. The reason we use interior (rather than mean) densities is because the traditional approach to habitat studies is to set up survey sites sufficiently far enough from edges so that their effects can be ignored. Since both the IDEAL and COMPLEX models return estimates for k, we needed to choose between the two values. To do this, we used an information-theoretic approach and chose the model with the lowest Akaike Information Criterion (AIC) score (Burnham and Anderson 1998).

Because the IDEAL and COMPLEX models are non-linear, fitting them requires supplying the procedure with starting parameters. To get initial parameters, we visually inspected graphs showing densities for each species at each edge type in each year. If no edge gradient was obvious in the graph, models were not run for that species/edge type/year combination. Where even a slight pattern was evident, we developed initial guesses as follows: Do was set to 0, Dmax was set to 200m, and e0 was set to 0.001 (positive or negative depending on whether the observed edge response gradient was positive or negative). Finally, k was set to 0.5, 1 ,or 1.5 based on visual inspection. Based on our initial results, model convergence was rare for the 4 parameter model (and was never chosen by AIC) and model convergence was sensitive to starting parameters. Therefore, after examining initial results and narrowing our focus to four target species, we performed an informal sensitivity analysis using the three parameter model (Malcolm 1994). To conduct this sensitivity analysis, we developed a factorial set of starting parameters for Dmax, k and e0. These parameters encompassed the range of possible Dmax distances based on our point count network (0m, 300m, 500m), densities based on the range of densities observed in the data (0, 1, 2 detections per survey), and a three-order-of-magnitude range for e0 (0.01, 0.001, 0.0001). This factorial design resulted in a set of 27 starting parameters that we used for fitting both the IDEAL and COMPLEX models for each species/edgetype/year combination.

The models with the lowest AIC scores are shown in Table 1. But our results show that when data are highly variable (as is the case on Ft. Hood), the models are highly sensitive to starting parameters. Both IDEAL and COMPLEX models often converged on multiple sets of parameters, and in many cases AIC did not support a single top model (based on a conventional threshold delta AIC value of two). However, this was not true for all models, especially those with the clearest edge patterns. Further, models sometimes converged with Dmax values far in excess of 500m (the maximum value of distance to the nearest edge within our data). These results could be interpreted to mean that there is no statistical support that interior densities have been reached. These results highlight one of the key challenges of designing edge response studies – until you have preliminary results suggesting actual Dmax, it is difficult to develop an appropriate study design. Indeed, Laurance (2004) suggested that many edge studies fail to find edge responses because they are not conducted at the proper scale. Further, our results suggest that when data are variable (as is usually the case in any habitat study), then a strong study design with high replication is necessary. We were fortunate to have so many points to work

Table 2. Parameters from three competing models to measure edge effects (DNC, INFINITE, COMPLEX) will be compared to a NULL model. The models with the lowest AIC score indicates the "best" model based on data fit and number of parameters.

		DNE			IDEAL EDGE				COMPLEX EDGES		
Edge Type	Year	slope	int	AIC	e0	Dmax	k	AIC	e0	Dmax	k
Golden-cheeked warbler (GCWA)											
WOODS|OPEN	Mean	0.002**	0.244	54.05	-0.0032	242**	0.91***	56.23	-0.0028**	314***	1.04***
WOODS|SCRUB	Mean	0.001	0.726**	38.86	-0.0044	208**	1.08***	37.36	-0.005	203**	1.08***
WOODS|SCTREES	Mean	0.006'	0.54*	63.39	-0.0014	460'	1.24**	65.18	-0.0014	402*	1.14***
Black-capped vireo (BCVI)											
SCRUB|WOODS	2003	0.003	0.444	59.75	-0.0076	149	1.21**	60.72	-0.0031	281*	1.35**
Black-and-white warbler (BAWW)											
WOODS|OPEN	2005	0.0006	0.228	59.47	-0.0033	174	0.42***	60.30	-0.0025	195*	0.45***
WOODS|SCRUB	Mean	0.0002	0.175	-1.29	-0.0052	93	0.23***	-0.49	-0.0026	128	0.23***
WOODS|SCTREES	Mean	0.0002	0.179	-0.36	-0.0031	151	0.27***	-0.63	-0.0035	135**	0.26***
Bewick's wren (BEWR)											
SCRUB|WOODS	Mean	0.0027**	0.0113	20.39	-0.0022**	370	0.94	22.42	-0.0016**	553***	1.08***

'$p<0.10$, *$p<0.05$, **$p<0.01$, ***$p<0.0001$

with at Ft. Hood to mitigate some of these problems, but because their network of sampling points was not designed specifically to measure complex edge responses, this limits our inference and weakens our results.

To deal with the problem of multiple, converging models we chose the model with the greatest support (lowest AIC score) for both IDEAL and COMPLEX models. Here, we only present results from a single year of data (or all years combined), depending on which set had the strongest patterns. However, most species showed similar responses from year to year, thus mean values from all years are presented in most cases. Parameters for all four models, along with AIC scores, are shown for each of the four species at the four edge types where they are sufficiently common for analysis (Table 2). Patterns and model fits for the four models are shown for the two main species of management concern at Ft. Hood, the GCWA and BCVI (Fig.

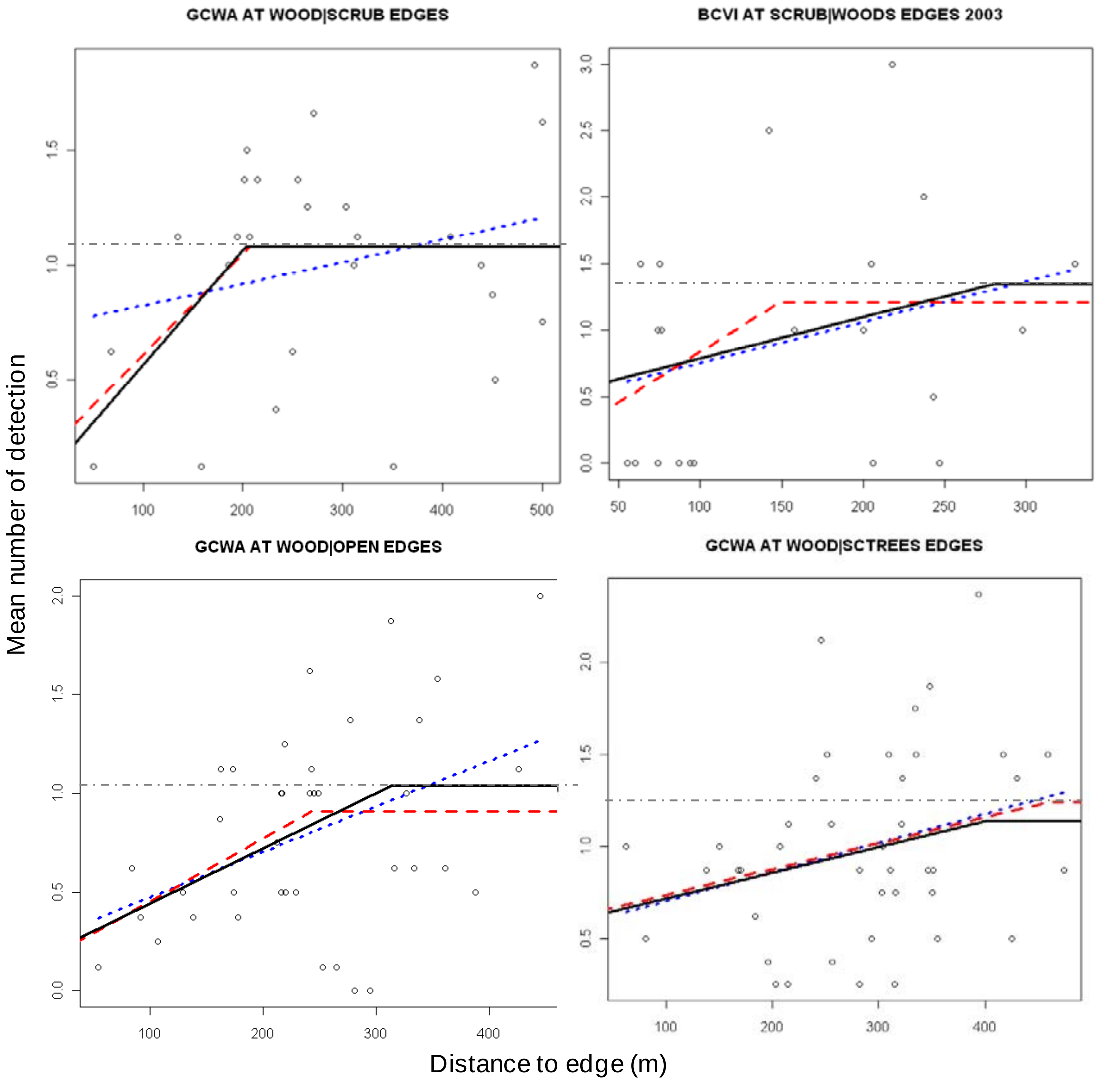

Figure 15. Edge responses for the two species of critical management concern (GCWA and BCVI) at Ft. Hood and the best fit lines from four competing models: COMPLEX (solid, black line), IDEAL (red, dashed line), DNE (blue, dotted line), NULL (grey dot-dash line).

15) and for two additional habitat-specific species, the BAWW and BEWR (Fig. 16). The fit for

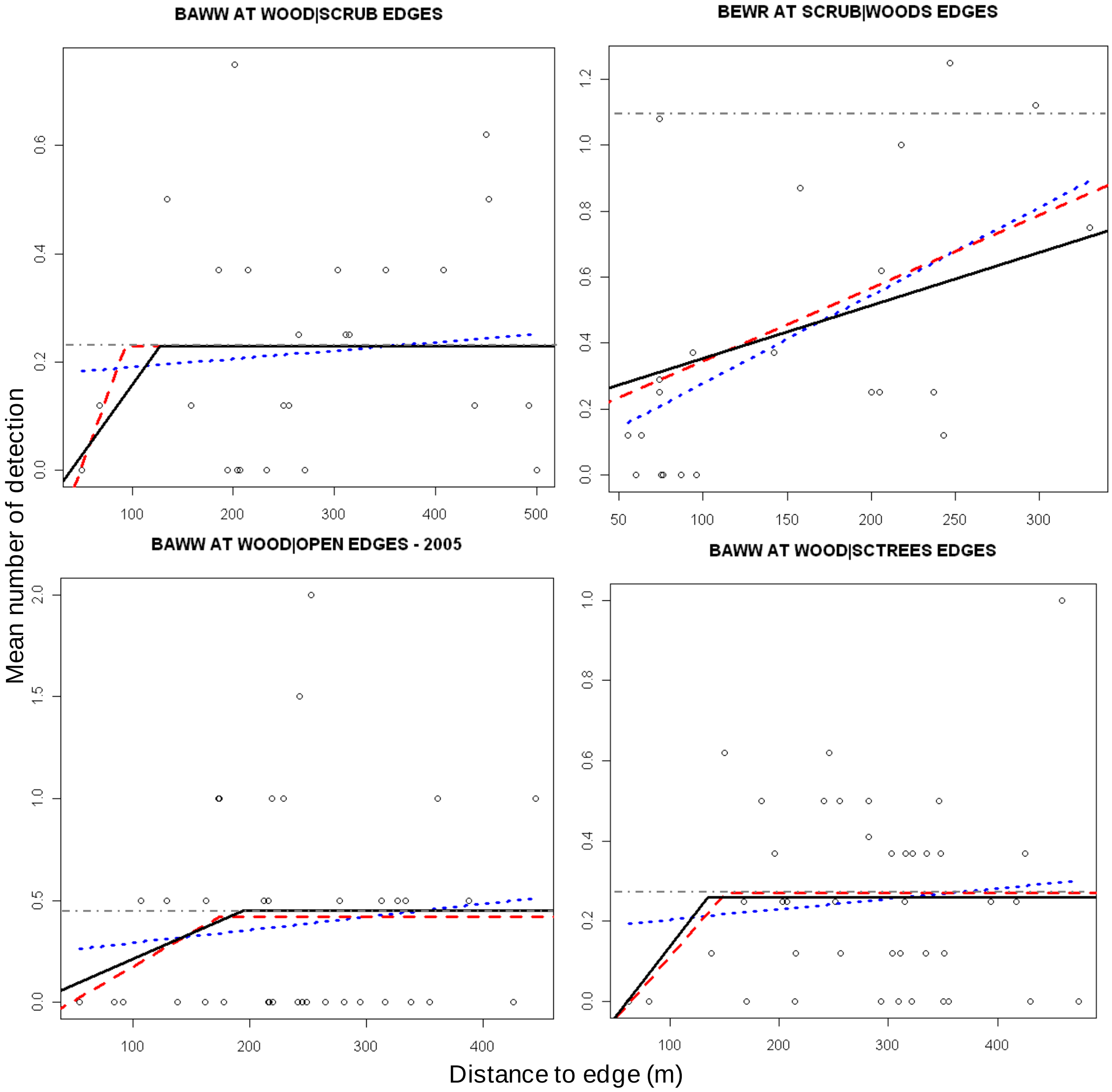

Figure 16. Edge responses for two additional species (BAWW and BEWR) at Ft. Hood and the best fit lines from four competing models: COMPLEX (solid, black line), IDEAL (red, dashed line), DNE (blue, dotted line), NULL (grey dot-dash line).

the COMPLEX model is included for comparison purposes only, but since it is not based on the distance to closest edge, its fit cannot fairly be judged visually by this display. Note that models often predict similar patterns, but may differ depending on whether and where thresholds are reached. Note that when Dmax is beyond 500m, both IDEAL and COMPLEX models are linear within the range of data collection (i.e., BEWR in Fig. 16). The model with the best fit, based on AIC score, is highlighted in Table 2 for comparison purposes only. We do not choose among the four models based on AIC, but instead based on which model does the best job predicting density values at our TEST points that are characterized by convoluted geometry.

Comparison of Observations to Predictions

In order to test the four competing models (NULL, DNE, IDEAL, COMPLEX) against field data, independent test points were identified separately from the points used to build parameters for the four models. We then used parameters from the four competing models (Table 2) to generate predicted densities for each of the test points. Those predicted densities were then compared to observations that had been measured in the field by technicians at Ft. Hood. To generate actual predictions from these parameters, we followed fixed procedures for each model's output. The NULL predictions remained constant for each species at each edge type. For DNE and IDEAL predictions, we simply plugged the parameter values into the model equations to generate values for comparison. For the COMPLEX model, we had developed a function in the "edgefx" R-package called "map.edge.effect," which applies the parameters given to the edge segments of a vector map (illustrated in Fig. 14) and implements Malcolm's model.

It is important to note that the deviation of COMPLEX predictions from an "idealized" realization of the same parameter set (i.e., if we used the parameters built from points where edge geometry was accounted for, but assumed that all the test survey points were along edges that are "ideal") shows the impact of including actual edge geometry in the implementation of Malcolm's model (Fig. 17). The magnitude of these deviations will vary depending on both the values in the parameter set and the shape of the edges near each sampling

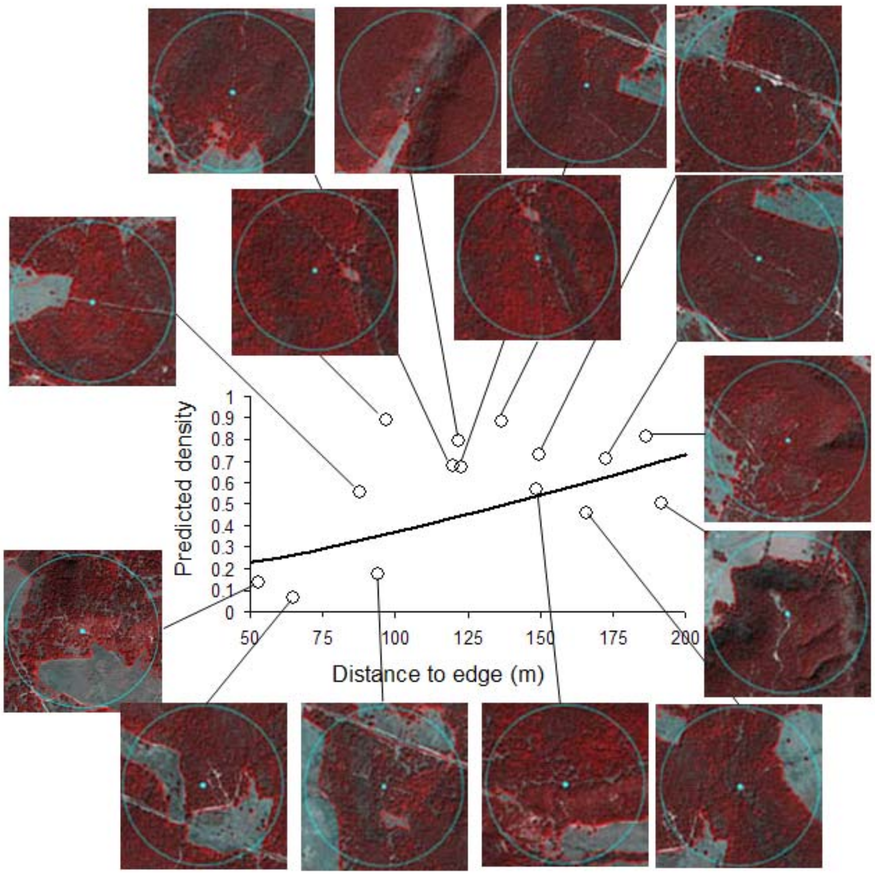

Figure 17. Deviation of predictions from Malcolm's model when parameters are implemented assuming that each point has ideal geometry (straight line) and when actual edge geometry is accounted for (circles). Each point represents a different point count location and remote imagery for each point is provided so that predicted deviations can be compared to actual edge geometry.

point. We illustrate the magnitude of these deviations for the GCWA at the 15 WOODS-OPEN test points (Fig. 17). This example shows that the magnitude of the difference in prediction can be quite substantial. It is also a reminder that the scatter of observations relative to distance to closest edge (as illustrated in Figs. 15 and 16) can give a misleading view of how important edges are in shaping ecological patterns. For instance, most edge studies fail to find a significant pattern (Ries and Sisk, *in press*), yet these studies never take edge geometry into account and rarely state to what extent edge geometry was "controlled" for (i.e., by seeking out straight edges with consistent adjacent habitat).

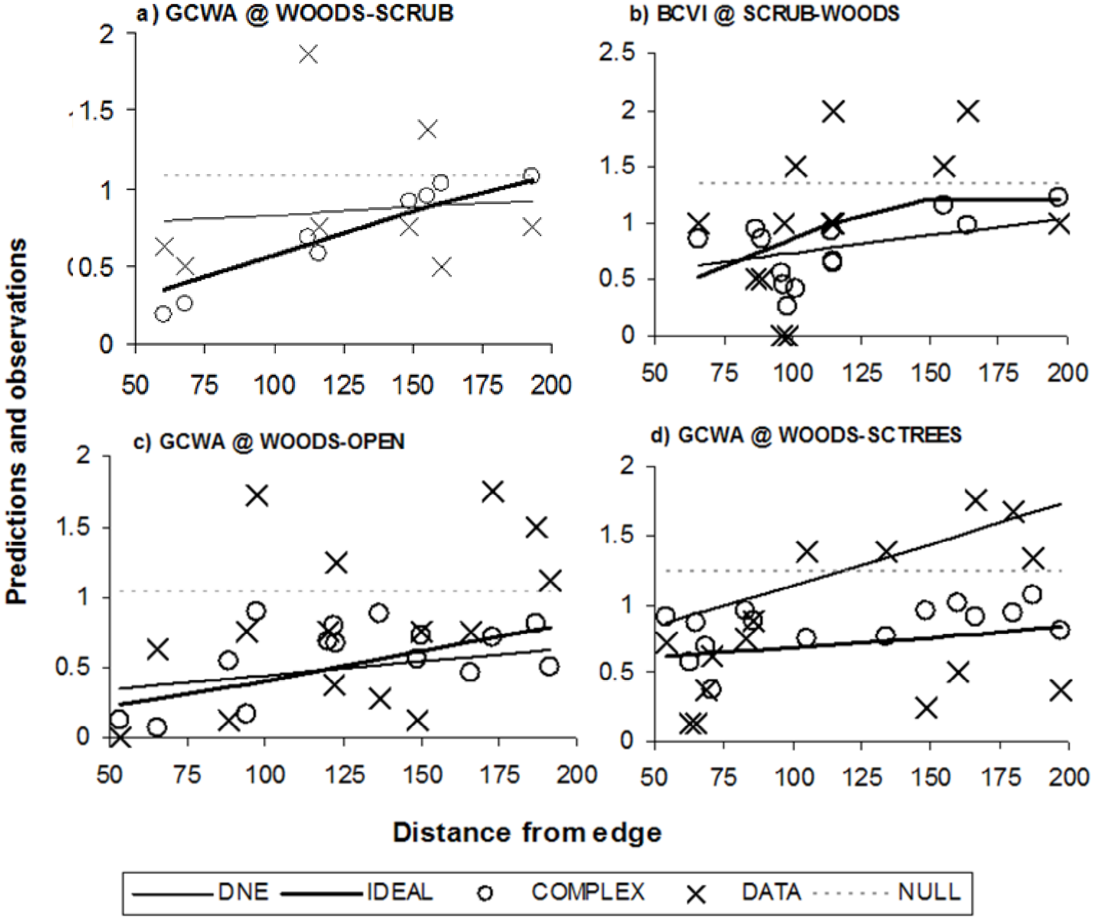

Figure 18. The predictions of four competing models (DNE, IDEAL, COMPLEX, and NULL) are compared to field observations (X's) for the two focal species, GCWA and BCVI, on Ft. Hood at multiple edge types.

The comparisons of observations to the predictions of the four models are illustrated in Fig. 18 for GCWA and BCVI and Fig. 19 for BAWW and BEWR. In almost all cases, the magnitude of variability seen in field observations swamps that predicted by the models, even the predictions of the COMPLEX model. Despite this, it is obvious from these figures that edge responses are also evident in these data sets that are independent of those used for parameter development. In almost all cases, lower densities are observed near the edge compared to further from the edge. The amount of scatter predicted by the COMPLEX model also differs among cases. In some cases, taking edge geometry into account provides substantial difference from the

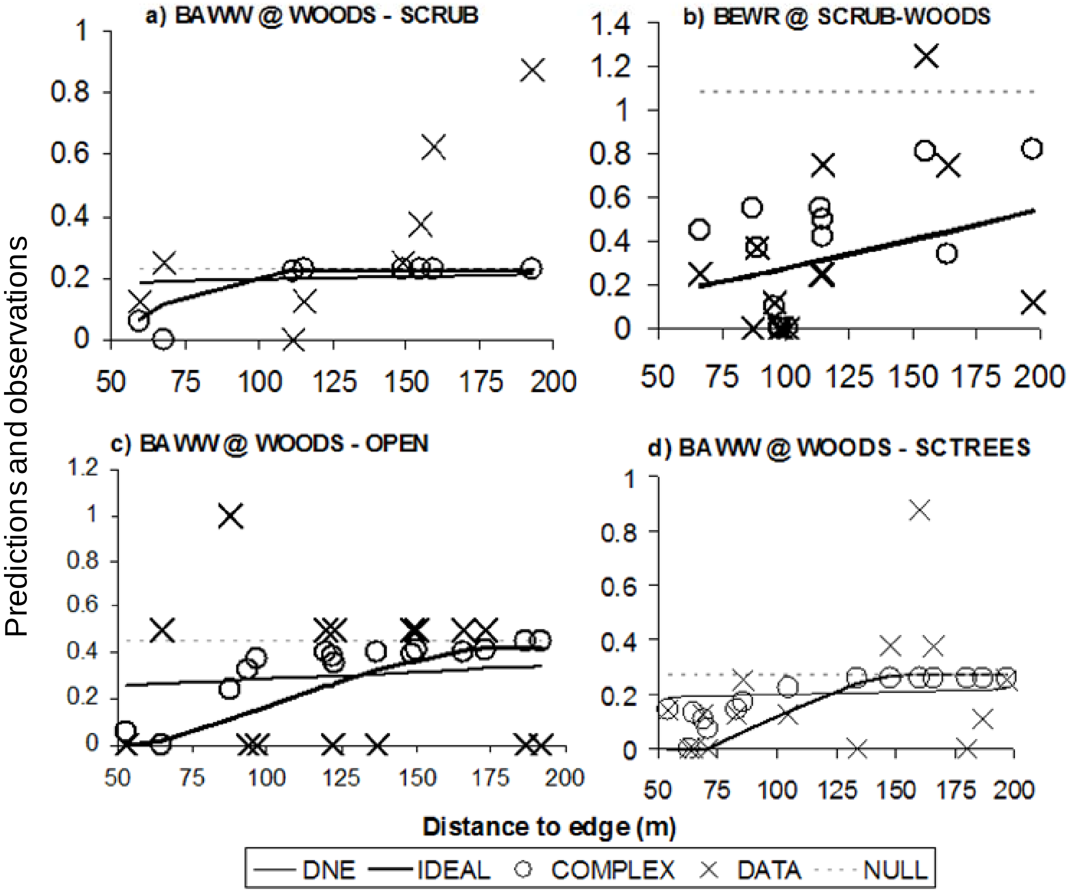

Figure 19. The predictions of four competing models (DNE, IDEAL, COMPLEX, and NULL) are compared to field observations (X's) for two additional species on Ft. Hood: BAWWs at Woods-Scrub edges (a) BEWRs at Scrub-Wood edges (b), BAWWs at Woods-Open edges (c) and Woods-Sctrees (d).

ideal version (as shown in Fig. 17 and also in Fig. 19b), but in other cases predictions are similar to the IDEAL model (i.e., Fig. 18a and Fig. 19a,c,d).

To compare observations to the predictions of the four models, we calculated the mean prediction error (PE = |obs-pred|; after Brand et al. 2006). Bootstrap methods are recommended to determine whether mean PEs of the four models differ significantly from each other (Brand et al. 2006), but we have not yet implemented that approach. The Malcolm model has the lowest mean PE when comparing the four models, although not always for the COMPLEX version of the model (Table 3). The NULL model almost always has the highest PE (Table 3) and therefore could be considered the worst model, suggesting that taking edges into account in predictions is usually helpful for species where significant edge responses have been demonstrated. In general, models that incorporated edges in some fashion were clearly better for GCWA, BCVI and BEWR, but not for BAWW which had the weakest edge responses as originally measured (see Table 2). Interestingly, there seemed to be little agreement between the "best" model for developing the parameters (Table 2) and the "best" model for testing the parameters (Table 3).

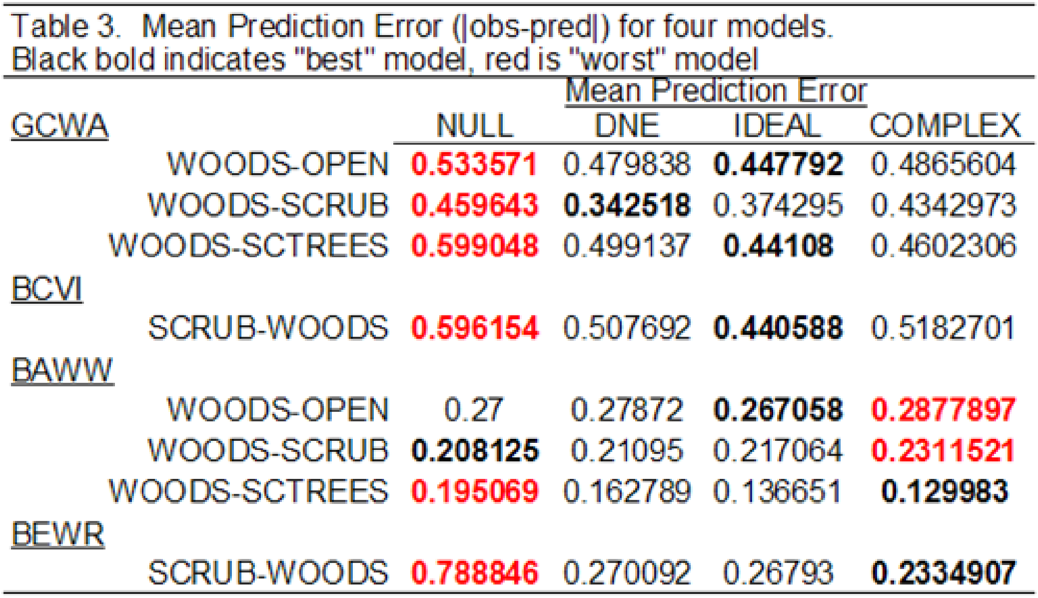

Table 3. Mean Prediction Error (|obs-pred|) for four models.
Black bold indicates "best" model, red is "worst" model

			Mean Prediction Error		
GCWA		NULL	DNE	IDEAL	COMPLEX
	WOODS-OPEN	**0.533571**	0.479838	**0.447792**	0.4865604
	WOODS-SCRUB	**0.459643**	**0.342518**	0.374295	0.4342973
	WOODS-SCTREES	**0.599048**	0.499137	**0.44108**	0.4602306
BCVI					
	SCRUB-WOODS	**0.596154**	0.507692	**0.440588**	0.5182701
BAWW					
	WOODS-OPEN	0.27	0.27872	**0.267058**	**0.2877897**
	WOODS-SCRUB	**0.208125**	0.21095	0.217064	**0.2311521**
	WOODS-SCTREES	**0.195069**	0.162789	0.136651	**0.129983**
BEWR					
	SCRUB-WOODS	**0.788846**	0.270092	0.26793	**0.2334907**

We examined two possible factors that may have influenced the magnitude of prediction error. The first was distance to edge, with the expectation that, if edges were important factors driving ecological patterns, then the closer the point was to the nearest edge, the better the predictions would be (i.e., the lower the prediction error) for models that consider edges (DNE, IDEAL, COMPLEX) but not the NULL model. This pattern was strongly found for BEWRs (Fig. 20a), but only weakly for GCWAs (results not shown). Patterns for BCVIs and BAWWs were more variable, although generally prediction error was somewhat lower near edges. Another factor we examined was how strongly predictions deviated from IDEAL when complex edge geometry was taken into account. These deviations are best illustrated in Fig. 17, and it might be expected that when edge responses are stronger based on edge geometry (so negative deviations from IDEAL) that prediction error would be lower. Again, a strong pattern in support of these predictions was only found for BEWRs (Fig. 20b), with a weak pattern again evident for GCWAs, and the opposite pattern found for BCVIs (results not shown). It is possible that an interaction between distance to edge and deviation from IDEAL is occurring, but we have not yet examined that possibility.

Our results suggest that predictions from Malcolm's model can differ strikingly from simpler measures, even when ideal geometry is assumed. Predictions are most strongly impacted when actual edge geometry is incorporated and these differences can be substantial (as in Fig. 17) or modest (as in Fig. 19a,c,d). However, incorporating edge geometry (the COMPLEX model) led to the best predictions in only 2 of 8 cases (Table 3). In half the cases, the IDEAL model performed best, with the DNE and NULL models each showing the best performance in one case each. This means that Malcolm's model, whether implemented assuming ideal geometry or incorporating complex geometry outperformed other models in 6 of 8 cases. This suggests that using Malcolm's approach may be valuable, but that accounting for actual edge geometry (the most difficult aspect of the model) may not be required, at least for some cases. However, since the design of the Ft. Hood survey network was not designed to test Malcolm's model (or any other edge model), local differences may have swamped important patterns, and tests designed specifically for this purpose may lead to stronger inferences about the importance of incorporating edge geometry into predictions of abundances across landscapes. Finally, predictions from the NULL model, which ignores edge dynamics, were the worst in 6 of 8 cases, stressing the importance of accounting for edge dynamics, even if only the simplest approaches are implemented.

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