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Habitat edge responses of generalist predators are predicted by prey and structural resources

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Abstract. Generalist predators are thought to be less vulnerable to habitat fragmentation because they use diverse resources across larger spatial scales than specialist predators. Thus, it has been suggested that generalist predators may respond positively to habitat edges or demonstrate no edge response, because they can potentially use prey resources equally well on both sides of the habitat edge. However, most predictions about generalist predator responses to the habitat edge are based solely on prey resources, without consideration of other potential drivers. For instance, structural resources are essential for some species to build webs to capture prey or to avoid intraguild predation and cannibalism. In this study, we used both prey and structural resources to predict the response of four predator functional groups (hunting spiders, web-building spiders, aerial predators, and epigeic predators that feed on the detrital/algal food web) to a habitat edge between two salt-marsh grasses (*Spartina alterniflora* and *Spartina patens*). We found that generalist predators largely demonstrated negative responses to the habitat edge and had distinct habitat associations. Positive edge responses were only observed in one functional group (hunting spiders), and this pattern was driven by the two most abundant species. Negative responses to the habitat edge were more common among taxa and were better explained by structural resources rather than prey resources in the two habitats. Although it is generally acknowledged that specialists decline in fragmented habitats, generalists are thought to be more resilient. However, our research demonstrates that even generalists have habitat structural or food resource requirements that may limit their resilience to habitat loss and fragmentation.

Key words: ecological boundary; edge effects; generalist predator; habitat fragmentation; predictive model; resource distribution.

Introduction

Habitat loss and fragmentation are considered to be the primary factors leading to species extinction worldwide (Wilson 2002). Yet, despite decades of research and literature reviews, it remains difficult to predict which species will be most vulnerable. To preserve biodiversity, it is essential that we understand species' responses to habitat fragmentation, which are influenced by three drivers: edge effects, area effects, and connectivity (Ewers and Didham 2006, Murphy et al. 2016, Ries et al. 2017, Fletcher et al. 2018). Edge effects are a key dynamic to understand how species respond to habitat fragmentation because fragmentation is associated with increased edge habitat (Sisk et al. 1997, Ries et al. 2017), and most patch-based area effects are simply scaled-up edge effects (Fletcher et al. 2007). In addition, species' responses to connectivity are often understood through their responses to edges; studies that test relative impacts of edge vs. connectivity find that edge responses dominate (Johnson and Haddad 2011, Evans et al. 2012), and models of functional connectivity often include edge responses as one of the key predictors (Pe'er et al. 2011).

Higher-trophic-level consumers are often negatively affected by habitat fragmentation because they are dependent on resources at lower trophic levels (Didham et al. 1998, Zabel and Tscharntke 1998, Holt et al. 1999, Dobson et al. 2006, Krauss et al. 2010). The predicted negative impact of fragmentation on predators is based on Island Biogeography Theory (MacArthur and Wilson 1967) and the trophic-rank hypothesis (Holt et al. 1999), which suggest that species losses that occur in smaller, more isolated patches should magnify up the food chain as each trophic level becomes increasingly vulnerable to the loss of resources at the level below. Thus, we might predict that habitat edges would negatively affect higher-trophic-level consumers such as predators. Although

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organisms at lower trophic levels may respond to resources at a microhabitat scale, generalist predators often use resources on a larger, macrohabitat scale (McCann and Rooney 2009) and often use spatially separated prey resources in order to meet their energy demands (Fagan et al. 1999, Rooney et al. 2006, McCann and Rooney 2009). Empirical research has also demonstrated that higher-order generalist predators and parasitoids spatially track multiple prey resources (Eveleigh et al. 2007). Such resource coupling by generalist predators could diminish the negative impact of habitat edges on higher trophic levels, which may lead to the widely held view that predation generally increases along habitat edges (e.g., Lahti 2001, Ries et al. 2017, and references therein). A recent meta-analysis of terrestrial arthropod food webs found that consumption rates (by predators, herbivores, or parasitoids) are higher at edges compared to interiors, but surprisingly this effect was weakest for predators (Martinson and Fagan 2014). When subjected to an empirical examination of the literature, the consensus emerges that predator densities and predation rates near edges are quite variable (as reviewed in Murphy et al. 2016, Ries et al. 2017). However, the single study that considered critical resources used by different predator species was able to predict edge responses of three predators, one generalist and two specialists, correctly (Wimp et al. 2011).

One key aspect of correctly predicting predator responses to habitat edges is the degree to which they are dietary specialists or generalists. For example, specialist predators in natural systems often demonstrate negative edge responses (Cronin 2009, Wimp et al. 2011), whereas generalist predators found in agricultural systems are more likely to spill over into the adjacent natural habitat relative to specialist predators (Rand and Lauda 2006, Rand and Tscharntke 2007, Blitzer et al. 2012, Frost et al. 2015). A recent meta-analysis showed that for herbivore consumers, generalists are less affected by bottom-up effects than are specialists (Vidal and Murphy 2018), but whether this is true for higher-trophic-level consumers is less clear. Although predictions for specialists that track their prey are fairly straightforward (Wimp et al. 2011), it is harder to predict responses for generalists with diverse prey resources. Whether critical resources may also be used to predict generalist predator responses to habitat edges is unknown.

Ries and Sisk (2004) created a simple set of predictions for any species at any edge type based on resource distribution in adjoining habitats. Predictions from this edge-resource model (hereafter referred to as the ERM) are based solely on known habitat associations, augmented by any information on resources gained from adjacent habitats. Resources in adjoining habitats can be supplementary (available in both habitats) or complementary (available only in one habitat). Some species have resources that are available only in a single habitat; these species may decline in density from the interior to the habitat edge, and this is a negative response to the habitat edge. Alternatively, species may have similar densities in both the habitat interior and edge, and thus although these species demonstrate a habitat response (they are only found in the habitat where their resources are found), they have no response to the habitat edge (also called a neutral edge response). It is important to distinguish between these two alternatives because how a species responds to fragmentation would differ depending on whether they have just a habitat response or both a habitat and an edge response. Because the edge-to-interior ratio of a habitat increases with a decrease in patch size, if a species is both restricted to its habitat and also negatively affected by the edge, then we would expect greater declines in density with habitat fragmentation relative to a species that has a habitat association, but no edge response. If resources are divided equally across habitats and are supplementary, then no habitat or edge response is predicted because the species is not adversely affected by changes in the habitat or edge. Finally, if a species has a resource that is found only in one habitat and not in the adjacent habitat, but a different resource is found in the adjacent habitat and not in the first habitat (i.e., complementary resources), then a positive edge response is predicted wherein densities are greatest along the habitat edge. Notably, there is nothing in the model construction that takes any species characteristic into account, including trophic level or degree of specialization. Although this framework therefore ignores the specifics of taxon biology or behavior, it has successfully predicted species' edge responses across diverse terrestrial taxa, including birds, mammals, plants, and butterflies (Ries et al. 2004, Ries and Sisk 2008), as well as species in aquatic systems.

We conducted a field experiment in which we tested the mechanisms that structure edge responses by four functional groups of generalist predators (hunting spiders, web-building spiders, aerial predators, and epigeic predators that feed on the detrital/algal food web); we performed our research in a naturally fragmented ecosystem, a well-studied intertidal marsh dominated by two grasses, *Spartina patens* and *Spartina alterniflora* (hereafter SP and SA, respectively). To make predictions for each predator functional group, we quantified two critical predator resources: prey density (47 prey species total, as seen in Appendix S1) and habitat structure. Although the benefits of prey resources are obvious, complex habitat structure is also considered a critical resource for predators in this system, because it provides a more favorable microclimate for predators (Uetz 1979), and refuge from cannibalism and intraguild predation (Langellotto and Denno 2004). Thus, differences in structural resources between adjacent habitats could ameliorate abiotic conditions or decrease antagonistic interactions among predators, thereby affecting predator responses to the habitat edge. We manipulated habitat complexity via the removal or addition of dead plant material (thatch) and tracked impacts on predator density. We then examined these two critical resources in combination (i.e., prey density and habitat structure) to examine generalist predator responses to habitat edge. Previously, we examined the responses of three predators, one generalist and two specialists in the system; we found that the ERM correctly predicted the edge responses of all three predators (Wimp et al. 2011). In this study, we focused on the much larger group of generalist predators to determine the generality of our findings (48 predator species across the four functional groups mentioned above; see Appendix S1). We use the ERM to make predictions about each predator functional group (Table 1; see Methods) in our system, and use the observed responses to ask two questions that will help us understand the ubiquity or lack thereof of predator edge responses: (1) Can the response of generalist predators to the habitat edge be predicted by prey and structural resources? (2) For the most abundant generalist predators, is prey density or habitat structure more important for predicting predator density at edges?

METHODS

Study site and organisms

We studied the edge responses of arthropod species at an expansive salt marsh near Tuckerton, New Jersey, USA (39°30.8′ N, 74°19.0′ W), that is dominated by natural monocultures of two grasses: SP and SA. Although each plant species grows in monoculture, these two species frequently co-occur; SP often grows in isolated patches completely surrounded by a "matrix" of SA. Where these two species meet, they form a distinct edge (Appendix S2: Figs. S1, S2; Wimp et al. 2011).

Generating predictions

Although sympatric food webs are always interconnected to some degree, there are two fairly distinct prey food webs for generalist predators that can be defined in the salt-marsh system: one based on live plant material (*Spartina*) and the other based on algae, detritus, and associated microbes (epigeic). A wealth of life-history information about preferred hunting targets and strategies already exists for salt-marsh predator functional groups (Döbel et al. 1990, Denno et al. 2002, 2003, Finke and Denno 2004, Lewis and Denno 2009, Murphy et al. 2012, Wimp et al. 2013). We collected data on prey densities and found that the herbivorous prey did not differ across SP interior, SP edge, SA interior, or SA edge habitats (Appendix S3); these results conflict with how we have found prey densities to differ across these habitats in the past (Wimp et al. 2011), but variability in prey availability is to be expected in most systems. However, epigeic prey were greater in the SP interior, declined

TABLE 1. Predicted and observed edge response for four groups of generalist predators (hunting spiders, web-building spiders, and aerial and epigeic predators) due to prey and habitat resources found in edge habitats of *Spartina alterniflora* (SA) and *Spartina patens* (SP). Throughout the table, the upward arrow is an abbreviation for "greater" and indicates in which habitat resources or densities will be greater compared to the other habitat. Using hunting spiders as an example, their prey and structural resources were greater in SP relative to SA. Thus, their edge response was predicted to be negative because resources are greater in SP. The "observed response to edge by functional group" column reports the responses observed in our experiment and the individual species response column shows how additive individual species' responses combined to produce the observed edge response for that entire functional group of predators. Continuing for hunting spiders, although the overall observed edge response for the functional group was positive, the response by individual species was mixed; only the most abundant species demonstrated a positive edge response, thus driving the overall pattern, but the rare species had negative edge responses with densities greater in SP, which follows our prediction.

Predator functional group	Prey resources	Structural resources	Predicted response to edge (prey and structure considered jointly)	Observed response to edge by functional group	Observed response to edge by individual species
Hunting spiders	↑ in SP	↑ in SP	Negative edge response (↑ in SP)	Positive edge response	Mixed across species *Positive edge response for abundant species* *Negative edge response (↑ in SP) for rare species*
Web-building spiders	↑ in SP	↑ in SA	Positive edge response	Negative edge response (↑ in SA)	Consistent across species *Negative edge response (↑ in SA) for both abundant and rare species*
Aerial predators	↑ in SP	Similar in SA and SP	Negative edge response (↑ in SP)	No edge response (↑ in SP)	Mixed across species *Negative edge response (↑ in SP) for abundant species* *Negative edge response (↑ in SA) or no edge response for rare species*
Epigeic predators	↑ in SP	↑ in SP	Negative edge response (↑ in SP)	No edge response (↑ in SP)	Mixed across species *Negative edge response (↑ in SP) for the most abundant species* *Negative edge response (↑ in SA) for second most abundant species* *Decreased abundance on both sides of the edge for rare species*

along the SP edge, and were lowest in the SA edge and interior habitats (Appendix S3). We then used these prey densities as one resource that may explain generalist predator responses to the habitat edge (Table 1).

In addition to prey resources, differences in habitat structure along the edge alter intra- and interspecific interactions among predators. Both SP and SA are perennials, but they differ in structure. SP retains a deep thatch layer for multiple years, whereas SA has a much sparser thatch layer (Denno et al. 1996). Thus, the deeper thatch layer in SP provides greater structural complexity. Thatch is a critical resource for predators not only because it provides a more favorable microclimate (Uetz 1979), but also because it offers refuge from cannibalism and intraguild predation (Langellotto and Denno 2004). Indeed, previous studies in the same system have found a decrease in intraguild predation and cannibalism among predators with an increase in thatch (Finke and Denno 2006, Langellotto and Denno 2006). Thatch thereby provides a spatial refuge from predation, which in turn increases the densities of hunting spiders (Finke and Denno 2006, Langellotto and Denno 2006); thus, structural resources for hunting spiders are greater in SP (Table 1). Another key difference in structural resources is that SA has erect culms that are ideal substrate for web-building spiders, whereas SP lays flatly with more flexible blades (Appendix S2: Fig. S2). Web-building spiders require a rigid plant architecture that creates scaffolding for web attachment, and the culm structure of SA provides this resource (Döbel et al. 1990); thus, structural resources for web-building spiders are greater in SA (Table 1). Although previous literature exists about the structural requirements of hunting, web-building, and epigeic predators, less is known about aerial predators in the salt-marsh system. The mobility of aerial predators suggests that they should not be affected by structural resources in either SA or SP, and thus we predicted that their structural resource requirements should be similar across these two habitats (Table 1).

We generated predictions about predator responses to the habitat edge based on both prey and structural resources (Table 1). Past implementations of the ERM model made predictions on a species-by-species basis, but we made predictions based on generalist predator functional groups. This is a useful approach because, as is found in most systems, many species were not abundant enough to test separately and are not well studied, and it is therefore difficult to make individual predictions. We predicted that generalist predator responses to the habitat edge would be a function of both prey density and habitat structure, and would differ according to the resource requirements of each group (Table 1). Hunting spiders feed on prey from both *Spartina* and epigeic food webs and overall prey densities are greatest in SP. Additionally, SP supports a more well-developed thatch layer, which decreases cannibalism among hunting spiders (Langellotto and Denno 2006). Thus, because prey and habitat resources for hunting spiders are concentrated in SP, we predicted hunting spiders would be more abundant in SP with a negative edge response (Table 1). Web-building spiders also feed from both food webs and overall prey densities are greater in SP, but structural resources are greater in SA (SA provides sites for web attachment). Thus, we predicted a positive edge response for web-building spiders because the resources found on either side of the edge are complementary (Table 1). Aerial predators (mostly Dolichopodidae) can similarly feed on prey from both *Spartina* and epigeic food webs (Ulrich 2004); thus, overall prey densities are greater in SP. Not much is known about the structural resource requirements of aerial predators, and so we therefore predicted that they would exhibit a negative edge response, because overall prey densities are greatest in SP (Table 1). Epigeic predators feed primarily on epigeic prey that have greater densities in SP, and the structural resources in SP provide a more favorable microclimate, so we predicted that epigeic predators would exhibit a negative edge response with higher densities in SP, because their prey and structural resources are concentrated in SP (Table 1).

Experimental design

In spring 2007, we established seven study areas that were separated from one another by a mean of 333 m (range: 71–576 m). Each area had 12 2 × 2 m plots (six per habitat type), for a total of 84 plots (Appendix S2: Figs. S3, S4). In each area, one plot was located in the center of a SP patch ranging from 6 to 18 m from the edge of the patch, and another plot was located within SA, the same distance from the edge as the associated plot in SP. These two plots were un-manipulated and measured arthropod densities and plant traits characteristic of the habitat interiors for these two *Spartina* species. The 10 other plots per area were located along the habitat edge and were used in the thatch manipulation experiment (see below). For all plots, we measured peak plant biomass and thatch on 13–17 July 2007 using 0.047-m^2 quadrats (following Denno et al. 2002).

We manipulated structural resources along the habitat edge by adding or removing dead *Spartina* plant material or “thatch” (thatch manipulation experiment; see Appendix S2 for details). Thatch biomass in SP is 40% greater than SA; to increase habitat structure in SA we added thatch and to reduce habitat structure in SP we removed thatch. This manipulative experiment provided us with a range of thatch densities and thus a way to determine whether habitat structure was an important predictor of generalist predator densities. We quantified the amount of thatch in each plot with our vegetation quadrats (see above).

Arthropod samples

We assessed arthropod density three times during the growing season (26 June, 17 July, and 4 August 2007), using a D-vac suction sampler (Rincon-Vitova Insectaries, Ventura, California, USA) with a diameter of 21 cm. For each plot, we collected arthropods with three 5-s placements of the D-vac head on the marsh surface. We stored all arthropods in ethanol and later sorted, counted, and identified all individuals to genus and species. New species were sent to experts for verification and identification.

Statistical analyses

To investigate the response of generalist predators and their prey to the habitat edge, we analyzed predator and prey densities from SP and SA edge and interior habitats using an analysis of covariance (ANCOVA; proc mixed, SAS 2002) with habitat (SA or SP) and edge (Edge vs. Interior) as fixed factors, and area and month of collection as random covariates. In this way, we could distinguish between arthropod responses to the two different habitats (SA or SP) vs. an overall response to the habitat edge itself (i.e., a significant difference in density between edge and interior habitats within either SA or SP). Insignificant interaction terms were dropped from the full ANCOVA model. We square-root-transformed the densities of hunting spiders, web-building spiders, and aerial predators, but no transformation was necessary for epigeic predators, which were normally distributed. Additionally, we square-root-transformed the densities of both herbivorous and epigeic prey to meet assumptions.

To examine the effects of prey and habitat structure (thatch) on each group of generalist predators, we performed a multiple regression for each group of generalist predators (hunting spiders, web-building spiders, aerial predators, and epigeic predators) with prey density and thatch as predictor variables. Because generalist predators feed on both herbivorous and epigeic prey, density in each of these groups was combined into a single prey value. To examine the importance of each predictor (prey density and thatch) for each predator group, we first examined the fit of the overall model and then calculated the significance of each partial regression coefficient using a *t*-test. We checked for collinearity between our predictor variables and found that these variables were not correlated (tolerance = 0.929).

RESULTS

Prey and structural resources

We found that densities of herbivorous prey did not differ between SA and SP habitats ($F_{1,12.8} = 0.12$, $P = 0.9$) and only marginally declined along the habitat edge ($F_{1,12.8} = 4.18$, $P = 0.062$; Appendix S3). Epigeic prey were more abundant in SP relative to SA habitats ($F_{1,45.1} = 94.78$, $P < 0.0001$) and declined along the habitat edge ($F_{1,45.1} = 11.64$, $P = 0.0014$; Appendix S3). Thus, combined densities of herbivorous and epigeic prey were greater in SP relative to SA (Appendix S3; Table 1). For structural resources, our thatch manipulation successfully created a range of thatch densities in both SA and SP ($F_{2,58} = 85.3$, $P < 0.0001$; Appendix S4).

Generalist predator edge responses

We predicted that hunting spiders should exhibit a negative edge response with higher densities in SP, because both prey and structural resources were higher in SP, but we observed a positive response by this group when all hunting spiders were considered together. Hunting spiders responded positively to the habitat edge ($F_{1,75} = 9.19$, $P = 0.003$, Fig. 1A), but overall densities were not greater in one habitat type relative to the other ($F_{1,75} = 2.35$, $P = 0.13$). However, this positive edge response was driven by the two most abundant hunting species (*Clubiona* sp. and *Pardosa littoralis*); the remaining 11 hunting spider species demonstrated a negative edge response with greater density in SP relative to SA, as we originally predicted (Fig. 2; Table 1).

We predicted that web-building spiders should have a positive edge response, because prey resources were greater in SP, but structural resources were greater in SA. However, web-building spiders were more abundant in SA ($F_{1,74} = 64.34$, $P < 0.0001$) and were not affected by edge vs. interior habitats ($F_{1,74} = 0.80$, $P = 0.37$; Fig. 1B), but there was a significant habitat-by-edge interaction ($F_{1,74} = 16.27$, $P = 0.0001$). Web-building spider density was greatest in the SA interior, lower along the SA edge, still lower along the SP edge, and lowest in the SP interior, which is a negative edge response. Unlike other predator groups, the response of web-building spiders to the habitat edge was consistent for abundant and rare species (Fig. 2; Table 1).

We predicted that aerial predators should demonstrate a negative edge response with higher densities in SP. Although aerial predator densities were greater in SP relative to SA ($F_{1,74} = 29.87$, $P < 0.0001$; Fig. 1C), they were not affected by the habitat edge ($F_{1,74} = 1.54$, $P = 0.2184$; Fig. 1C). The lack of an edge response may be explained by variation in edge responses among species. The two most abundant aerial predators demonstrated a negative edge response, as predicted, whereby they were more abundant in SP and declined in SA. However, the rare aerial predator species were more abundant in SA, contrary to predictions, or demonstrated no edge response (Fig. 2; Table 1). These contrasting responses among aerial predators resulted in no overall edge response when species were combined as a functional group.

Finally, we predicted a negative edge response by epigeic predators, because prey and structural resources were both found in SP. Epigeic predator densities were indeed greater in SP relative to SA ($F_{1,81.1} = 8.73$, $P = 0.004$; Fig. 1D), but were not affected by edge vs. interior habitat ($F_{1,81.1} = 0.02$, $P = 0.8$). This group exhibited some of the most widely divergent responses among species. Although the two most abundant epigeic

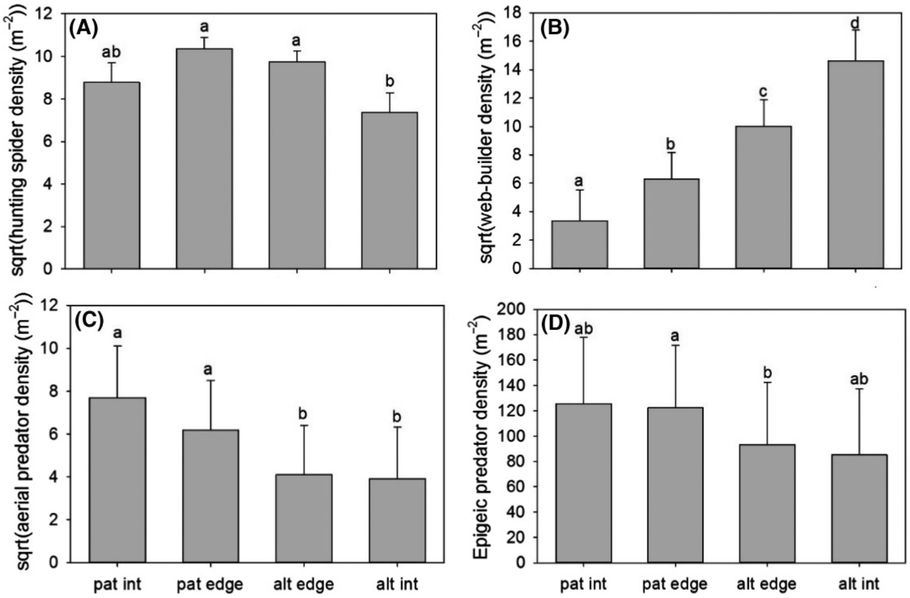

FIG. 1. Response of four groups of generalist predators to the habitat edge: (A) Hunting spiders demonstrated a positive response, (B) web-building spiders demonstrated a negative response, and (C) aerial and (D) epigeic predators demonstrated a neutral response. Shown are mean density ± 1 SE (pat int = *Spartina patens* interior; pat edge = *S. patens* edge control; alt edge = *Spartina alterniflora* edge control; alt int = *S. alterniflora* interior).

predators both demonstrated a negative edge response, one species was more abundant in SP and the other species was more abundant in SA. The rare epigeic predator species demonstrated yet a third pattern, whereby they were more abundant in the interior habitat of both SP and SA and declined along the habitat edge (Fig. 2; Table 1). Together, these mixed responses resulted in no edge response by the functional group when all species were considered together.

Effects of prey density and habitat structure on generalist predators

We found that predator responses to prey density and habitat structure (thatch) varied by functional group. Neither prey density ($t = 0.75$, $P = 0.45$) nor thatch ($t = 0.89$, $P = 0.38$) affected the densities of hunting spiders. Prey density ($t = 1.16$, $P = 0.25$) also did not affect web-building spider densities; as predicted these spiders responded negatively to thatch ($t = -2.63$, $P = 0.01$). Aerial predator densities were positively affected by both prey density ($t = 4.77$, $P < 0.001$) and thatch ($t = 2.52$, $P = 0.014$). Finally, epigeic predators were not affected by prey density ($t = 0.23$, $P = 0.816$), but thatch had a marginal positive effect on their densities ($t = 1.964$, $P = 0.053$).

DISCUSSION

Generalists have often been predicted to be able to survive fragmentation better than specialists (Fagan et al. 1999, Bagchi et al. 2018) because they can use diverse resources and seem to do equally well when feeding on a variety of prey (Rooney et al. 2006, McCann and Rooney 2009, Vidal and Murphy 2018). Thus, we may anticipate that generalist predators would exhibit positive responses to edges (if resources are divided) or no edge response if they can use resources equally well on both sides of the edge. However, we found that only the two most abundant species of hunting spiders demonstrated a positive edge response. Indeed, six out of eight common species demonstrated a negative edge response, and all of the rare taxa demonstrated a negative edge response. Thus, being a dietary generalist with the ability to consume multiple resources does not preclude that many “generalists” actually do exhibit habitat associations; we therefore need to distinguish between species that are dietary generalists and habitat generalists. Many predator species in our study were dietary generalists (rare hunting spiders, abundant aerial predators, and the most abundant epigeic predator), but exhibited habitat associations and were found most commonly in the grass species *Spartina patens* (SP); SP is rapidly disappearing in many marsh habitats because of sea level rise (Donnelly and Bertness 2001), especially where SP is surrounded by a matrix of SA, and disappearance of this key habitat will have important implications for these generalist predators.

The ERM has been extremely useful in predicting individual species’ responses to the habitat edge (Ries and Sisk 2004, Ries et al. 2004, Ries and Sisk 2010), but we found that it was less useful for predicting responses

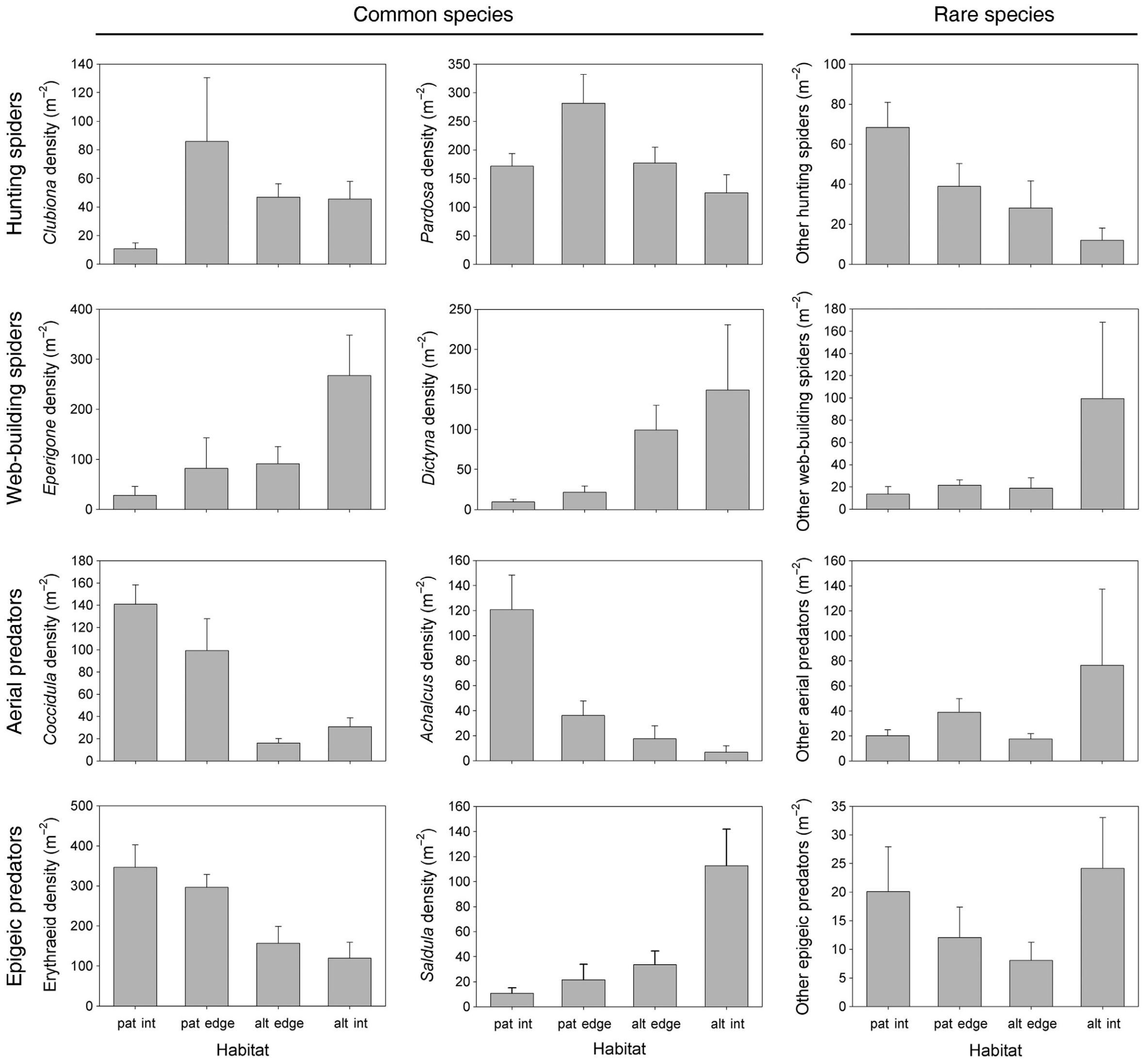

FIG. 2. Edge responses of common and rare predators across four functional groups. To determine whether the positive response of hunting spiders to the habitat edge was driven by a few abundant species or represented a common response among predators, we plotted the edge response of the two most abundant species in two separate histograms, and the remaining rare species in a single histogram. Shown are means ± 1 SE (pat int = *Spartina patens* interior; pat edge = *S. patens* edge; alt edge = *Spartina alterniflora* edge; alt int = *S. alterniflora* interior).

of an entire functional group. We considered both prey and structural resources to be of equal value to predators, but the predators clearly did not value these resources equally. Furthermore, we found that the abundant and rare species had different edge responses for all of our functional groups except the web-building spiders. Our results are consistent with previous studies that have found diverse edge responses among different predator species within the same family (Martin and Major 2001, Marshall et al. 2006). Because rare species are by nature uncommon, we hoped to be able to use the responses of abundant species in each functional group to predict edge responses by rare species, but our results show that the divergent responses of these taxa make this impossible.

When predictions do not match our observations, we can use this to understand where our predictive model failed us. First, we equated prey abundance with ease of prey capture. However, the response of the two most abundant hunting spiders was likely driven by differences in prey susceptibility, rather than overall prey density. We know from research in this system that the most abundant hunting spiders (*Clubiona* sp. and *Pardosa littoralis*) are better able to capture prey in SA (Denno et al. 2003). Thus, the positive edge response we observed may have been driven by greater structural resources in SP, as predicted, but greater prey susceptibility in SA for visually hunting spiders. Second, we undervalued the importance of structural resources to the predators. Rather than exhibiting a positive edge response, web-building spiders negatively responded to the habitat edge and had higher densities in SA. The assumption that prey and structural resources were equally important to web-building spiders was incorrect; structural resources outweighed prey resources in importance for these spiders that use the erect culm structure of SA for web scaffolding. Notably, this was the only functional group that had consistent edge responses for abundant and rare species. Third, as noted above, the responses of rare and common species are not consistent and thus cannot be lumped into functional groups. Importantly, rare species consistently demonstrated negative edge responses. Because habitats become increasingly dominated by edge effects as they decrease in size (Ries et al. 2004), rare species are likely to be disproportionately affected by habitat loss.

There are two ways in which predictions for generalist predator responses to habitat edges may be improved. First, an understanding of prey resources requires more than quantifying the abundance of potential prey items, at least in some cases. In the *Spartina* system, it requires a more detailed knowledge of the actual prey consumed by a predator and the relative susceptibilities of these prey. Although such an understanding may have been daunting in the past, stable isotope (McNabb et al. 2001, Halaj et al. 2005, Wise 2006, Kuusk and Ekbom 2010, Wimp et al. 2013), and DNA-based techniques (Agustí et al. 2003) now give us the ability to determine which prey are actually consumed by a predator, and make predictions based on the density of such prey. Second, our findings suggest that generalist predators do not weigh prey and structural resources equally, and understanding this will improve predictions for generalist predator edge responses in the future. For instance, we failed to understand the degree to which habitat structure trumped food resources in explaining web-building spider densities. Previous studies in agricultural habitats have found that web-building spiders demonstrate positive, negative, and neutral responses to the habitat edge; however, in each case, it was the distribution of suitable vegetation for web scaffolding that explained edge responses (Baldissera et al. 2004). Notably, structural resources are not only important for web attachment; structural complexity has also been shown to reduce intraguild predation and cannibalism among predators in the salt-marsh system (Finke and Denno 2006, Langellotto and Denno 2006). Thus, structural resources may also be especially valued by species susceptible to top-down pressure from other predators. These studies not only demonstrate the importance of using resource distribution to predict predator edge responses, but also the importance of considering structural resources as a primary driver, even compared to prey resources.

Habitat loss and fragmentation is one of the primary factors leading to species extinctions worldwide, and predators may be especially susceptible to extinction relative to other groups of organisms (Terborgh et al. 2001). We found that the most consistent response of diet-generalist predators to the habitat edge was a negative response. Thus, habitat fragmentation and the creation of edges will lead to changes in community composition of predators. Such alterations to predator composition are important because predator composition, rather than predator richness, has recently been suggested as best explaining prey suppression (Alhadidi et al. 2018). Predator identity often plays a large role in prey suppression, and the loss of different predator species from the same functional guild can impact ecosystem processes, even when other members of the guild are present in the community (Duffy et al. 2007, Griffin et al. 2013).

In considering generalist species, we as ecologists usually think about dietary generalism, and here we show that species can be dietary generalists, but have a habitat association. Although prey availability is necessary for understanding predator distribution, we emphasize that it is also important to consider habitat structural resources in combination with prey resources. Importantly, structural resources were often more useful in predicting responses of species to the habitat edge than overall prey density, especially for web-building spiders. For species with negative edge responses or strong habitat associations (web-building spiders, aerial predators, and epigeic predators), structural resources were much more significant (or nearly so for epigeic predators) and consistent predictors of predator responses to the habitat edge. Thus, as long as prey are available in both habitats, structural resources may be a stronger and more consistent driver of predator edge responses.

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DATA AVAILABILITY

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.2cb125v