



What is an edge species? The implications of sensitivity to habitat edges

Leslie Ries and Thomas D. Sisk

L. Ries (lries@umd.edu), Dept of Biology, Univ. of Maryland, College Park, MD 20742, USA. – T. D. Sisk, Environmental Sciences, Northern Arizona Univ., Flagstaff, AZ 86011, USA.

For decades, researchers have categorized species as “edge-loving” or “edge-avoiding”, but recent studies that show inconsistencies in responses have called these labels into question and led to a sense that edge effects are idiosyncratic and difficult to understand. We suggest that species would be better categorized according to their sensitivity to edges, not the direction of observed responses because no species should be expected to show the same response to all edge types. Measures of edge sensitivity will apply widely across taxa and landscapes and allow metrics that are broadly comparable, making generalities easier to discern. Finally, while the direction of observed edge responses remains a critical (but largely understood) dynamic, most reported edge responses are neutral, so discovering when species are least likely to respond to edges will increase our understanding of edge ecology and associated fragmentation effects. We offer a case study that measures edge sensitivity of 15 butterfly species at 12 edge types. We found that sensitivity is weakly related to vulnerability to predation, but more importantly we show how our results generate new predictions about edge sensitivity that can be explored in future studies.

Throughout the long history of edge studies, many researchers have tried to pigeonhole certain species as either intrinsically “edge-loving” or “edge-avoiding” (Hansen and Urban 1992, Villard 1998, Imbeau et al. 2003). Broader classifications for higher taxonomic groups or guilds have also become popular. For instance, carnivores, game, weedy plants and songbirds are often associated with higher densities at edges, while habitat specialists are generally thought to avoid edges (Ries et al. 2004). With further scrutiny, however, it is often found that these groups do not respond as consistently as previously assumed (Villard 1998, Baker et al. 2002, Chalfoun et al. 2002) especially when looking beyond forest-open edges (Schlossberg and King 2008). This may debunk common wisdom regarding edges, which is largely drawn from the forest literature, but in doing so it contributes to a general sense that edge responses are idiosyncratic and not easy to predict or understand (Ries et al. 2004, Ewers and Didham 2006).

We believe that attempts to label species according to a particular directional edge response are fundamentally flawed because no species should be expected to show the same response at all edge types. Indeed, an extensive review shows that much of the variability in observed edge responses can be explained by the fact that different responses are observed at different edge types, suggesting edge responses are not as idiosyncratic as previously thought (Ries et al. 2004). Further, we recently presented a model that predicts that all species are likely to show a mixture of edge responses (e.g. positive, negative and neutral) depending on the type of edge encountered (Ries and Sisk 2004). Here, we define

edge as the boundary between two vegetation cover classes (which are often broadly referred to as “habitat”), although many other definitions are possible (Lidicker 1999, Strayer et al. 2003). We have not advocated for defining habitat or edge strictly from an organism’s point of view because that is challenging when researchers are dealing with a community of organisms. Instead, it is important for researchers to define the cover classes in a way that is meaningful for the community that is being studied.

Ultimately, much of the confusion about whether a certain species is “edge-loving” or “edge-avoiding” comes from observing different responses at different edge types. A recent article by Schlossberg and King (2008) illustrates this tendency. They show that shrub-nesting birds, a group typically classified as “edge-loving,” in fact consistently avoid forest edges, but only when compared to the open, shrubby habitat interiors that they prefer. The authors make the point that the edge-loving label came from a history of studies of forest fragmentation. Indeed, from the reference point of the forest interior, shrub-nesting birds often do show higher densities along forest edges. This result led to a lack of conservation focus on these habitat-sensitive birds since it was assumed that if they preferred edges, they were not at risk of decline due to habitat fragmentation. That most shrub-nesting species decline near forest edges despite their consistent labeling as an “edge” species led the authors to question the validity of labeling any species as being intrinsically associated with edges (Schlossberg and King 2008).

If species should not be classified as “edge-loving” or “edge-avoiding,” then how can we grapple with the complex array

of species-specific edge responses that has been reported by hundreds of past (and likely future) edge studies? We suggest that instead of labeling species as to their specific edge responses (positive or negative), that species may be labeled according to their general sensitivity to edges. In other words, do they respond to edges or do they ignore them completely? The advantage of this definition is that it can be widely applied to any species or group of species without the unrealistic expectation of observing the same response at all edge types. Within this framework, the type of edge response (positive or negative) is not specified, only a species' general sensitivity to the presence of edges. While understanding the direction of observed edge responses remains a critical goal (as described below), we believe these patterns should not be used to label species.

We suggest that edge sensitivity is a useful label because, while many species are known to respond strongly to edges, many others do not. In fact, a lack of detectable edge response is the most common result reported in the edge literature (Ries et al. 2004) and suggests that many species ignore edges. However, to justify labeling a species as insensitive, one should be able to demonstrate a consistent lack of response at several edge types. This is because most species should not be expected to show responses at all edge types, and even the most consistent edge responders sometimes fail to exhibit a response to edges they are known to be sensitive to. For instance, brown-headed cowbirds *Molothrus ater* are famously drawn to forest-pasture edges (Lowther 1993), but some studies have shown no pattern relative to edges (Goquen and Mathews 2000). Further, an extensive review of the edge literature show that when variability is reported in edge responses, it is almost always that neutral responses are mixed with uni-directional edge responses, rather than an edge response changing direction (i.e. from positive to negative, or vice-versa). This "neutral response" is often the result of confounding factors (such as edge orientation or contrast) that tend to weaken edge responses and make them harder to detect (Ries et al. 2004), but may also be due to low statistical power. Our objectives here are to 1) define edge sensitivity, 2) describe, based on current knowledge, which species might be considered edge sensitive or insensitive, 3) develop a framework for studying edge sensitivity, and 4) provide an example based on our own field work on butterflies in southeastern Arizona.

What is edge sensitivity?

We define edge-sensitive species as those that show edge responses to one or more edge types. In contrast, we define edge-insensitive species as those that rarely, if ever, show responses to any edge type. Like most classifications presented as a dichotomy, in reality most species probably exist along a 'sensitivity spectrum' and we propose that the most useful approach is to rank where species lie along this spectrum and understand the factors associated with the probability of observing or not observing edge responses. We propose a general approach to ranking below, and give a specific method in our case study. Factors that correlate with these rankings might be extrinsic, meaning environmental conditions influence the probability of observing an edge

response, or intrinsic, meaning that a particular species or group tends not to perceive or respond to habitat edges. It is important to stress that if considering sensitivity a continuous rather than a dichotomous trait, it is not necessary for a species to always (or never) show a response to edges to be considered edge sensitive (or insensitive). As more species are ranked according to their edge sensitivity, it becomes possible to determine the consistency of edge sensitivity patterns and if certain extrinsic conditions or intrinsic characteristics are associated with the probability of observing an edge response.

While more general than past categorical approaches, this approach acknowledges the fact that most edge-sensitive species show a variety of responses (positive, negative and neutral). Of course, the direction of observed edge responses (i.e. increased or decreased abundances near the edge) remains critical information and will predict how a species is likely to respond to fragmentation. We therefore suggest that efforts to identify edge-sensitive species should be paired with models that are successful in predicting or understanding the direction of observed edge responses. We presented a model (Fig. 1 in Ries and Sisk 2004) that suggests that organisms should avoid edges with habitats they do not prefer and should ignore edges where habitat quality is equal on both sides. Organisms may prefer edges if their resources are found in greatest abundance there, or if their resources are divided between the two adjacent habitats. Another predictive model for birds at forest-open edges was based on an extensive meta-analysis of the literature (Brand 2004) and found that positive and negative responses were predicted largely by habitat use.

The success of these models argues against abandoning efforts to predict edge responses, but the results also suggest that it is unrealistic to label species or groups of species relative to the direction of their edge responses. Despite this, we suggest that any framework that helps us grapple with the complexity of multiple species responses in heterogeneous landscapes – where edges abound – is valuable. Furthermore, as we hope to demonstrate, taking our suggested approach has the potential to help us understand why certain species seem to be sensitive or insensitive to edges, and whether those species share any biological traits that would make their response patterns more predictable.

According to an exhaustive review of the edge literature (Ries et al. 2004), species from diverse taxa show no response to edges about 70% of the time. This may underestimate edge sensitivity, however, since many of these studies have low replication and, therefore, insufficient statistical power to detect subtle responses. Additionally, some studies may not be designed to detect edge responses at the scale at which they occur (Laurance 2004). For instance, a recent study of edge effects in beetles found that of the 78 most common species, almost 90% showed a significant edge response, and many of these responses penetrated up to 1 km into patch interiors (Ewers and Didham 2008). Nevertheless, it is clear that weak or absent edge responses are common in nature, indeed the most common outcome according to an extensive, 60-year literature. Therefore, it is crucial that we not only understand species' edge responses where they do occur, but also where and why they do not occur (Ries et al. 2004). Understanding where edge responses do not occur, and what

factors control edge sensitivity, may help us identify circumstances where species are less subject to the negative impacts of fragmentation (separate, of course, from related habitat loss).

There is strong evidence in the literature that extrinsic factors influence the likelihood of observing edge responses. The factors most often identified as either weakening or eliminating edge effects are edge orientation and structural edge contrast (Ries et al. 2004). Edge responses tend to be stronger, and thus more likely to be detected at south-facing edges (in the Northern Hemisphere) and at edges with greater structural contrast, which is generally defined by relative vegetation height. These variables may strengthen or weaken edge responses, depending on the species, and are rarely controlled for in field studies. It is important to note that over multiple studies, when species and edge type are held constant, significant responses are almost always in the same direction, but are usually mixed with some neutral responses (Ries et al. 2004). This could be due to low statistical power, confounding variables such as those listed above, or other ecological factors that may weaken or negate edge responses. Therefore, a species need not always show significant edge responses to be considered edge sensitive, although sensitivity to environmental variables may underlie lower sensitivity to edges in general. While such extrinsic factors may explain some of the within-species variability in edge responses reported in the literature, a general lack of response may be due to an intrinsic insensitivity to edges.

Identifying intrinsically edge-insensitive species is less straightforward than identifying edge-sensitive ones. First of all, little attention has been given to species that do not respond to edges, so consistent non-responders have generally not been noted in the literature. Secondly, species are rarely measured at multiple edge types, making it difficult to establish that there is a general lack of response. One way to gauge edge insensitivity is to examine cases where species do not respond to an edge under conditions where an edge response is most expected (i.e. near edges of preferred and non-preferred habitat or an edge between habitats that contain divided resources). Another approach is to measure responses at several edge types, especially the edges commonly found in habitats where the species is most abundant. Species that rarely, if ever, show an edge response, especially where they are most expected, should be considered edge insensitive.

Edge sensitivity as a framework for future research

Understanding when edge responses are more or less likely to occur should become a focus of future edge studies. This does not mean that we should abandon efforts to develop models and frameworks to understand the circumstances under which we observe positive versus negative edge responses. There has been substantial progress in predicting the direction of particular responses (Brand 2004, Ries et al. 2004), as well as in explaining the mechanisms underlying observed positive and negative edge responses (Fagan et al. 1999, Lidiker 1999). However, there has been little effort to understand why species fail to respond – that is, why they are insensitive – despite this being the most common out-

come from studies of edge effects. Confounding, extrinsic landscape factors, such as edge orientation and structural contrast between adjoining habitats, deserve more attention because these factors have been shown to weaken or eliminate edge responses (Ries et al. 2004). Furthermore, orientation and contrast are factors that can be easily quantified and, along with information on vegetative composition and structure, can be important descriptors of conditions and resources encountered at edges, factors that undoubtedly affect responses.

Intrinsic factors, those directly related to the species' biology, may cause certain species to be generally insensitive to edges, no matter the extrinsic conditions. Some authors have proposed biological traits that might be associated with edge sensitivity, including negative relationships with home range and body size (Wiens et al. 1985) and mobility (Wiens et al. 1985, Ewers and Didham 2006). A recent meta-analysis of the bird literature showed that there were some traits associated with the probability of showing responses to forest edges, including nest type and placement, body size and ecological plasticity (Brand 2004), supporting the idea that some intrinsic traits are associated with edge sensitivity. Identifying the life-history or ecological characteristics that are associated with intrinsic sensitivity to edges will help to improve future predictions of species-level responses to fragmentation and landscape change. We therefore suggest that ranking species as to their edge sensitivity and determining the circumstances under which they exhibit edge responses should be a focus of future edge research. However, even if no unifying characteristics can be found, simply knowing that certain species tend to ignore edges will be helpful in understanding their ecology and planning for their management. Ideally, a system for evaluating edge sensitivity will be based on responses at multiple edges, incorporate expectations based on habitat associations and take into account the statistical power of the study, and we present one such metric below. However, this level of rigor may not be achievable in many studies, so we do not propose a standard metric for ranking edge sensitivity. Instead, we suggest that multiple approaches inspired by the information available can be employed to generate rankings that are broadly comparable. As information accumulates, these rankings can be revised, standardized and expanded.

Case study: butterflies in southeastern Arizona

From 1999–2001 we studied the edge responses of the 15 most common butterfly species at twelve edge types in riparian habitat along the San Pedro River in southeastern Arizona (Ries and Sisk 2008). The objective of that study was to test the predictions of our model of edge responses (Ries and Sisk 2004). Like other tests of our model (Ries et al. 2004), unpredicted neutral responses (where we observed no response under conditions where we predicted a positive or negative edge response) were the most common source of unexplained variation. When edge responses were observed, however, they were almost always in the direction predicted. Here, we explore both extrinsic and intrinsic factors that may have contributed to the abundance of unexplained neutral responses observed in our study. In so doing, we hope to provide a framework for future studies of edge sensitivity.

In order to carry out our study, the mosaic of habitats comprising the riparian corridor along the San Pedro River was divided into three zones: floodplain forests, upland riparian and surrounding desert scrub (Ries and Sisk 2008). The upland riparian zone was further divided into three different classes based on woody vegetation structure: open grassland, mesquite forest and a 'mix' of grassland and mesquite that could be characterized as mesquite savannah. These categorizations resulted in five vegetation classes that captured two axes of variability that are known to be important to butterflies: moisture and canopy closure (Scoble 1992). The juxtaposition between these five vegetation classes created six habitat pairs (forest–grassland, forest–mix, forest–mesquite, grassland–scrub, mix–scrub, mesquite–scrub), and edge responses were measured separately on each side of the discrete boundary between each pair. Mean vegetation height varied greatly between the habitat types and the juxtaposition of habitats resulted in a range of structural edge contrasts. We modeled edge responses separately on each side of the edge, resulting in twelve edge types.

At each of the 12 edge types, we measured densities of 15 species in transects composed of contiguous 10 × 10 m plots that were placed perpendicular to the edge and extended 50–100 m into habitat interiors. On average there were 13 transects in four or five independent study areas for each edge type, and surveys were conducted over the course of three years. Using information on mean densities (excluding edge plots) within each habitat and also information on the distribution of host and nectar plant resources, we generated predictions from our model for each of the 15 species at each edge type. Model predictions were generated based on whether there were significantly higher or lower detections in the adjacent patch (predicting negative or positive edge responses respectively) or if there were complementary resources (either host or nectar resources concentrated in the adjacent patch). In that case, positive edge responses were always predicted regardless of observed vegetation class associations. Predictions were categorical (positive, negative, or neutral) and we then compared observed categorical responses to those predicted (Table 1). Full descriptions of the methods used to develop edge response predictions and to measure and compare observed edge responses are detailed in Ries and Sisk (2008). It is worth noting that of the 15 species studied, 12 showed positive, negative and neutral responses, depending on the edge type (Ries and Sisk 2008), again reinforcing the point that most species will show different edge responses depending on the type of edge studied.

We developed a database that recorded, for each species at each edge type in each year, what edge response was predicted and what edge response was observed. The resulting database contains 211 records for the 15 species at 12 edge types over three years. We created a 3 × 3 contingency table for each species where we organized negative, neutral and positive predictions in rows and negative, neutral and positive observations in columns (Table 1) and quantified the number of times each of the nine outcomes was observed. Outcomes were scored as 'correct' if the predicted response was observed, 'wrong' if a significant edge response was observed that was not predicted, or 'neutral' if no response was observed where a positive or negative edge response was

Table 1. Evaluation of model performance. A 3 × 3 contingency table illustrates cases where the model is correct (the predicted edge response was observed), 'wrong' (an unpredicted positive or negative response was observed) or 'neutral' (a neutral response was observed when a positive or negative response was predicted). Reprinted from Ries and Sisk (2008).

Prediction	Observation		
	–	0	+
–	correct	neutral	wrong
0	wrong	correct	wrong
+	wrong	neutral	correct

predicted (Table 1). It is this last category ('neutral') that we focus on for this analysis; because it quantifies the prevalence of edge responses only where they are most expected, it is the best indicator of sensitivity. All following analyses were done in R ver. 2.10.0 (R Development Core Team 2009).

Extrinsic factors

Our study design allowed us to explore the impact of edge contrast, classified by the magnitude of differences in vegetative composition and structure into categories of low, medium and high. We were not able to examine the impact of orientation because our edges were oriented east–west rather than north–south. Low-contrast edges were identified as occurring at grassland–scrub and forest–mesquite habitat pairs. Medium-contrast edges were identified as those edges between forest–mix and mix–scrub habitat pairs. High-contrast edges were found at forest–grassland and mesquite–scrub habitat pairs. We only included the 121 cases where we made directional predictions (i.e. predicted a positive or negative edge response). We used Fisher's exact test to determine if the occurrence of correct, 'neutral' and 'wrong' outcomes (Table 1) differed in proportion among low, medium and high contrast edges. There was no statistical support ($p = 0.17$) that our ability to predict edge responses differed among any of the categories; and specifically, the proportion of 'neutral' outcomes was very similar between all three contrast levels (68%, 71%, and 72% for low, medium and high contrast edges respectively).

Intrinsic factors

We hypothesized that increased body size would be associated with decreased edge sensitivity (*sensu* Wiens et al. 1985), that greater hostplant specificity would be associated with increased edge sensitivity (based on a past association with edge sensitivity and habitat specificity, Ries et al. 2004), and that greater vulnerability to predation would be associated with increased edge sensitivity (based on a strong association with edges and increased predation rates, Chalfoun et al. 2002). To test these relationships, we used residual scores for 'neutral' outcomes, adjusted to cell totals, to determine if we observed more 'neutral' outcomes than expected due to chance. The specific measure is from Agresti (1996):

$$\sum_{i=1,3} \frac{o_{i,2} - e_{i,2}}{\sqrt{e_{i,2}(1 - p_{i+})}(1 - p_{+2})} \quad (1)$$

where o = observed cell value, e = expected value if observations were randomly distributed (but holding fixed the marginal row and column totals), p_{i+} = marginal row total divided by the grand total and p_{+j} = marginal column total divided by the grand total. These adjusted residuals are calculated from the two cells in the 3×3 contingency table that represent cases where either positive or negative responses were predicted, but no response was observed (Table 1). In our case, the two cells with these 'neutral' outcomes were in positions 1,2 and 3,2, but that may not always be, so subscripts in Eq. 1 should be adjusted accordingly.

There are two major advantages to this measure. The first is that it allows us to ignore cases where we observed a predicted neutral response (in other words, cases where no response was observed, and none predicted). We believe these cases are not informative about edge sensitivity because edge responses were not expected. Second, the residuals are adjusted to the overall number of neutral responses observed in the entire study, thereby taking statistical power into account. The resulting residual scores show which species exhibited more 'neutral' outcomes (meaning that a neutral response was observed when a significant negative or positive response was expected) than expected by chance, given the total number of times neutral responses were recorded in the study. Residual scores for neutral outcomes, taken from Ries and Sisk (2008, Table 2) and reproduced here in Table 2, provide a means of ranking edge sensitivity, by developing a 'neutrality' score. Negative 'neutrality' scores mean that neutral outcomes were less frequent than expected by chance, thus these species are relatively more edge sensitive. Conversely, a positive 'neutrality' score means that more neutral responses were recorded than expected, and these species are less edge sensitive.

To explore hypothesized mechanisms underlying edge sensitivity, each of the fourteen species was given an ordinal

score to indicate body size, hostplant specificity and vulnerability to predation. Scores are displayed and explained in Table 2. Kendall's coefficient of rank correlation, a non-parametric test of association (Sokal and Rohlf 1981), was used to compare the sensitivity rankings to the scores in each of the three categories of ecological characteristics. Tests were two-tailed since any observed pattern would be of interest (Lombardi and Hurlbert 2009), but we did make a priori predictions regarding the direction of association and so paid closer attention to trends in the hypothesized direction. Vulnerability to predation was the only factor tested that showed any relationship with edge sensitivity. More vulnerable species showed a non-significant trend towards greater sensitivity to edges ($p = 0.15$, Table 2), which is in the direction predicted. We also noticed, post-hoc, a relationship between edge sensitivity and wing coloration. The most edge-sensitive species had relatively lighter-colored wings, while the least edge-sensitive butterflies in this study were predominately brown or black. We included information about wing color in Table 2, but we did not carry out a formal analysis since we did not make any a priori predictions about wing coloration.

Discussion

Edge responses have been studied for decades because they are increasingly common in most landscapes (Sisk et al. 1997), critical to our understanding of how habitat mosaics influence species' distributions (Ewers and Didham 2006, Laurance 2008) and important for conservation planning (Lindenmayer et al. 2008). More recently, edge responses have been shown to be the most common mechanism underlying area sensitivity and indeed many area effects are really just scaled-up edge effects (Fletcher et al. 2007). Classifying

Table 2. Species traits and edge sensitivity rankings by neutrality score (more sensitive species have a lower score).

Species	Neutrality score*	Family	Dominant wing color	Size [†]	Host plant specificity [‡]	Vulnerability to predation [§]
<i>Eurema proterpia</i>	-2.4	Pieridae	orange	2	1	4
<i>Nathalis iole</i>	-2.2	Pieridae	yellow	1	2	4
<i>Euptoieta claudia</i>	-1.9	Nymphalidae	orange/brown	2	3	3
<i>Colias eurytheme</i>	-1.4	Pieridae	yellow	2	2	4
<i>Phoebis sennae</i>	-0.6	Pieridae	yellow	3	1	4
<i>Colias cesonia</i>	-0.3	Pieridae	yellow	3	2	4
<i>Danaus gilippus</i>	-0.2	Nymphalidae	orange/black	3	2	1
<i>Pyrgus albescens</i>	0	Hesperiidae	black/white	1	2	2
<i>Brephidium exilis</i>	0	Lycaenidae	bronze	1	2	4
<i>Battus philenor</i>	0	Papilionidae	black	3	1	1
<i>Eurema nicippe</i>	0.5	Pieridae	orange	2	1	4
<i>Pholisora catullus</i>	0.8	Hesperiidae	brown	1	3	2
<i>Libytheana carinenta</i>	0.9	Libytheidae	brown	2	1	2
<i>Chlosyne lacinia</i>	1	Nymphalidae	black	2	2	3
Correlation of ranks [¶]				-0.05 ($p = 0.81$)	-0.04 ($p = 0.85$)	-0.3 ($p = 0.15$)

*a score based on the adjusted residuals indicating whether neutral responses were more or less abundant than expected based on independent distribution of observations. See text for details.

[†]1 = small (~2–4 cm wingspan), 2 = medium (~4–7 cm wingspan), and 3 = large (usually > 6 cm wingspan).

[‡]1 = only known to use a few species or generally restricted to one genus, 2 = generally restricted to one plant family, 3 = known to commonly use more than one family.

[§]1 = poisonous, 2 = camouflaged or hidden, 3 = unpalatable larvae, 4 = palatable/conspicuous.

[¶]Kendall's coefficient of rank correlation.

species according to what is assumed to be a 'typical' edge response is a common approach to untangling the observed complexity of edge responses, yet it is fundamentally flawed because species should not be expected to show the same edge response at different edge types (Ries and Sisk 2004). Instead, the consideration of a species' overall sensitivity to edges provides a more useful way to classify species. The need to better understand edge sensitivity is illustrated by the fact that most reported edge responses are neutral (Ries et al. 2004), yet current understanding of mechanisms underlying edge responses suggests that species should show responses at most edges (Ries and Sisk 2004). How consistently species respond to edges in situations where responses are most expected provides an indication of the edge sensitivity of a particular species.

While many species have been identified as regularly responding to edges, no species has yet been identified as being edge insensitive. This is due to a general bias against negative results, and because most edge studies do not measure responses at enough edge types to support a determination of insensitivity. We suggest that one future focus for edge research and literature reviews should be comparing observed responses with predicted responses, thereby allowing the determination of the edge sensitivity for a suite of species. As appropriate theoretical constructs are developed and refined, and as more species are classified based on their sensitivity, it will be possible to identify ecological traits correlated with and, potentially, driving edge sensitivity. This approach is necessarily distinct from efforts to understand the direction of observed edge responses, because edge response direction is dependent largely on the specific edge studied, while sensitivity may be a species-level trait. Our case study of edge responses of butterflies in desert riparian habitat shows the value of this approach. We have previously shown that the direction of observed edge responses for these butterflies is highly predictable, but that understanding neutral responses remains the dominant source of unexplained variation (Ries and Sisk 2008). This is true for other tests of our model as well (Ries et al. 2004). Here we demonstrated how sensitivity can be scored by evaluating the prevalence of neutral outcomes, relative to those expected under a null model and ignoring cases where no response was expected (Eq. 1). This sensitivity measure is a useful response variable for evaluating ecological traits thought to be associated with edge sensitivity.

The only factor we examined that showed any relation to edge sensitivity was vulnerability to predation, with more vulnerable species showing a trend towards higher edge sensitivity (Table 2). Edges have long been associated with increased predation and parasitism (Chalfoun et al. 2002), although species often congregate at edges despite higher predation rates (Battin 2004). We are not aware of any study that shows increased edge-related predation in butterflies, although bird predation has been shown to be higher for mantids at edges (Ries and Fagan 2003). In our study, species that were more vulnerable to predation seemed to be more sensitive to edges. However, it is also worth noting that most edge-sensitive, vulnerable species were from the sub-family Coliadinae within the family Pieridae (Table 2). It is therefore possible that other factors common to this sub-family may explain their increased sensitivity to edges.

For instance, we noticed post-hoc that lighter colored butterflies (such as all Coliadinae) were more edge-sensitive compared to the darker species showing lower edge-sensitivity (Table 2). Lighter colored butterflies absorb radiation more slowly than darker butterflies (Scoble 1992) and so may be relatively inefficient at capturing radiant heat. Therefore, sensitivity to microclimate is an alternative explanation for the edge sensitivity of these butterflies. Future studies of edge sensitivity in butterflies should be designed to test whether vulnerability to predation or wing coloration is affecting edge responses in butterflies, ideally with a suite of species that allow these factors to be disentangled from phylogenetic associations.

There have been great strides in understanding the direction of observed edge responses in nature (Brand 2004, Ries and Sisk 2004), while the vast majority of unexplained variability remains unexpected neutral responses. We propose a research approach that will help generate predictions that relate to mechanisms underlying this lack of edge sensitivity. Predictive models help advance the study of edge effects by allowing tests of hypothesized relationships and underlying mechanisms, resulting in a more efficient and quantitative assessment of typically variable edge responses. The vast majority of reported edge responses are neutral, and little progress has been made in understanding or predicting these outcomes. Although non-responsiveness is generally not a target of most studies, in the context of habitat fragmentation it is important to know which species are likely to be sensitive to the proliferation of edge habitat. By identifying the species which are most likely to ignore edges – as well as those that are most sensitive – we can increase our understanding of the landscape-level factors that drive edge effects, while identifying the species that are most and least likely to be the most vulnerable to the dynamics of ongoing landscape change.

Acknowledgements – This research was supported by the Strategic Environmental Research and Development Project (CS-1100 and SI-1597). Helpful comments were offered by James Battin, Robert M. Ewers, Shannon Murphy and Louis Imbeau.

References

- Agresti, A. 1996. An introduction to categorical data analysis. – Wiley.
- Baker, J. et al. 2002. The edge effect and ecotonal species: bird communities across a natural edge in southeastern Australia. – *Ecology* 83: 3048–3059.
- Battin, J. 2004. When good animals love bad habitat: ecological traps and the conservation of animal populations. – *Conserv. Biol.* 18: 1482–1491.
- Brand, L. A. 2004. Prediction and assessment of edge response and abundance for desert riparian birds in southeastern Arizona. PhD. thesis. – Colorado State Univ., Fort Collins, USA.
- Chalfoun, A. D. et al. 2002. Nest predators and fragmentation: a review and meta-analysis. – *Conserv. Biol.* 16: 306–318.
- Ewers, R. M. and Didham, R. K. 2006. Confounding factors in the detection of species responses to habitat fragmentation. – *Biol. Rev.* 81: 117–142.
- Ewers, R. M. and Didham, R. K. 2008. Pervasive impact of large-scale edge effects on a beetle community. – *Proc. Natl Acad. Sci. USA* 105: 5426–5429.

- Fagan, W. F. et al. 1999. How habitat edges change species interactions. – *Am. Nat.* 153: 165–182.
- Fletcher, R. J. et al. 2007. The role of habitat area and edge in fragmented landscapes: definitively distinct or inevitably intertwined? – *Can. J. Zool.* 85: 1017–1030.
- Goquen, B. C. and Mathews, E. N. 2000. Local gradients of cowbird abundance and parasitism relative to livestock grazing in a western landscape. – *Conserv. Biol.* 14: 1862–1869.
- Hansen, A. J. and Urban, D. L. 1992. Avian response to landscape pattern – the role of species life histories. – *Landscape Ecol.* 7: 163–180.
- Imbeau, L. et al. 2003. Are forest birds categorised as "edge species" strictly associated with edges? – *Ecography* 26: 514–520.
- Laurance, W. F. 2004. Do edge effects occur over large spatial scales? – *Trends Ecol. Evol.* 15: 134–135.
- Laurance, W. F. 2008. Theory meets reality: how habitat fragmentation research has transcended island biogeographic theory. – *Biol. Conserv.* 141: 1731–1744.
- Lidicker, W. Z. 1999. Responses of mammals to habitat edges: an overview. – *Landscape Ecol.* 14: 333–343.
- Lindenmayer, D. et al. 2008. A checklist for ecological management of landscapes for conservation. – *Ecol. Lett.* 11: 78–91.
- Lombardi, C. M. and Hurlbert, S. H. 2009. Misprescription and misuse of one-tailed tests. – *Austral Ecol.* 34: 447–468.
- Lowther, P. E. 1993. Brown-headed cowbird (*Molothrus ater*). – In: Poole, A. (ed.), *The birds of North America online*. Cornell Lab of Ornithol.
- Ries, L. and Fagan, W. F. 2003. Habitat edges as a potential ecological trap for an insect predator. – *Ecol. Entomol.* 28: 567–572.
- Ries, L. and Sisk, T. D. 2004. A predictive model of edge effects. – *Ecology* 85: 2917–2926.
- Ries, L. and Sisk, T. D. 2008. Butterfly edge effects are predicted by a simple model in a complex landscape. – *Oecologia* 156: 75–86.
- Ries, L. et al. 2004. The ecology of habitat edges: mechanisms, models and variability explained. – *Annu. Rev. Ecol. Evol. Syst.* 35: 491–522.
- Schlossberg, S. and King, D. I. 2008. Are shrubland birds edge specialists? – *Ecol. Appl.* 18: 1325–1330.
- Scoble, M. J. 1992. *The Lepidoptera*. – Oxford Univ. Press.
- Sisk, T. D. et al. 1997. Bird assemblages in patchy woodlands: modeling the effects of edge and matrix habitats. – *Ecol. Appl.* 7: 1170–1180.
- Sokal, R. R. and Rohlf, F. J. 1981. *Biometry* (2nd ed.). – W. H. Freeman and Sons.
- Strayer, D. L. et al. 2003. A classification of ecological boundaries. – *BioScience* 53: 723–729.
- Villard, M. A. 1998. On forest-interior species, edge avoidance, area sensitivity, and dogmas in avian conservation. – *Auk* 115: 801–805.
- Wiens, J. A. et al. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. – *Oikos* 45: 421–427.