

# Habitat edges as a potential ecological trap for an insect predator

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**Abstract.** 1. Ecological traps, where animals actively select poor habitat for reproduction over superior habitat, are generally associated with birds at forest edges. This study examines oviposition preference, predation, and parasitism rates in the mantid *Stagmomantis limbata* to determine the potential generality of this phenomenon.

2. Egg case (oothecae) densities were measured across two edge types (cottonwood and desert scrub) within desert riparian ecosystems. A positive edge effect in oothecae density was found with an approximate three-fold increase in density at cottonwood ( $X_{\text{edge}} = 0.05$  oothecae/100 m<sup>2</sup> vs.  $X_{\text{interior}} = 0.015$  oothecae/100 m<sup>2</sup>) and desert scrub ( $X_{\text{edge}} = 0.20$  oothecae/100 m<sup>2</sup> vs.  $X_{\text{interior}} = 0.06$  oothecae/100 m<sup>2</sup>) edges ( $P < 0.01$ ).

3. Rates of bird predation were significantly higher for oothecae at desert scrub edges and showed a trend of higher predation rates at cottonwood edges, suggesting that riparian habitat edges may be acting as an ecological trap for this mantid species. There was no effect of edges on oothecal parasitism rates.

4. These results provide an example of the effect of habitat edges on a generalist insect predator and indicate that an ecological trap may exist with respect to one of its natural enemies.

**Key words.** Bird predation, ecological trap, egg parasitism, habitat edges, oviposition choice, *Podagrion*, *Stagmomantis limbata*.

## Introduction

The concept of ecological traps, where animals actively select poor habitat for reproduction over superior habitat, has been developed largely within the avian edge literature. The discovery that woodland edges were acting as ecological traps for some songbirds, attracting high densities of reproductive individuals whose nests were then subjected to increased rates of predation and parasitism (Gates & Gysel, 1978; Chasko & Gates, 1982; Flaspohler *et al.*, 2001), helped form the modern, negative perception of landscapes featuring high edge densities (Yahner, 1988). This maladaptive habitat selection is generally attributed to a change in an organism's environment (often anthropogenic) that is out-

side of their evolutionary experience and leads individuals to use misleading cues of habitat quality (Schlaepfer *et al.*, 2002). The ecological trap phenomenon brought considerable attention to the problem of habitat fragmentation (Brittingham & Temple, 1983) and led to numerous studies examining the impacts of edge habitat on both distribution and fecundity of many taxa (for reviews, see Paton, 1994; Murcia, 1995; Lahti, 2001; Chalfoun *et al.*, 2002; Sisk & Battin, 2002).

Although ecological traps were first described 30 years ago, and several empirical studies have been published, both within and outside the edge literature, it is only in the past couple of years that ecological traps have received extensive theoretical treatment (Delibes *et al.*, 2001; Donovan & Thompson, 2001; Kokko & Sutherland, 2001; Schlaepfer *et al.*, 2002; J. Battin, unpubl. obs.). Recent models suggest that ecological traps can lead deterministically to population extinction, although this depends on factors such as the strength of selection (Donovan & Thompson, 2001), starting

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population level (Kokko & Sutherland, 2001), and the proportion of trap habitat in the landscape (Delibes *et al.*, 2001). For systems where edges may be acting as ecological traps, the latter two factors are potentially critical. As fragmentation increases, the proportion of edge habitat increases, and associated habitat loss is likely to cause population declines that are separate from any dynamics associated with edge proliferation. Therefore, ecological traps occurring at habitat edges may interact synergistically with such losses, and can become more severe as habitat fragmentation progresses.

The ecological trap phenomenon has not been well explored within the insect literature. Indeed, studies of the fitness consequences of reproductive choice in insects are largely confined to the preference–performance literature. These studies seek a linkage between oviposition choice (usually differentiating among host-plant species or among plant parts) and offspring fitness. Several reviews indicate that preference–performance linkages range along a continuum, including positive, neutral, and negative relationships (see Thompson, 1988; Courtney & Kibota, 1990; Mayhew, 1997 for reviews), although field tests are rare (Mayhew, 1997). Ecological traps are analogous to negative preference–performance linkages; however, reproductive choices are being made at the landscape, rather than the individual-plant, scale. A few studies on insects have shown spatial linkages between increased abundance and mortality, although none have been placed in the framework of ecological traps. One study describes a fly species (*Phytomyza ilicis* Curtis) that showed both increased abundance and mortality near forest edges (McGeoch & Gaston, 2000). In another example, two butterfly species (*Battus philenor* L. and *B. polydamus* L.) preferred ovipositing in sunny rather than shady patches, despite lower survivorship for eggs (Rauscher, 1979).

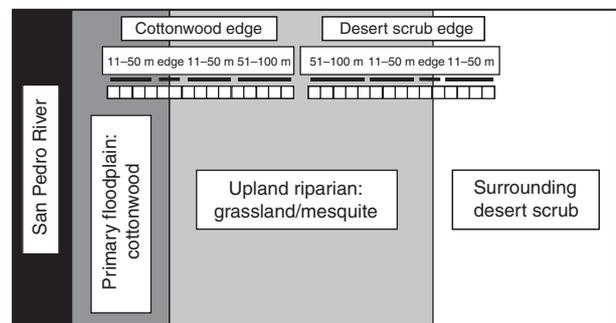
Even in the absence of evidence for active selection of edge habitat, studies of mortality rates near edges are important in order to determine the generality of increased predation and parasitism rates that have commonly been shown for birds (Paton, 1994; Lahti, 2001; Chalfoun *et al.*, 2002). Peltonen and Heliövaara (1999) found no effect of edges on predation for 10 species of bark beetle (Coleoptera: Scolytidae), and Roland and Kaupp (1995) demonstrated *decreased* mortality at edges for tent caterpillars (*Malacosoma disstria* Hübner). Here, evidence is provided that riparian habitat edges may be acting as an ecological trap for an insect predator, the mantid *Stagmomantis limbata* (Hahn). While an increase in bird predation on mantid oothecae is shown, there was no effect on egg parasitism.

#### Study system: mantids in riparian habitat

Riparian habitat in arid ecosystems is an ideal system in which to study edge phenomena. The narrow structure of riparian habitat leads to high perimeter to area ratios, so that any edge impacts are likely to exert a strong influence on the overall ecology of the system. In arid systems, riparian habitat has a strikingly different structure compared to

the surrounding desert, leading to well-defined edges. Riparian areas are also ideal in that they provide critical habitat for the vast majority of wildlife in arid ecosystems (Naiman *et al.*, 1993) so their dynamics are a crucial component of the area's ecology. Most riparian habitat in desert areas of North America have been severely degraded by water diversions, agriculture, and grazing, causing the habitat to become increasingly narrow and more fragmented. This study took place on the San Pedro River in southeastern Arizona, the last remaining free-flowing river in the region. All data were collected within the boundaries of the San Pedro National Conservation Area where grazing and agriculture have been excluded since 1986.

Despite its high level of protection, the San Pedro River has undergone dramatic transformations since European settlement in the mid-1800s. Although historically dominated by open, marshy habitat, the San Pedro is now increasingly characterised by woody vegetation (Stromberg, 1998). The riparian corridor now exists as a two-tiered system with a primary flood plain and an upland riparian zone surrounded by desert scrub (Fig. 1). The primary flood plain is dominated by Fremont cottonwood (*Populus fremontii* Watson) with some Gooding willow (*Salix goodingii* Ball). The upland riparian zone, which is dominated by a mixture of grassland and mesquite (*Prosopis velutina* Wooton), generally exists on a raised terrace above the primary flood plain. The presence of these three adjacent habitat types (cottonwood, mesquite/grassland, and desert scrub) creates distinct habitat edges that were the focus of this study (Fig. 1). The structure of the two focal edge types differ in that the cottonwood edges have a higher structural contrast than the desert scrub edges, due to a much greater difference in vegetation height between the adjacent habitats.

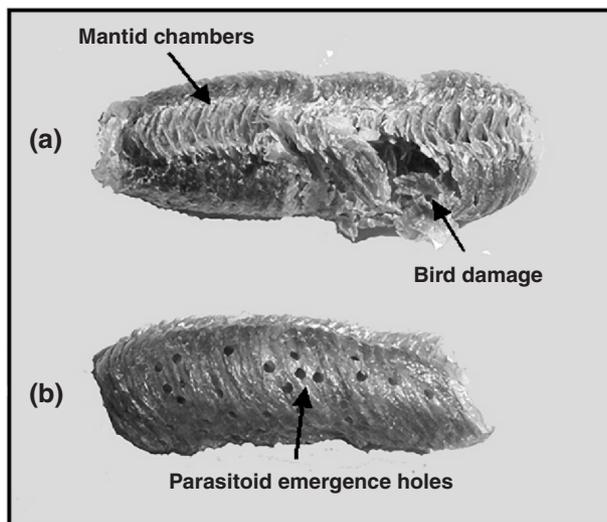


**Fig. 1.** Habitat structure of the study area. There are two zones of riparian habitat on each side of the river: the primary floodplain dominated by cottonwood (*Populus fremontii*) and an upland riparian zone dominated by grasslands and mesquite (*Prosopis velutina*). The riparian zone is surrounded by expansive desert scrub habitat. Edges between these three habitat types are the basis of this study. Transects of contiguous 10 × 10 m plots span both edges between the riparian zones and extend from 50 to 100 m into the interior depending on width. The plots were grouped into three classes based on distance to the nearest edge (0–10, 11–50 and 51–100 m). Distance and habitat categories used for analysis are shown.

*Stagmomantis limbata* is a common mantid native to the southwestern U.S.A. and northern Mexico (Helfer, 1987). In southern Arizona, *S. limbata* is univoltine, with nymphs hatching in spring and oothecae (egg cases) being deposited from August to November by adults that do not overwinter (Roberts, 1937). Mantid oothecae are preferentially deposited on thin woody branches of shrubs from 1 to 5 m off the ground (Fagan, 2002) and are relatively obvious when present. Oothecae are subject to bird predation as well as attacks by Torymid parasitoids from the genus *Podagrion* (Breland, 1941; Grissell & Goodpasture, 1981; Fagan & Folarin, 2001; Fagan, 2002). Because oothecae remain where they were originally deposited, and show easily quantifiable signs of bird predation and wasp parasitism (Fig. 2), this is an excellent system in which to examine the impacts of edges on habitat selection, predation, and parasitism. Although the coupling of increased density and mortality are suggestive of an ecological trap, to truly demonstrate this phenomenon, detailed information on habitat selection and lifetime fitness are required (Schlaepfer *et al.*, 2002); measures that are difficult to obtain in field settings. As in many studies, this one uses density and mortality rates (predation and parasitism) as proxies for habitat selection and fitness.

## Materials and methods

Oothecal densities and rates of predation and parasitism were assessed using transects established throughout the National Conservation study area. Transects were linear in structure and composed of contiguous 10 × 10 m plots that were centred on either cottonwood or desert scrub edges and extended into either habitat for 50–100 m depend-



**Fig. 2.** Top (a) and side (b) views of oothecae (egg cases) of *Stagmomantis limbata* showing mantid emergence chambers, bird damage, and emergence holes of parasitoid *Podagrion* wasps.

ing on the width of the habitat (Fig. 1). Two to six transects were established in each of 10 study areas along 65 km of river. Study areas were chosen based on width and access, but transect placement within areas was determined by a random number generator, although only edges with abrupt transitions were used. Study areas were separated by at least 1 km. In 2000, 44 transects were surveyed in 10 study areas, and in 2001, 28 transects were surveyed in seven study areas.

In 2000, transects were searched (as part of another study) in July and August and all oothecae located were flagged for later collection. By September, however, some flagged oothecae could not be recovered. Off-transect oothecae were collected to offset those missing for scoring predation and parasitism rates, but were not used for density calculations. These off-transect oothecae were collected up to 100 m into desert scrub (50 m beyond established transects) allowing extended measurements for predation and parasitism rates in desert scrub habitat. In 2001, searches and collections were conducted simultaneously in September and confined to established transects. Most egg cases exhibited the degree of deterioration typical of those that have been exposed to the elements for 1 year. Excluded from the analyses were a few badly deteriorated oothecae that were likely 2 years old and another small number that were freshly laid and hence not exposed to overwinter parasitism.

Collected oothecae were brought to the lab to determine parasitism and predation rates following the procedures detailed in Fagan and Folarin (2001) and Fagan (2002). Emergence potentials of oothecae were estimated volumetrically; parasitoid exit holes were counted to obtain an accurate index of parasitism rates; and oothecae were scored for evidence of physical damage due to bird predation.

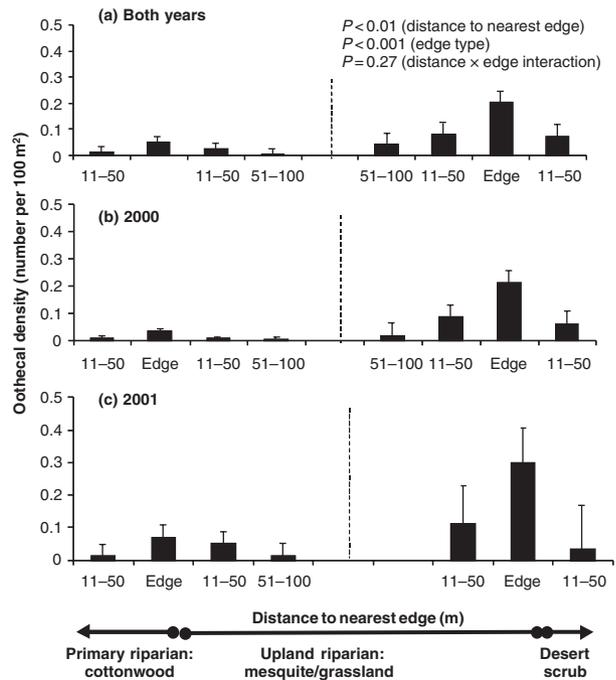
## Data analysis

Because the entire region was affected by a La Niña event that greatly reduced productivity of the desert grasslands, densities of oothecae were generally very low in comparison with prior studies in the area (Fagan & Folarin, 2001; Fagan, 2002). Consequently, oothecae were assigned to one of three broad classes based on distance to edge (0–10, 11–50, and 51–100 m) and pooled among years to increase sample sizes. In each area, the number of oothecae found in each distance class was divided by the total area searched (summed across years) to arrive at a density of oothecae per 100 m<sup>2</sup>. Because the oothecal density data most closely matched a Poisson distribution, a square-root transformation was applied to facilitate analyses via parametric tests (Zar, 1996). Data on proportion of eggs parasitised were angularly transformed (Zar, 1996) before testing for differences. A two-way ANOVA tested for differences in mean density and parasitism rates among edge-type, distance class, as well as the associated interaction (edge × distance) using a mixed model with study area as a random effect to account for the lack of independence within areas (Littell *et al.*, 1996). Because predation rates

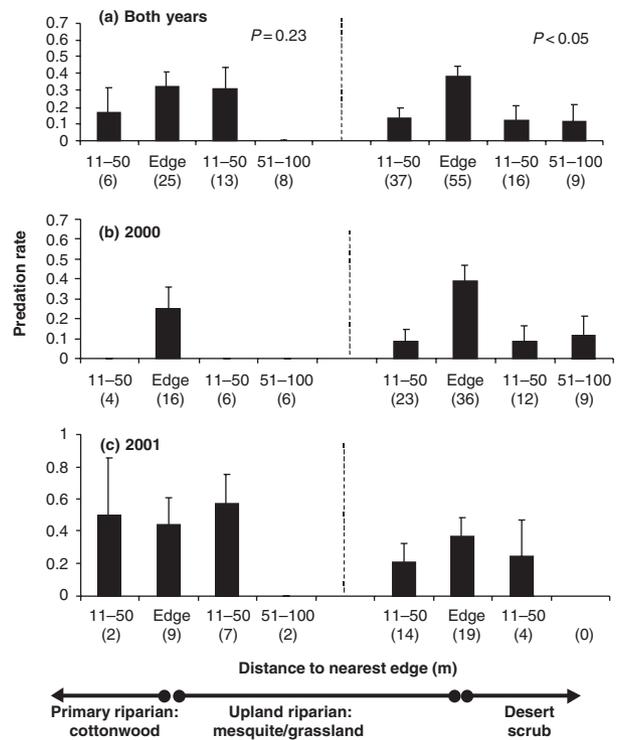
were based on a binomial distribution, Fisher's exact test was used to compare rates among distance classes (Zar, 1996). This test was performed separately at each edge type with the alpha-level adjusted to 0.025 via a Bonferroni correction to account for the multiple comparisons (Sokal & Rohlf, 1995). Although data were pooled among years for analysis, results from each year are illustrated separately so that year-to-year consistency in patterns can be considered.

**Results**

Oothecal densities increased at both cottonwood and desert scrub edges ( $F = 4.19$ , d.f. = 3,  $P < 0.01$ ) and the pattern was consistent between years (Fig. 3). There was an approximate three-fold increase in density at edge vs. interior habitat (pooled among 11–50 m and 51–100 m distance classes) at both cottonwood ( $X_{\text{edge}} = 0.05$  oothecae/100 m<sup>2</sup> vs.  $X_{\text{interior}} = 0.015$  oothecae/100 m<sup>2</sup>) and desert scrub ( $X_{\text{edge}} = 0.20$  oothecae/100 m<sup>2</sup> vs.  $X_{\text{interior}} = 0.06$  oothecae/100 m<sup>2</sup>) edges. Densities were higher at desert scrub compared with cottonwood edges ( $F = 12.74$ , d.f. = 1,  $P < 0.001$ ) but there was no interaction between edge type and distance from edge, indicating a consistent pattern at both edge types ( $F = 1.35$ , d.f. = 3,  $P = 0.27$ ). Predation by birds also showed a significant increase (Fig. 4) near desert scrub edges ( $P < 0.05$ ) and a trend of higher predation rates



**Fig. 3.** Density of oothecae with standard errors at each distance class within habitat types. Tests were run only on data pooled among years (a). *P*-values are based on a two-way ANOVA (with interaction) using a mixed model (with study area as a random effect) run on square-root transformed densities. For illustration purposes only, data are provided separately for 2000 (b) and 2001 (c).

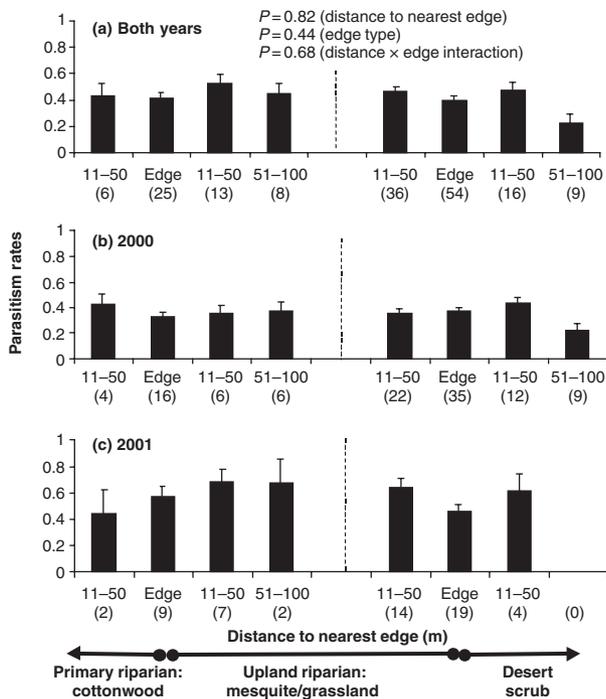


**Fig. 4.** Bird predation rates on oothecae with standard errors at each distance class within habitat types. Tests were run only on data pooled among years (a). *P*-values are based on Fisher's exact test. For illustration purposes only, data are provided separately for 2000 (b) and 2001 (c). The number of oothecae scored at each distance category is shown in parentheses.

at cottonwood edges ( $P = 0.23$ ); however, only the increase at desert scrub edges was consistent between years (Fig. 4b,c). Predation at cottonwood edges suggested a strong edge effect in 2000 (Fig. 4b), but no pattern was evident in 2001 (Fig. 4c). There was no pattern in parasitism rates (Fig. 5) based on either edge type ( $F = 0.64$ , d.f. = 1,  $P = 0.44$ ) or distance to edge ( $F = 0.38$ , d.f. = 3,  $P = 0.82$ ).

**Discussion**

The increase in oothecal density coupled with increased bird predation suggests that riparian edges may be acting as an ecological trap for *S. limbata*. A consistent effect was seen at desert scrub edges, with local increases in both oothecal density and the rate of oothecal predation by birds. A consistent effect in densities was seen at cottonwood edges and suggested for oothecal predation in one year. The fact that there were edge effects, both in abundance and predation at two edges with strikingly different structures, suggests that this may be a general phenomenon for *Stagmomantis* in desert riparian ecosystems. These results strengthen three previously reported patterns associated with edges: the potential presence of an ecological trap (Gates & Gysel, 1978; Chasko & Gates, 1982; Brittingham & Temple, 1983) and increases in



**Fig. 5.** Parasitism rates of oothecae by *Podagrion* wasps with standard errors at each distance class within habitat types. Tests were run only on data pooled among years (a). *P*-values are based on a two-way ANOVA (with interaction) using a mixed model (with study area as a random effect) run on arcsin-transformed parasitism rates. For illustration purposes only, data are provided separately for 2000 (b) and 2001 (c). The number of oothecae scored at each distance category is shown in parentheses.

predation rates and predator densities (Lahti, 2001; Chalfoun *et al.*, 2002) and extend them to include a species of generalist arthropod predator.

Definitive demonstration of an ecological trap requires data showing active selection of one habitat type over another coupled with detailed demographic data showing decreased fitness in the preferred habitat (Schlaepfer *et al.*, 2002). This type of evidence is rare in the ecological trap literature, with most studies using surrogates such as nest site location and nest success (J. Battin, unpubl. obs.). For this study, oviposition site was used as a surrogate for habitat selection, and predation and parasitism rates as a surrogate for fitness. For mantids, the second assumption is more questionable than the first, in that being near edges may confer unrecognised advantages that could offset overwinter losses of offspring to natural enemies. For example, there may be a fitness advantage to adult female mantids in the form of increased prey availability near edges. In other mantids, capture of late season prey is known to strongly determine the number of eggs per ootheca (Eisenberg *et al.*, 1981). Alternatively, edge habitats may provide increased prey densities in the spring that would confer a key advantage to emerging nymphs, which are routinely prey-limited (e.g. Hurd & Eisenberg, 1984; Hurd & Rathet,

1986), although in one experimental test, food supplementation did not increase survivorship (Moran & Hurd, 1997). In either case, females may be cueing in on increased prey availability that may either be misleading them to choose poor habitat or offsetting increased predation through higher offspring survivorship. Ultimately, studies that follow mantid success through a complete life cycle are necessary to determine if habitat edges are truly acting as an ecological trap in this system. Given suitable densities of oothecae for stocking, this kind of study is actually possible in the San Pedro because many areas of suitable habitat are effectively devoid of mantids, possibly due to a history of habitat disturbances coupled with severe limitations on the recolonisation potential of gravid female mantids (Eisenberg *et al.*, 1992).

Whether or not mantids are actively choosing edge habitat, evidence presented here suggests that predation, but not parasitism, increases near edges. This is consistent with past studies that have generally shown either an increase in predation or parasitism rates, or no effect (Paton, 1994; Lahti, 2001) with decreases in predation and parasitism rare near edges (Chalfoun *et al.*, 2002). This suggests the possibility that a common ecological consequence of fragmentation in birds may apply to insects as well; however, there is not yet sufficient data to determine this for insects or any other group, and results are likely to remain highly variable no matter how well replicated. In order to determine the generality of these patterns near edges and make more sense of the variability in results, a mechanistically-based framework needs to be developed to predict when positive, neutral, and even negative mortality rates should be expected near edges. In this study, increased bird predation on mantid oothecae near edges may be due to higher densities of birds, or simply be a density-dependent response to increased availability of prey. Differences in oothecal height have previously been shown to be associated with differing rates of bird predation (Fagan, 2002), but this was not evident in the data. In contrast, *Podagrion* egg parasitoids appear to respond to habitat spatial structure quite differently than do the mantids whose oothecae they are searching for (Fagan & Folarin, 2001), so it is not surprising that a spatial effect of egg parasitism was not identified among the three distance classes.

## Conclusions

This study suggests that habitat edges may be acting as an ecological trap for the generalist insect predator, *S. limbata*; however, detailed demographic data are necessary to determine more rigorously if edges are acting as an ecological trap for *S. limbata* and, if so, the ecological consequences for it and the rest of the community. A more mechanistic understanding of how species interactions change across habitat edges is critical to make sense of the patterns and variability reported in the edge literature (Fagan *et al.*, 1999). Progress toward this goal will allow predictions of how predation or parasitism rates are likely to change near edges, and of when ecological traps are most likely to occur.

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