Habitat edges, within-patch dispersion of hosts, and parasitoid oviposition behavior

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Abstract. Although density–edge effects are commonly reported, we have only scratched the surface in understanding the mechanisms underlying how habitat edges mediate species interactions. Here, I use a combination of field surveys and experiments to explore the linkages between the presence of host-plant edges (*Scolochloa festucacea*), the within-patch distribution of planthopper eggs (*Delphacodes scolochloa*), and the oviposition behavior of their egg parasitoids (*Anagrus* spp.). The field surveys revealed that densities of hosts and parasitoids at the edge were ≥2.5 times lower than densities in the patch interior and that the effect was independent of patch size. As a consequence of its edge-avoidance behavior, host within-patch dispersion was significantly more aggregated in the presence, as compared to the absence, of an edge. Also, as patch size decreased, the proportion of the patch that was core (i.e., beyond the influence of the edge) decreased, and the degree of host aggregation increased. In a subsequent field experiment, I found that the dispersion of hosts affected *Anagrus* oviposition behavior only when hosts were present on islands with discrete edges. Under these circumstances, the proportion parasitized and per capita parasitized were 2.3 and 3.4 times higher, respectively, when hosts were clumped as compared to when hosts were uniformly or randomly distributed. Based on a laboratory experiment using small *S. festucacea* patches, I found that *Anagrus* had 40% shorter step lengths, spent 52% more time in the patch, and parasitized 84% more hosts when hosts were clumped as compared to uniformly distributed. These results were indicative of area-restricted search by *Anagrus*, which is an effective foraging strategy when hosts are clumped. This is the first study to demonstrate that predator foraging behavior in response to prey dispersion can be mediated by the presence of a patch edge. Also, because edge-averse behavior is commonly reported in the literature, an underappreciated effect of fragmentation on predator–prey interactions and stability could arise from edge-mediated effects on prey within-patch aggregation.

Key words: aggregation; Anagrus *spp.; area-restricted search;* Delphacodes scolochloa; *egg parasitoid; fragmentation; host–parasitoid interactions; prairie potholes;* Scolochloa festucacea.

INTRODUCTION

Alteration of edge habitat is concomitant with a variety of anthropogenic activities, most notably, habitat fragmentation (Groom and Schumaker 1990, Lande 1998, Fagan et al. 1999, Tscharntke et al. 2002). In recent years, the study of edge effects has progressed beyond simply identifying patterns of changing abundance, species richness, or composition at habitat edges to include quantifying how population, community, and ecosystem processes are mediated by the presence or nature of edges (reviewed by Fagan et al. 1999, Ries et al. 2004). For example, studies have revealed that habitat edges can serve as filters or barriers to dispersal (e.g., Wiens et al. 1985, Ovaskainen 2004, Haynes and Cronin 2006), affect predation and parasitism rates (e.g., Ries and Fagan 2003, Albrecht 2004, Patten et al. 2006), pollination rates (e.g., Aizen and Feinsinger 1994, Burgess et al. 2006, Gabriel and Tscharntke 2007),

competitive interactions (e.g., Remer and Heard 1998, Hickerson et al. 2005), and influence cross-boundary subsidies (e.g., Janzen 1986, Rand et al. 2006). To date, we have only scratched the surface in understanding the mechanisms that underlie these various edge-mediated effects (Bierregaard et al. 1992, Fagan et al. 1999). In particular, there are few studies that have deciphered the mechanisms generating altered species interactions in response to the presence of patch edges, e.g., the cause for altered predation rates (but see, e.g., Kareiva 1987, Roland 1993, Ibarzabal and Desrochers 2004).

One way that habitat edges can mediate predator–prey interactions is by altering the within-patch distribution of prey, which in turn can affect predator foraging success. Harrison and Shepp (1981) demonstrated that edge-sensitive skew in models of population diffusion can result in the accumulation of individuals along the patch edge. Random walks with biased movement at the boundary can have a similar effect (Ovaskainen and Cornell 2003, Ovaskainen 2004, Reeve et al. 2008). In support of these models, numerous empirical studies have found that organisms cluster at

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the patch edge (e.g., Bider 1968, Kaiser 1983, Blouin-Demers and Weatherhead 2001). Alternatively, the edge may be strongly reflective, causing organisms to aggregate in the interior of the patch (e.g., Wolf and Batzli 2004, Fletcher 2005, Hickerson et al. 2005). Regardless of whether a species accumulates at, or is reflected away from the patch edge, these edge effects can influence a species' dispersion at the scale of the whole patch. As patch size decreases, the influence of the edge on within-patch dispersion should increase (i.e., the core habitat, or area that is unaffected by the edge, should become a smaller proportion of the patch as patch size decreases; Temple and Cary 1988, Laurance and Yensen 1991, Ohman and Erikson 1998).

The dispersion of a prey species within a patch can significantly influence its risk of predation. Prey aggregation can provide protection against predators by confusing attacking predators (e.g., schooling behavior; Neill and Cullen 1974), improving detection of predators (e.g., Kenward 1978, Coleman et al. 2004, Fernandez-Juricic et al. 2004), mobbing attacking predators (e.g., Groom 1992, Weatherhead and Summerer 2001), or via the dilution effect (Turchin and Kareiva 1989, Aukema and Raffa 2004, Sandin and Pacala 2005). However, the benefits of prey aggregation may be negated by the occurrence of a strong aggregative response by predators (Turchin and Kareiva 1989). A number of studies have demonstrated that clumped prey suffer higher predation or parasitism rates than randomly or uniformly distributed prey (e.g., Kaiser 1983, Lode 2000, Pitt and Richie 2002, Nachman 2006a, b). One possible explanation for this result is that predators exhibit area-restricted search (i.e., the tendency of predators to concentrate their foraging effort to areas where they have had recent success; Kareiva and Odell 1987), which is a highly efficient foraging behavior when prey are clumped (see Godfray 1994). Numerous examples exist of predators and parasitoids foraging in this way (e.g., Waage 1978, Lode 2000, Klaassen et al. 2006, Pinaud and Weimerskirch 2007).

Because smaller patches should be more strongly influenced by edge effects, we might expect prey to be more strongly aggregated, and predation rates to be higher, in small as compared to large patches. This may represent a novel explanation for why, in some study systems, mortality from predators is greater in smaller than larger patches (e.g., Doak 2000, Hovel and Lipcius 2001, Cronin et al. 2004).

In this study, I used a combination of field surveys and experiments to explore the linkage between the presence of a habitat edge, prey distribution, and predator foraging behavior. The target organisms are the patchily distributed wetland grass *Scolochloa festucacea* (Willd.) Link (sprangletop), its specialist herbivore *Delphacodes scolochloa* Cronin and Wilson (Hemiptera: Delphacidae), and the egg parasitoids *Anagrus nigriventris* Girault and *A. columbi* Perkins (Hymenoptera: Mymaridae). First, I surveyed planthopper egg densities

and parasitism at different distances from the patch edge to determine if an edge effect existed. Second, I examined whether the strength or spatial extent of the edge effect varied with patch size. Given the occurrence of a host density edge effect, I was particularly interested in testing the prediction that the aggregation of hosts increased with decreasing patch size. In addition, by comparing discrete patches with equivalent-sized areas within much larger continuous sprangletop habitat containing no edges, I also determined whether the presence of an edge was associated with a more aggregated distribution of hosts. Third, I conducted a field experiment to examine the effects of planthopper density, within-patch dispersion (uniform, random, clumped), and presence of a sprangletop edge on parasitoid density, proportion of hosts parasitized, and the per capita number of hosts parasitized. Last, I conducted a laboratory experiment to examine how planthopper dispersion (uniform vs. clumped) affected the foraging behavior of individual parasitoids. This study illustrates the complex and indirect mechanisms by which habitat edges can mediate predator–prey interactions.

METHODS

Study system

The prairie pothole region of northeastern North Dakota is a formerly glaciated area characterized by numerous seasonal and permanent ponds or potholes (van der Valk 1989). A dominant wetland plant associated with these potholes is the native grass, *Scolochloa festucacea*. Sprangletop often encircles pothole margins, or occurs as smaller patches (<5 m^2) in open water of shallow ponds and in scattered minor depressions (Smith 1973, Cronin and Wilson 2007).

The planthopper *Delphacodes scolochloa* is an abundant specialist herbivore of sprangletop (Cronin 2007, Cronin and Wilson 2007). Planthoppers overwinter as nymphs in the senescent leaf sheaths. In early May, nymphs emerge and begin feeding and reach peak adult densities at the end of May. A second generation follows, with maximal adult densities occurring in the middle of July. All of the adult males and only 9% of the adult females are macropterous and capable of sustained flight (Cronin and Wilson 2007). Brachypterous females have small wing buds that limit them to dispersing predominantly by walking and hopping.

Eggs are inserted beneath the stem epidermis in clusters of 1–15 and are parasitized by two fairyfly parasitoids, *Anagrus nigriventris* and *A. columbi* (Cronin 2007, Cronin and Wilson 2007). *A. nigriventris* is the dominant egg parasitoid accounting for 92% of the parasitized hosts. Because of the difficulty in distinguishing these two minute parasitoids, they are referred to henceforth by their genus, *Anagrus*. Over the course of six generations, parasitism of *D. scolochloa* eggs was 21.7% ± 4.2% (Cronin 2007).

Survey of edge effects, within-patch dispersion, and parasitoid performance

The first field survey took place in August 1997 and focused on whether there was an edge effect with regard to sprangletop stem or planthopper egg density or parasitism of *D. scolochloa* eggs, and if an edge effect was present, how far it extended into the interior of large sprangletop patches. For eight potholes, I harvested sprangletop stems at five distances (ranging from 0 to 3 m) from the patch edge. Stems were dissected to determine egg density and proportion of hosts parasitized. Details regarding sampling methods are found in Appendix A. Differences in stem density, egg density, and proportion parasitized with respect to the position in the patch were determined with separate profile ANOVAs with no between-subjects effects (see Appendix A).

In the second field survey, I examined whether an edge effect in stem density, planthopper egg density, and parasitism was evident in different-sized sprangletop patches. Also, I determined whether patch size or the presence of a habitat boundary influenced the spatial distribution of planthoppers, per capita number of hosts parasitized, and proportion of hosts parasitized. Sprangletop patches were chosen to represent three nonoverlapping size classes (small, 0.7–1.1 m^2; medium, 3.2–4.8 m^2; and large, 8.9–24.5 m^2) and were separated from any other sprangletop by ≥ 5 m. Stem densities, *D. scolochloa* egg densities, and parasitism were sampled at the patch edge and at random locations within the patch (see Appendix A). In addition, I sampled adult female *Anagrus* density in patches by capturing them on sprangletop stems coated with sticky Tanglefoot (Tangletrap, Grand Rapids, Michigan, USA; Appendix A). Because I did not place a subset of sticky traps at the patch edge, I was not able to assess whether there was an edge effect in parasitoid density. The proportion of hosts parasitized, and the per capita number of hosts parasitized, a measure of parasitoid performance (Cronin and Strong 1999, Cronin 2003a), were estimated for each patch. For the latter measure, the mean number of parasitized hosts per sample (from the stem collections) was divided by the mean number of female parasitoids per sample (from the sticky stem traps).

To quantify the degree of aggregation of host eggs (k_H) and *Anagrus* females (k_P), I fit the count data (excluding supplemental samples) to a negative-binomial model using MATLAB 4.0 (Mathworks, Natick, Massachusetts, USA) and solved for the clumping parameter k. If $k < 1$, insect distributions were strongly clumped. As k becomes smaller, the degree of aggregation of insects becomes greater; $k \to \infty$ when the distribution of insects is random (Poisson).

The influence of patch size on planthopper and parasitoid density and aggregation, proportion of hosts parasitized, and per capita hosts parasitized were determined using separate ANCOVA models. Different covariates were used depending on the test (see

Appendix A). To determine if patch size influenced the occurrence or strength (i.e., mean difference between the patch edge and interior) of a planthopper density edge effect, I used a profile ANOVA (see Appendix A). Here, a significant patch size × position within-patch interaction would indicate that the strength of the edge effect varied with patch size.

If a density edge effect exists, we would expect that as patch size decreases there should be a corresponding decrease in the percentage of the patch that is unaffected by the edge (i.e., the core area of the patch; Laurance and Yensen 1991, Ohman and Erikson 1998). Moreover, if hosts or parasitoids are edge averse, the impact of the edge on within-patch dispersion should be greatest in the smaller patches. To assess whether the presence of a patch edge influenced the aggregation of planthoppers, I compared the aggregation of planthoppers in the small- and medium-sized patches with the aggregation for equivalent-sized areas of sprangletop embedded within very large sprangletop patches ("mainland habitat") using profile ANOVA (Appendix A).

Planthopper dispersion and parasitoid performance experiment

I conducted a field experiment to test whether the within-patch dispersion of *D. scolochloa* eggs affects *Anagrus* density, proportion of hosts parasitized, and per capita hosts parasitized. Small patches of sprangletop (in 0.16-m^2 bus pans) were created in May of 2000. Each patch was divided into a 3 × 5 grid with a cell size of ~1 dm^2. I manipulated the density and dispersion of *D. scolochloa* eggs within patches through the use of small stem cages (Appendix B). I used two density levels (0.6 or 2.0 infested stems/cell; 31.1 ± 0.14 eggs/infested stem, mean ± SE, $n = 1872$ stem cages) and three dispersion patterns (uniform, random, and clumped). For the uniform treatment, infested stems were evenly distributed among cells. In the random treatment, the distribution of infested stems among cells was Poisson and for the clumped treatment, the distribution was negative binomial with $k = 0.3$ (represents the lower 10th percentile from the survey study). A third treatment was the location of the bus pans, either 3–5 m from any other sprangletop (island patches with a discrete edge), or embedded within a >250-m^2 mainland habitat (no distinct edge) and spaced ≥ 5 m apart. The three treatments were fully crossed and each treatment combination was replicated eight times. Additional details are provided in Appendix B.

Near the end of the *D. scolochloa* egg-laying period in early August, when *Anagrus* is most abundant and adult planthoppers are becoming scarce, the bus pans were transported to the field. I applied Tanglefoot to the base of five stems per bus pan (uniformly spaced apart) in order to estimate *Anagrus* density. The bus pans were left in the field for 10 days to allow parasitoids to colonize the patches and parasitize host eggs. Afterward, the infested stems and sticky trap stems were processed

as described in Appendix A. I determined the proportion of hosts parasitized and computed an index of the per capita number of hosts parasitized (total number parasitized/total number of female *Anagrus*) for each bus pan. The effects of planthopper density, dispersion, and bus pan location on *Anagrus* density, the proportion parasitized and per capita parasitized were determined with a full factorial ANCOVA (see Appendix B).

Within-patch oviposition behavior of Anagrus

I conducted a laboratory experiment to examine how the dispersion of hosts affects the oviposition behavior of individual *Anagrus* females. The experimental area consisted of 19 ~1-dm^2 pots of sprangletop arranged in a circular patch (see Appendix C for details). Experimental patches were infested with planthopper eggs to achieve one of two dispersion patterns, uniform (1 infested stem/pot) or clumped (2–3 infested stems of seven centrally located pots; $k = 0.47$). Both treatments had the same number of infested stems ($n = 19$) per patch and equivalent numbers of host eggs per infested stem (24.7 ± 1.2, $n = 103$). There were 13 and 12 replicates for the uniform and clumped treatments, respectively.

Anagrus adults were reared from field-collected stems that were cut into 10-cm sections and placed in 1-L bowls with a lid. The ends of the stem were inserted into small water-filled tubes to keep them from drying out (see Cronin and Strong 1990). Female *Anagrus* that emerge from these stems were quickly mated by the at large population of males (J. T. Cronin, *unpublished data*). An experimental replicate involved gently releasing a single <8 h-old female *Anagrus* onto an infested stem in the central pot (pot no.1). After the female was released, an observer would inspect the base of all stems (where eggs are laid and parasitoids tend to forage) at 5-min intervals. We recorded the time on each stem, the pot number associated with that stem, the sequence of stems visited, and the total time in the patch (patch time; time to last observation). The trial was terminated when no parasitoid could be found after 30 min. Five days after the end of the trial, the stems were dissected and the number of healthy and parasitized hosts was counted for each of the visited and infested stems. This procedure was used successfully by Cronin and Strong (1993) to study *A. sophiae* ovipositing in *Prokelisia marginata* host eggs.

A total of seven search/oviposition behaviors were reported for *Anagrus*: number of stems and number of infested stems visited, mean time (minutes) spent and number of hosts parasitized per visited infested stem, mean step length (distance in centimeters between consecutive infested stems visited), patch time, and number of hosts parasitized in the patch. Differences in behaviors between patches with uniform and clumped hosts were determined with separate *t* tests. To guard against inflated Type I errors associated with multiple tests, I used a sequential Bonferroni correction to adjust the critical value of α.
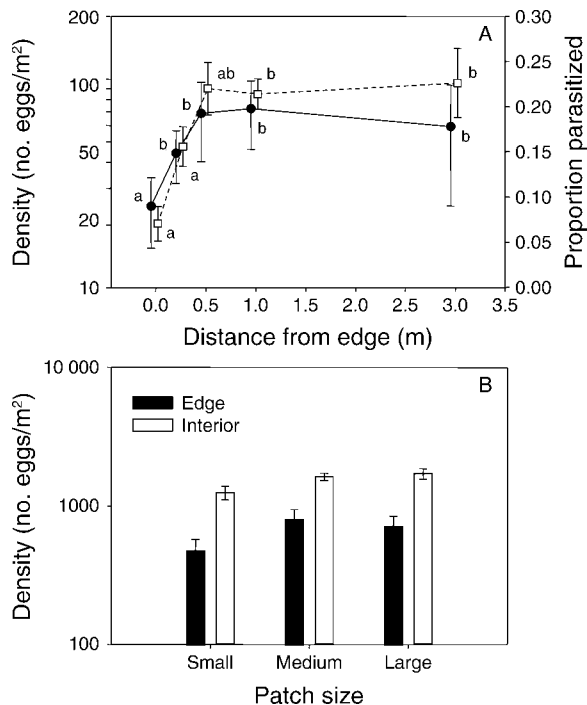

FIG. 1. Edge effects in planthopper density and parasitism. (A) Density (solid circles and solid lines) and parasitism (open squares and dashed lines) of planthopper eggs at different distances from the patch edge (0 m). (B) Relationship between patch size (small, 0.7–1.1 m^2; medium, 3.2–4.8 m^2; large, 8.9–24.5 m^2) and planthopper egg density at the patch edge and interior ($\geq$0.25 m from edge). For each variable, significant differences between categories were determined with separate paired *t* tests and are denoted with different letters ($P \leq 0.01$). Prior to analyses, density was ln-transformed, and parasitism was arcsine square-root transformed. Values shown are means $\pm$ SE.

RESULTS

Survey of edge effects, within-patch dispersion, and parasitoid performance

A strong edge effect was evident for planthopper density and the proportion of hosts parasitized (Fig. 1A). Host density and proportion parasitized at the edge averaged 2.5 and 2.9 times lower than at all other distances, respectively. There was no significant difference in egg density at all distances $\geq$0.25 m from the edge. For parasitism, the edge effect was still evident at 0.25 m. The similarity in edge effects for host density and parasitism does not appear to be the result of parasitoids tracking hosts. I detected no density-dependent parasitism at the scale of a 15 $\times$ 15 cm sampling frame when all patches and locations were combined ($R^2 = 0.085$, $P = 0.072$, $n = 39$). Finally, the cause for these edge effects cannot be attributed to differences in stem density; stem densities were similar among all locations sampled ($F_{4,28} = 0.73$, $P = 0.58$).

Planthopper and parasitoid densities and dispersions were significantly influenced by patch size. Small patches
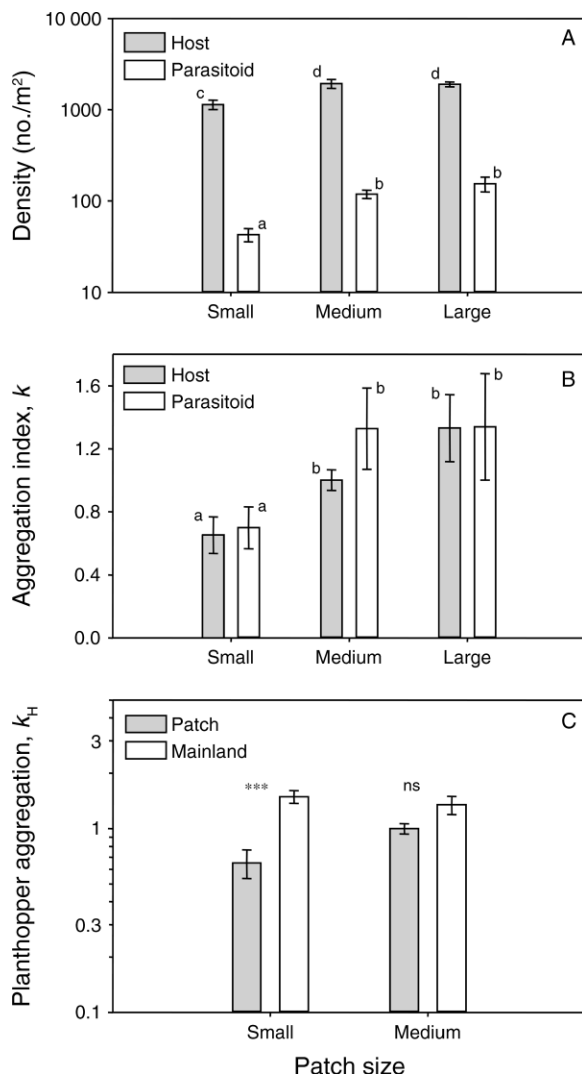
FIG. 2. Effects of patch size on (A) host and parasitoid density and (B) host and parasitoid aggregation (k_H, k_P). (C) Planthopper aggregation in response to patch size and whether the habitat has an edge (discrete patch) or does not have an edge (mainland habitat). Different letters denote significant differences ($P \leq 0.01$) between patches of different sizes (within the same bar type). For panels A and B, statistical tests were performed to assess the differences between patch sizes within a species, not between species. In panel C, asterisks (***) indicate a highly significant difference ($P = 0.001$) between small patches with and without edges. For the medium-sized patches, there was no significant difference. Values shown are means ± SE.

had planthopper egg densities that were 41% lower than the densities in either the medium or large patches (Fig. 2A; one-way ANOVA, $F_{2,20} = 9.51$, $P = 0.001$). There was no difference in density between medium and large patches (Tukey's test, $P = 0.99$). When no other factors were considered, Anagrus density also increased significantly with increasing patch size (Fig. 2A; ANOVA, $F_{2,18} = 7.44$, $P = 0.004$). However, after accounting for a significant positive effect of host density on Anagrus

density, the effect of patch size on Anagrus density was no longer significant (Appendix D). The edge effect in planthopper egg density was consistently strong regardless of patch size (Fig. 1B; profile ANOVA; position, $F_{1,20} = 34.98$, $P < 0.001$; size, $F_{2,20} = 5.34$, $P = 0.014$; position × size: $F_{2,20} = 0.39$, $P = 0.68$). Finally, stem densities did not vary significantly with regard to patch size ($F_{2,20} = 2.12$, $P = 0.14$) or location within the patch (edge vs. interior; $F_{1,20} = 0.39$, $P = 0.54$).

Hosts and parasitoids were strongly aggregated in all patches, and the degree of aggregation was similar between species ($k_H = 0.94 \pm 0.09$, $k_P = 1.07 \pm 0.15$; mean ± SE; paired t test, $t_{21} = 0.88$, $P = 0.387$). For the planthopper, the degree of aggregation increased with increasing host density ($F_{2,18} = 6.23$, $P = 0.023$) and decreasing patch size (Fig. 2B; $F_{1,18} = 10.46$, $P = 0.001$). Parasitoid aggregation increased significantly with patch size when no other sources of variation were considered (Fig. 2B; $F_{2,19} = 3.61$, $P = 0.047$). When other covariates were included in the model, only host aggregation was associated with k_P ($P = 0.051$, Appendix D). In this case, host and Anagrus aggregation were positively correlated. When comparing habitats with and without edges (small and medium patches vs. mainland habitat, respectively), I found that the degree of aggregation averaged 80% greater in the former than latter habitat (Fig. 2C; $F_{1,15} = 19.26$, $P = 0.001$). As expected, the difference in aggregation between small patches and equivalent-sized mainland habitats was much greater than the difference between medium patches and the mainland habitats (Fig. 2C; habitat type × patch size interaction, $F_{1,15} = 5.90$, $P = 0.028$).

The proportion of hosts parasitized by Anagrus was independent of patch size and host and parasitoid density per patch (Appendix D). The prediction that the proportion of hosts parasitized would increase with increasing host aggregation was not upheld ($P = 0.438$), although the trend was in the right direction (Appendix D). In contrast, the per capita number of hosts parasitized increased significantly with the degree of host aggregation (k_H; Fig. 3) and declined significantly with increasing density of adult female parasitoids (Appendix D).

Planthopper dispersion and parasitoid performance experiment

Anagrus density within a bus pan of sprangletop was not affected by the density or dispersion of hosts, but was strongly influenced by the location of the bus pan (Appendix E). As expected, the island bus pans were visited by 43% fewer female Anagrus than the mainland bus pans. The proportion of hosts parasitized was most strongly influenced by Anagrus density (16% of the model variance explained); higher parasitoid densities resulted in a greater proportion parasitized (Appendix E). Bus pans that were islands or had a low host density tended to have higher proportions of hosts parasitized than bus pans that were in the mainland or had a high
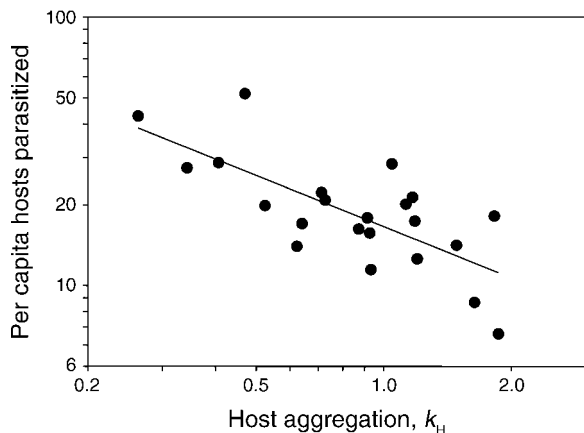
Fig. 3. The relationship between the degree of host aggregation, k_H, and the per capita number of hosts parasitized by *Anagrus*. The line is fit by least-squares regression ($R^2 = 0.52$, $P < 0.001$, $n = 21$). Based on an analysis of studentized residuals ($=10.68$), one data point was omitted from the analysis.

host density (Fig. 4A). There was also a highly significant location × dispersion interaction (Appendix E, $P = 0.004$). In this case, parasitism differed between the islands and mainland when hosts were clumped ($F_{1,83} = 24.6$, $P < 0.001$), but not when hosts were uniformly or randomly distributed ($F_{1,83} = 1.77$, $P = 0.187$ and $F_{1,80} = 0.55$, $P = 0.459$, respectively). Clumped hosts on islands suffered 2.2 times more parasitism than clumped hosts on the mainland (based on least-squares means). When island and mainland bus pans were considered separately, there was a significant effect of dispersion treatment on parasitism in islands ($F_{2,39} = 7.57$, $P = 0.002$), but not in the mainland ($F_{2,40} = 1.83$, $P = 0.173$). For the former bus pans, parasitism was 2.3 times greater when hosts were clumped than when hosts were randomly or uniformly distributed (Tukey test, $P < 0.008$ for both tests).

The per capita number of hosts parasitized was most strongly influenced by the location of the bus pans (Appendix E, 15% of variance explained). On island pans, 9.1 ± 1.2 hosts were parasitized per parasitoid as compared to 2.5 ± 1.2 hosts for mainland pans (based on least-squares means; Fig. 4B). The per capita number parasitized also averaged 2.5 times higher in the high, as compared to the low, density treatment (7.5 ± 1.2 vs. 3.1 ± 1.1 hosts parasitized per parasitoid, respectively). The dispersion of hosts, alone, had no effect on the per capita parasitized, but there was a highly significant dispersion × location interaction (Appendix E). Similar to the proportion parasitized, the per capita number parasitized by *Anagrus* was 3.7 times greater on islands than the mainland when the distribution of hosts was clumped ($F_{1,80} = 25.1$, $P < 0.001$), but there was no significant difference between locations when hosts were uniformly ($F_{1,80} = 3.58$, $P = 0.062$) or randomly ($F_{1,80} = 2.25$, $P = 0.130$) distributed. When separate ANOVAs were performed for each location, I found a significant

effect of dispersion treatment on the per capita parasitized on islands ($F_{2,38} = 5.15$, $P = 0.010$) but not in the mainland ($F_{2,40} = 1.82$, $P = 0.176$). With regard to the island patches only, the per capita number parasitized averaged 3.4 times higher for the clumped hosts than for the uniform or randomly distributed hosts (combined); although, the only significant difference was between the clumped vs. uniform hosts (Tukey's test, $P = 0.009$).

Within-patch oviposition behavior of *Anagrus*

Anagrus females exhibited very different searching and oviposition behaviors in patches that differed only with respect to the dispersion of hosts (Table 1). On average, parasitoids visited the same number of stems (4.1 stems), spent approximately the same amount of time per infested stem (52 min), and parasitized the same number of hosts per visited infested stem (6.9 hosts) regardless of the dispersion of hosts. However, for parasitoids on patches with clumped host distributions, a much higher percentage of visited stems were infested with planthopper eggs, 96% vs. 52%, respectively. Also,
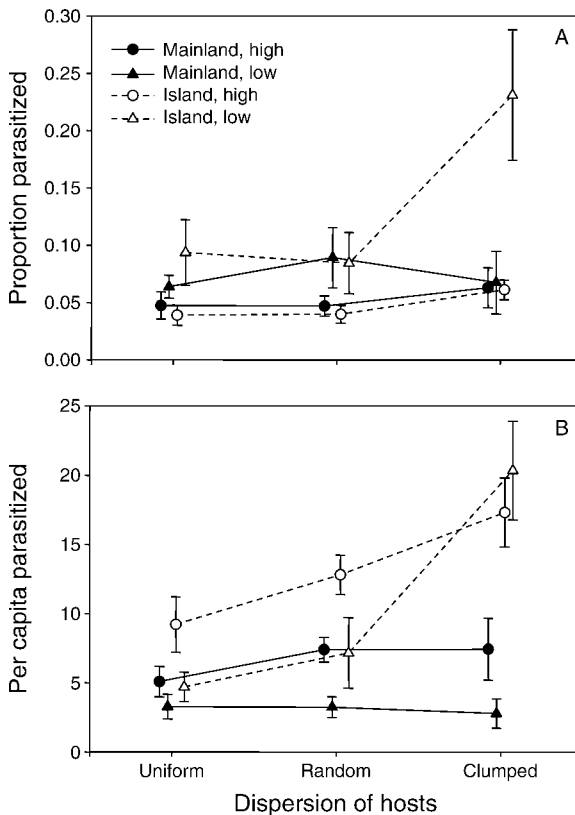

Fig. 4. Effect of host dispersion (uniform, random, or clumped) and density (high or low) on the (A) proportion of hosts parasitized and (B) the per capita number of hosts parasitized in bus pans of sprangletop. Bus pans were either embedded within large sprangletop habitats (mainland) or placed ≥3 m from any sprangletop (islands). Values shown are means and SE.

TABLE 1.　*Anagrus* foraging behavior in experimental patches (cluster of 19 pots) of sprangletop.

Behavior	Uniform	Clumped	df	T	P
Total stems visited	4.7 ± 0.7	3.5 ± 0.3	23	1.54	0.137
Infested stems visited	2.0 ± 0.3	3.3 ± 0.3	23	3.09	0.001†
Mean time per infested stem (min)	52.1 ± 2.6	53.4 ± 6.3	23	0.18	0.863
Mean hosts parasitized per stem	6.9 ± 1.1	7.0 ± 0.5	23	0.07	0.946
Mean step length (cm)	10.7 ± 1.2	6.3 ± 0.8	20	2.97	0.008†
Total time in patch (min)	114 ± 16	174 ± 15	23	2.72	0.012†
Total hosts parasitized	12.2 ± 2.3	22.5 ± 2.4	21	3.08	0.006†

Note: Values in uniform and clumped columns are mean ± SE. Those *P* values marked with a dagger (†) indicate a significant difference in behavior means between the uniform and clumped treatment (based on sequential Bonferroni test).

the mean step length, or distance moved between consecutively visited stems, was 41% shorter in the clumped than uniform patches. At the patch level, *Anagrus* females stayed 52% longer and laid a total of 84% more eggs when hosts were clumped as compared to when hosts were uniformly distributed (Table 1).

DISCUSSION

Through a combination of survey data and field and laboratory experiments, I have deciphered the basic elements of how sprangletop patch edges influence the interaction between *D. scolochloa* and its *Anagrus* egg parasitoids. Planthopper egg density and parasitism were each more than two times lower on the patch edge than at any other point further than 0.25 m from the edge. As a consequence, the presence of a sprangletop edge resulted in an increase in the aggregation of planthopper eggs when measured at the scale of the whole patch. In fact, as patch size decreased, the proportion of the patch that was within the sphere of influence of the edge increased, and consequently the aggregation of planthopper eggs within the patch increased. *Anagrus* parasitoids performed best in discrete patches with strongly aggregated hosts, owing to area-restricted oviposition behavior.

Lower densities at the patch edge are commonly reported and underlie some of the concerns about habitat fragmentation (e.g., Wolf and Batzli 2004, Fletcher 2005, Hickerson et al. 2005). The mechanism that generates this pattern in *D. scolochloa* is not well understood. For my survey and experimental data, the boundary between sprangletop and the matrix (composed of shorter grasses) was quite distinct and I rarely observed planthoppers in the matrix (J. T. Cronin, *unpublished data*). Lower edge densities could arise if within-patch movement is diffusive and the edge is strongly reflective (based on model by Reeve et al. 2008; J. D. Reeve and J. T. Cronin, *unpublished data*). Alternatively, lower densities at the patch edge than interior could be attributed to harsher abiotic conditions (e.g., Chen et al. 1995, Baldi 1999, McGeoch and Gaston 2000), higher predator densities or predation rates (e.g., Blouin-Demers and Weatherhead 2001, Ries and Fagan 2003, Ibarzabal and Desrochers 2004, Patten et al. 2006), or negative interactions with other herbivore species (i.e., interspecific or apparent competition;

Suarez et al. 1998, Hickerson et al. 2005, Cronin 2007) at the patch boundary. Parasitism by *Anagrus* was not responsible for the planthopper edge effect because parasitism rates were lower at the edge than interior of the patch. At present, I have no information on other sources of mortality or microclimatic conditions at the patch edge and interior that may explain the density edge effect in *D. scolochloa*.

The planthopper density–edge effect was narrow and extended only to ~0.25 m from the patch edge. Moreover, the edge effect was present regardless of patch size. Based on this information, the core area of a patch, i.e., the area unaffected by the habitat edge (e.g., Temple and Cary 1988, Laurance and Yensen 1991, Ohman and Erikson 1998), was expected to become proportionally smaller as patch size decreased. For example, the proportion of the patch that was core was estimated to be 79%, 62%, and 26% for the large, medium and small patches, respectively (calculations based on a circular patch). A meta-analysis by Bender et al. (1998) indicated that species that avoid habitat edges tend to have higher densities in larger patches, a pattern supported by my study.

Owing to the edge effect, planthopper eggs were primarily concentrated within the core area of the patch. As a consequence, at the scale of the whole patch, planthopper eggs were significantly more aggregated in small as compared to medium or large patches. Evidence that the change in aggregation with patch size can be attributed to the density–edge effect comes from the comparison of similar-sized habitats with and without an edge. Relative to an equivalent area within the sprangletop mainland, the small patches had an aggregation index *k* that was 80% lower (a lower *k* implies greater clumping). As expected, the medium-sized patches, which had proportionally more area in the core, did not have egg distributions that were significantly more clumped than equivalent sized mainland habitats. Therefore, it appears that there is a threshold patch size, between ~1 and 4 m², above which the density–edge effect is unimportant to the within-patch aggregation of planthoppers. Sprangletop patches below this threshold are abundant within the shallow waters of large potholes and in small depressions between large sprangletop-bordered potholes (J. T. Cronin, *unpublished data*). These small patches may be

important to planthopper spatial spread, connectivity among larger patches, and the rescue of other populations from extinction (see Laurance 1991, Crone et al. 2001, Murphy 2001).

The aggregation of *Anagrus* adult females also increased with decreasing patch size. This result could indicate that the parasitoid is edge averse like its host, which caused parasitoids to be concentrated into a proportionately smaller area within the patch as patch size decreased. Alternatively, *Anagrus* simply may be responding to the distribution of its host. Statistically, it is difficult to distinguish among hypotheses because a strong correlated response to patch size by the host and parasitoid would make it impossible to ascertain whether the host distribution or patch size itself were the causal factor generating the aggregation–patch size relationship. However, *Anagrus* attacks at least one other host species that feeds on a different plant species in the pothole region (Cronin 2007). With potential hosts in the surrounding grass matrix, it seems unlikely that the parasitoids would exhibit edge-avoidance behavior (see Ries and Sisk 2008). Also, in a previous study with the less common *A. columbi*, I found that this species readily crossed patch boundaries when the matrix was composed of other grasses (Cronin 2003b). I conclude that *Anagrus* in this study is most likely responding to its host, not the patch edge.

Edge-averse species, such as *D. scolochloa*, should generally exhibit a pattern of increased aggregation with decreasing patch size. However, to my knowledge, this prediction has not been evaluated for any other species. Given that edge-averse species are common (106 species spanning a broad diversity of taxa [see review by Ries et al. 2004]), an increase in within-patch aggregation is likely to be a common indirect effect of habitat fragmentation.

The field survey, in combination with the host dispersion experiment, provided a clear picture of how the presence of habitat edges and the aggregation of prey influenced parasitism by *Anagrus*. The field survey suggested that an increase in planthopper aggregation within a patch was associated with an increase in *Anagrus* per capita number of hosts parasitized. However, the experiment indicated that host dispersion was only important when the habitat had a distinct edge. When bus pans of sprangletop were embedded in large natural patches, host dispersion had no effect on the per capita number or proportion of hosts parasitized by *Anagrus*. In contrast, the per capita number and proportion parasitized on islands were 3.4 and 2.3 times higher, respectively, when hosts were strongly clumped as compared to when hosts were uniformly or randomly distributed. This is the first study to demonstrate that predator foraging behavior in response to prey dispersion can be mediated by the presence of a patch edge.

The greater performance of *Anagrus* when hosts were aggregated on islands was not a consequence of long-range attraction of parasitoids to patches with clumped hosts. Recruitment of *Anagrus* females to these bus pan islands did not differ among dispersion or host density treatments. Studies with several other parasitoid species also have found that colonization of a patch is independent of the density of hosts (e.g., Cronin and Strong 1999, Sutterlin and van Lenteren 2000, Cronin 2003a). In this study, once *Anagrus* encountered a discrete island patch, its oviposition behavior changed in response to the dispersion of hosts. In laboratory-created patches, *Anagrus* step lengths were 40% shorter when hosts were clumped as compared to uniformly distributed. This behavior is indicative of area-restricted search and has been reported for numerous species (e.g., Waage 1978, Lode 2000, Klaassen et al. 2006, Pinaud and Weimerskirch 2007). As expected when a predator discovers an aggregation of prey, area-restricted search can result in a greater per capita number of prey killed than when prey are uniformly or randomly distributed (Bell 1991, Godfray 1994, Nachman 2006b, Bommarco et al. 2007). In fact, *Anagrus* females spent 52% more time and parasitized 84% more hosts in the experimental arena when the host distribution was clumped relative to when it was uniform. These results correspond very well with my findings from the surveys of natural patches in which the per capita number of hosts parasitized increased with the degree of host aggregation. The shorter time spent in patches with uniformly distributed hosts could be due to the longer step lengths by *Anagrus*, increasing the probability that they lose contact with the patch (Turchin 1998). Alternatively, parasitoids may have given up the patch sooner because of the lower rate of host encounters in the uniform patches (Stephens and Krebs 1986).

If edges affected prey mortality only through their impact on prey dispersion, then there should have been no difference between mainland and island locations in the per capita number and proportion of hosts parasitized. However, independent of the effects of host dispersion and host density, islands had per capita numbers and proportions of hosts parasitized that were 2.4 and 1.5 times higher, respectively, than the mainland. These findings indicate that the habitat edge per se enhances parasitoid success. The most likely explanation for the location effect is that *Anagrus* is disinclined to cross a patch boundary, and thus remained longer ovipositing within island bus pans. At least for one of my parasitoids, *A. columbi*, we see this response when host-plant patches have a high-contrast edge (Cronin 2003b). Another contributing factor could be an increase in the oviposition rate by *Anagrus* following their dispersal to islands. This response, predicted by optimal foraging theory (reviewed by Cronin and Strong 1999), is known to occur in *A. columbi* (Cronin 2003a). However, islands were only isolated from the mainland by 3–5 m, making it unlikely that such short flights would elicit a more than twofold increase in number of ovipositions.

The cause for the large difference in parasitism between mainland and island bus pans that had aggregated hosts (hence the strong location × dispersion

interaction; Fig. 4) is more difficult to explain. It would require that the edge be most effective in enhancing oviposition success when hosts are clumped. Area-restricted search could be made more effective if the parasitoid's encounter with, or movement across the edge caused her to often return to the vicinity of her last oviposition (i.e., a foray loop; Conradt et al. 2003). This response would increase ovipositions on islands in general, but the increase would be greatest when hosts are clumped. In the absence of an edge, parasitoids may more readily drift away from clusters of hosts, weakening the relationship between host aggregation and per capita number parasitized. Because *Anagrus* parasitoids are so small, it would be quite difficult to observe their flight behavior and test this hypothesis. Currently, theoretical models of within-patch foraging focus on when to leave a patch (see Stephens and Krebs 1986, Stephens et al. 2007) and pay little attention to how patch edges might mediate foraging behavior.

I note here that the field experiment and survey differed with regard to the effect of host aggregation on percentage parasitism. In both cases the proportion of hosts parasitized tended to increase with the degree of host aggregation in discrete patches, but the relationship was only significant for the experimental patches (islands). The lack of a significant population response in the survey data could be explained by the heterogeneity inherent in the availability of hosts to parasitoids in natural patches. Hosts in the experiment were all even aged (differing by <2 d) and therefore relatively equal in their suitability to parasitism (*Anagrus* successfully parasitizes hosts in the first one-half of the 2–3 week development period; Cronin 2003a; J. T. Cronin, *unpublished data*). In contrast, hosts on natural plants varied in age by as much as three weeks, and the peak in *Anagrus* adult densities often appeared well after the peak in host densities (Cronin 2007). The resulting heterogeneity in susceptibility to parasitism easily could have obscured the relationship between host aggregation and the proportion parasitized. Provided that susceptible hosts are relatively abundant when parasitoids are active, a strong signal in the relationship between host aggregation and the per capita parasitized would be expected.

From a population dynamics perspective, area-restricted search by predators can contribute to the stability of predator–prey interactions by generating a type III functional response (Holling 1959, Murdoch and Oaten 1975) or by increasing the variance in parasitism risk (Chesson and Murdoch 1986, Pacala et al. 1990, Ives 1992). Stability through the former mechanism seems unlikely because there is no evidence that the proportion or per capita parasitized was density dependent (Appendix D; Cronin and Wilson 2007). Regarding the second mechanism, area-restricted search by *Anagrus* for aggregated hosts is likely to lead to considerable heterogeneity in parasitism risk. Although the stability consequences of heterogeneous parasitism risk is debatable (see Murdoch et al. 1992, Taylor 1993, Gross and Ives 1999), risk is an important issue with regard to pest suppression (Chesson and Murdoch 1986, van Veen et al. 2002).

Ecologists have generally overlooked the possibility that habitat edges can mediate predator movement or oviposition behavior, and prey risk by indirectly affecting prey dispersal (but see Cronin 2003a). In fact, the recent review of predator responses to fragmentation and loss of prey habitat by Ryall and Fahrig (2006) did not consider the possible importance of increased fragmentation to prey dispersal within a patch and predator performance. However, as stated previously, species that exhibit edge-averse behavior should tend to have more aggregated distributions in smaller patches. For predators employing an area-restricted search strategy, we might expect predation rates to be higher in smaller as compared to larger patches. This may represent a novel explanation for why, in some study systems, mortality from predators is greater in smaller than larger patches (e.g., Doak 2000, Hovel and Lipcius 2001, Cronin et al. 2004). However, to my knowledge, the underlying mechanisms behind these patterns have typically been attributed to more traditional factors such as increased exposure to predators in the matrix (e.g., Albrecht 2004, Ibarzabal and Desrochers 2004, Rand et al. 2006). Clearly, more studies are needed that explore the linkages between habitat edges, prey dispersal, and predator foraging success, as well as how changes in these linkages influence predator–prey population dynamics and response to increased habitat fragmentation.

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APPENDIX A

Detailed description of field-survey methods and statistics used (*Ecological Archives* E090-012-A1).

APPENDIX B

Description of experimental methods and statistics used to determine the effect of host density and dispersion, and presence of a habitat boundary, on *Anagrus* performance (*Ecological Archives* E090-012-A2).

APPENDIX C

Detailed methods used in the assessment of *Anagrus* oviposition behavior (*Ecological Archives* E090-012-A3).

APPENDIX D

ANCOVA table for the effects of patch size, host density, and degree of aggregation on several variables associated with the parasitoid *Anagrus* (*Ecological Archives* E090-012-A4).

APPENDIX E

ANCOVA table results for the effects of three experimental treatments (location, host dispersion, and host density) on parasitoid density and parasitism (*Ecological Archives* E090-012-A5).