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# PATCH STRUCTURE, OVIPOSITION BEHAVIOR, AND THE DISTRIBUTION OF PARASITISM RISK

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*Abstract.* To date, almost no experimental field studies have attempted to assess the factors that generate heterogeneity in the distribution of parasitism risk, a putative indicator of host–parasitoid stability. In this study, I examined the interaction between a planthopper *Prokelisia crocea* and its egg parasitoid *Anagrus columbi* among discrete patches of prairie cordgrass, *Spartina pectinata*. In particular, I examined how patch geography and host distribution within a patch influenced the distribution of adult parasitoids, parasitoid oviposition behavior, the proportion of hosts parasitized, and the aggregation of parasitism ($CV^2$) and adult parasitoids.

Based on six generations of census data, the distribution of parasitism was strongly aggregated within ($CV^2 = 3.58$), but not among ($CV^2 = 0.58$) cordgrass patches. Parasitism was also spatially and temporally density independent. To determine what influences the distribution of parasitism risk, I selected 26 discrete cordgrass patches, removed all sources of *A. columbi*, and then quantified the immigration and subsequent oviposition behavior of *A. columbi* colonists. I found that the number of immigrants significantly increased with patch size and decreased with patch isolation. Patch size had no influence on the per capita hosts parasitized per leaf, but there was a significant twofold increase in per capita attacks from the least to the most isolated patches. The isolation effect was likely due to an optimal oviposition response to dispersal distance by *A. columbi*. For these experimental patches, substantial within-patch aggregation of parasitism ($CV^2 = 1.63$) did not translate into strong among-patch aggregation ($CV^2 = 0.13$). Searching adult parasitoids were randomly distributed within and among patches and thus did not explain the high $CV^2$ within patches. Interestingly, the aggregation of parasitism risk within a patch was significantly negatively correlated with patch size and positively correlated with patch isolation. The distribution of parasitism risk could be divided into two general components. The within-parasitoid component was attributable to individuals engaging in multiple ovipositions within a leaf and the distance-dependent oviposition response. The latter response was likely the cause for the variation in $CV^2$ with respect to patch size and isolation. Within-parasitoid aggregation has no effect on host–parasitoid stability. The among-parasitoid component of aggregation appears to have been due to heterogeneity in the vulnerability of hosts and an edge effect (parasitism risk is 60% more heterogeneous at the edge than interior of a patch) and is in theory stabilizing. Consequently, a change in landscape structure that leads to an increase in cordgrass edge habitat may promote a more stable host–parasitoid interaction.

*Key words: aggregation;* Anagrus columbi; *dispersal distance; edge effects; host–parasitoid interaction; immigration; oviposition behavior; patch isolation; patch size;* Prokelisia crocea; *pseudointerference; stability.*

## INTRODUCTION

The milieu of predator–prey interactions is a heterogeneous, spatially subdivided landscape. Over the past several decades a paradigm has emerged regarding the role of spatial subdivision: it can promote predator–prey coexistence (for reviews, see Hanski and Gilpin 1997, Tilman and Kareiva 1998, Turchin 1998). Such a generalization must be viewed with considerable circumspection because the stability of an interaction can depend on the details of the dispersal behavior, life history, and demography of both the predator and prey. For example, Kareiva (1987) found that aphid populations were more prone to localized outbreaks (i.e., unstable dynamics) in experimentally fragmented, relative to continuous, goldenrod habitat. Patchiness in this study apparently interfered with the searching and aggregation behavior of ladybird predators of the aphids. Clearly, one way to further our understanding of the role of spatial subdivision in predator–prey population dynamics would be to emphasize a mechanistic-based experimental approach.

Insect parasitoids and their hosts have been popular model organisms in spatial ecological studies of consumers and their resources (Godfray 1994, Hassell 2000). While the literature is replete with theoretical treatises of the effects of spatial subdivision on host–

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parasitoid interactions (e.g., Reeve 1988, Comins et al. 1992, Hassell and Wilson 1998), field studies are primarily restricted to an examination of the relationship between host density and the proportion of hosts parasitized among host-plant patches (Stiling 1987, Walde and Murdoch 1988). Very few field studies have addressed how features of the landscape (size, isolation, or perimeter-to-area ratio of patches, or aspects of the intervening habitat) influence the dispersal and oviposition behavior or the distribution of parasitoid attacks (Roland 2000). In one such study, Doak (2000) found that parasitism of the geometrid moth, *Itame andersoni*, was strongly influenced by patch size and isolation, with the smallest patches having the highest overall proportion of hosts parasitized (see also Sheehan and Shelton 1989, Lei and Hanski 1997, Cronin and Strong 1999, Lei and Camara 1999). The cause for this heterogeneous distribution of parasitism is not well understood.

The fact that patchiness influenced the distribution of parasitism in the previous example is of great importance because highly heterogeneous distributions of parasitism have been directly linked to theoretically stable host–parasitoid interactions (Pacala et al. 1990, Hassell et al. 1991, Ives 1992*a*). Heterogeneity in the risk of parasitism can result from variations among patches in the distribution, foraging time, or oviposition behavior of parasitoids, or in the density, accessibility, or susceptibility of hosts (Bailey et al. 1962, Pacala et al. 1991, Taylor 1993, Cronin and Strong 1999, Gross and Ives 1999). How patch structure influences these factors, and in turn affects the distribution of parasitism, is largely unknown. One exception is the study by Cronin and Strong (1999) in which it was found that the number of hosts parasitized per patch by the minute egg parasitoid, *Anagrus sophiae* (Hymenoptera: Mymaridae), increased with patch isolation distance and corresponded to a more aggregated distribution of parasitism in isolated relative to nonisolated host patches.

A widely accepted method for quantifying heterogeneity in the risk of parasitism among host patches is the $\mathrm{CV}^2$, the coefficient of variation squared in the probability of parasitism across host patches. Larger values of the $\mathrm{CV}^2$ indicate more aggregated distributions of parasitism risk. It has been argued that for an extensive array of discrete-time models a $\mathrm{CV}^2 > 1$ is sufficient to stabilize a host–parasitoid interaction (Pacala et al. 1990, Hassell et al. 1991). However, this $\mathrm{CV}^2 > 1$ rule can be made invalid if model assumptions are violated, e.g., if hosts and parasitoids have overlapping generations (Murdoch and Stewart-Oaten 1989, Ives 1992*b*, Murdoch et al. 1992, Reeve et al. 1994*a*) or if attacks per parasitoid are also aggregated within patches (i.e., multiple ovipositions per parasitoid within a patch; Gross and Ives 1999). Violation of assumptions can affect the minimum level of aggregation necessary for stability. While the use of the $\mathrm{CV}^2$ as an absolute indicator of stability is questionable, it can nevertheless be used as a relative measure of the distribution of parasitism risk (Taylor 1993, Cronin and Strong 1999).

In this study, I examined how several aspects of host-plant patch structure, the size, isolation, and proximity of hosts to the edge of patches, influence the density distribution and oviposition behavior of a parasitoid and the distribution of parasitism risk within and among host patches. The study system is the patchily distributed prairie cordgrass (*Spartina pectinata* Link; Poaceae), a specialist planthopper of cordgrass (*Prokelisia crocea* [Van Duzee]; Hemiptera: Delphacidae), and the planthopper's specialist egg parasitoid (*Anagrus columbi* Perkins [Hymenoptera: Mymaridae]). I first present census data spanning six planthopper–parasitoid generations and 7–12 prairie sites that indicate highly heterogeneous distributions of parasitism within, but not among, cordgrass patches. I then describe two field experiments that quantify the influence of the distribution of adult parasitoids, their oviposition behavior, and various aspects of patch structure on the aggregation of parasitism risk. Finally, I address how changes in the structure of cordgrass habitat could influence parasitoid behavior and the aggregation of parasitism risk, and consequently the spatial and temporal dynamics of this host–parasitoid interaction.

## METHODS

### *Life history*

A common native plant species of relatively hydric grasslands is prairie cordgrass, *S. pectinata* (Hitchcock 1963). Cordgrass occurs in very discrete patches ranging in size from well less than 1 $\mathrm{m}^2$ to several hectares, and in isolation by up to 46 m from the nearest cordgrass patch (Cronin 2003*a*). An extensive insect assemblage has been reported to feed on prairie cordgrass (Holder 1990, Johnson 1995, Wheeler 1996), and the delphacid planthopper, *P. crocea*, appears to be the most abundant (Holder 1990, Holder and Wilson 1992, Cronin 2003*a, b*). *Prokelisia crocea* is monophagous (Holder and Wilson 1992) and has two distinct generations per year in North Dakota; one in which adult densities peak in mid–late June and another in which adult densities peak in early August (*unpublished data*). Adults live for two weeks and lay eggs along the midrib of the adaxial surface of cordgrass leaves. In the field, planthopper egg densities range from 0 to 253 eggs per leaf (24.7 ± 0.8 eggs/leaf, mean ± 1 SE, $n = 1394$; *unpublished data*). The suite of natural enemies that attack *P. crocea* is typical of most other delphacids (Cronin and Strong 1993*c*). The most obvious source of mortality is egg parasitism by the mymarid *A. columbi*, which accounts for ~21% host mortality on average (*unpublished data*).

The host range of *A. columbi* is poorly known, but appears restricted to just a few species of planthoppers (Krombein et al. 1979). Within the prairies where this research was conducted, I have never reared a species resembling *A. columbi* from any other host plant (Cronin 2003*b*). *Anagrus columbi* is proovigenic (ecloses as an adult with its total egg complement mature and available for oviposition) and has an average load of 46.9 ± 2.2 eggs ($n = 37$; *unpublished data*). The foraging behavior of this egg parasitoid is quite similar to that of the congener *A. sophiae*, a parasitoid of the salt-marsh planthoppers *P. marginata* and *P. dolus* (Cronin and Strong 1990*a, b,* 1993*a, b,* 1994, 1999, Reeve et al. 1994*b*). In general, *A. columbi* searches for hosts at random within a cordgrass leaf, demonstrates no ability to avoid superparasitism, and displays a type I functional response over the range of hosts normally found in the field (*unpublished data*). The $\mathrm{CV}^2 > 1$ rule is based on the assumption that parasitoids behave in this way (Hassell et al. 1991, Pacala and Hassell 1991, Taylor 1993).

### *Natural distribution of parasitism*

For six planthopper generations, spanning three years (1998–2000), I made cordgrass leaf collections from 7 to 12 sites to determine host egg density, the proportion of hosts parasitized, and the distribution of parasitism risk. The sites containing cordgrass were located in northeastern North Dakota, USA, and were separated from one another by 450 m to 70 km. The number and identity of sites varied from year to year due to changes in their accessibility. At the end of each planthopper generation, when the oviposition period for both the planthopper and parasitoid was virtually complete (as determined from regular sweep samples and sticky traps in each site), 25–40 host-infested cordgrass leaves were collected from a wide area within each site. Through careful dissection of the leaves, it was possible to identify unparasitized and parasitized hosts, and those host eggs that successfully emerged planthopper nymphs and parasitoid adults (Cronin and Strong 1990*a*). Thus, each leaf provided a complete record of the cumulative history of planthopper and parasitoid attacks during that generation. Parasitism in this study was based on that complete record.

Within each site, I examined the relationship between host-egg density and the proportion of hosts parasitized per leaf, and quantified the aggregation of parasitism among leaves using the $\mathrm{CV}^2$ (see *Methods: Computing aggregation* for calculation). I henceforth refer to the scale of these spatial analyses as the ''among-leaves scale.'' Temporal density dependence in parasitism across six planthopper generations was evaluated from the relationship between the mean proportion of hosts parasitized per leaf and mean host density per leaf. Separate tests were performed for each cordgrass site (only eight sites had data for all six generations).

I conducted an additional census within a large prairie site (17 km west of Grand Forks, North Dakota) that focused on the distribution of parasitism ''among patches.'' During the second planthopper generation of 1999, I collected 10 host-infested leaves (in some patches fewer infested leaves were available) from each of 25 cordgrass patches and determined host density and proportion parasitized from each. I returned to these same patches in both the first and second generations of 2000, but also added another 81 patches to the census. Among these 106 patches, sizes ranged from 0.08 to 48.50 $\mathrm{m}^2$, and averaged 3.50 ± 0.80 $\mathrm{m}^2$ (mean ± 1 SE). The relationship between mean host density per leaf and the mean proportion parasitized per leaf among the cordgrass patches was determined for each of the three generations. The among-patch $\mathrm{CV}^2$ was also determined for each generation.

### *Parasitoid response to patch structure*

To evaluate how patch structure influences the interaction between *P. crocea* and *A. columbi*, I experimentally manipulated planthopper egg density among cordgrass patches within a single prairie fragment. Number of *A. columbi* immigrants, number of hosts parasitized per female parasitoid, proportion of hosts parasitized, the aggregation of parasitism, and the aggregation of adult parasitoids were estimated for each patch.

The prairie fragment was located within the Kelly's Slough National Wildlife Refuge 16 km west of Grand Forks, North Dakota, and was ~22 ha in size. For the experiment, I selected 26 discrete patches that were chosen to represent a broad range of sizes and degrees of isolation. To accurately quantify patch size, I photographed each patch from 3 m above, digitally traced their boundaries, and then computed the area using ImageTool 2.0 (Wilcox et al. 1996). Patch isolation, which is dependent upon the linear distance to, and size of, neighboring patches (Hanski 1994, Hanski and Kuussaari 1995), was determined only from the nearest patch in each of four quadrats (NE, NW, SE, and SW). Here, my index of isolation, $I$, was computed as

$$I = \frac{1}{\sum_{i}^{4} A_i e^{-D_i}}$$

where $A_i$ and $D_i$ are the area of (square meters) and distance to the nearest patch in the $i$th quadrat, respectively. Larger values of $I$ indicate greater patch isolation. There is a high correlation between $I$ and a much more inclusive measure of isolation based on all of the cordgrass patches within a 40-m buffer area surrounding the focal patch ($R = 0.80$, $n = 25$, $P < 0.001$). The 26 patches used in this study ranged in size from 0.3 to 6.1 $\mathrm{m}^2$ and in isolation from 0.028 to $1.07 \times 10^7$ (the maximum linear distance to a nearest neighbor was 17 m) (Fig. 1). Patches within this size range represented the majority of patches or 52% of the total number within this site (Cronin 2003*a*).

Late in the second planthopper generation of 2000 (mid-August), when planthopper eggs and parasitoids

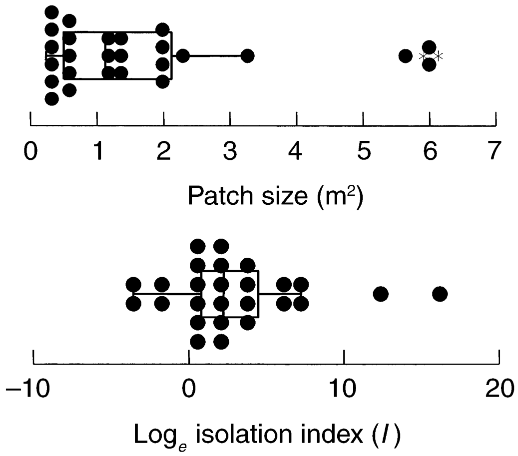

FIG. 1. Distribution of patch sizes and isolation indices (ln-transformed) for 26 experimental cordgrass patches. Data points are superimposed upon a box-and-whisker plot (Sokal and Rohlf 1995).

were just past peak abundances, a team of researchers carefully removed all leaves with visible planthopper oviposition scars (evident after ∼7 d) from each of the 26 cordgrass patches. This procedure led to the removal of all well developed planthopper embryos and parasitoids in advanced developmental stages. Consequently, the within-patch source of adult *A. columbi* was effectively eliminated. What remained in each patch was leaves bearing young planthopper eggs (a stage suitable for parasitoid attack; Cronin and Strong 1990*a*) and early instar parasitoid larvae that would not eclose for at least another 10–14 d. I note here that even in the smallest cordgrass patches, the leaves removed from a patch accounted for only a very tiny fraction of the total number of leaves in that patch.

Within each of the 26 patches, I placed potted cordgrass plants that bore experimentally established clutches of planthopper eggs for *A. columbi* to attack. Eight female and two male adult planthoppers were placed in a 50 mm long by 26 mm diameter tubular clip cage (see Cronin and Strong 1990*a*) that was positioned at the base of a single leaf of a potted cordgrass stem (16 cm diameter pots). The planthoppers were given 48 h to lay eggs, during which time they produced a discrete host-egg clutch with an average of 54.4 ± 1.6 eggs (mean ± 1 SE, $n = 401$). Experimental clutch sizes were larger on average than natural clutch sizes (mean = 24.7 eggs) but well within the range found in the field (1–253 eggs; Cronin 2003*a*). Two clutches were established on opposite-facing leaves of a single stem per pot, and there were 3–5 stems per pot. By using experimentally created egg clutches, I minimized the variation in host age, density per leaf, and distribution of hosts within a leaf. Also, variation in cordgrass plant quality, which may influence parasitism (e.g., Price 1986), was minimized by using plants propagated under identical conditions. I did not attempt to control the variation among naturally occurring planthopper eggs, except to eliminate older host embryos from the patch.

Eight potted cordgrass plants, each with two host-egg clutches, were placed in each of the 26 cordgrass patches. Four pots were positioned along the patch border (edge pots), one at each cardinal direction, and the remaining four pots were placed near the patch center (interior pots). All pots were sunk flush to the ground.

To estimate the density of *A. columbi* immigrants in each cordgrass patch, I captured wasps on trap plants. Within each cordgrass pot, a thin layer of Tanglefoot (Tanglefoot Company, Grand Rapids, Michigan) was applied to the basal 10 cm of two opposite-facing leaves of a host-free cordgrass stem. As I have found with the congeneric *A. sophiae* (Cronin and Strong 1993*a*), female *A. columbi* walk or alight onto host-infested leaves and leaves coated with Tanglefoot with equal frequency (*unpublished data*). Because all within-patch sources of adult *A. columbi* had been removed, these captures provide an estimate of the number of immigrants per cordgrass leaf. Laboratory evidence supports the notion that these trap leaves within a patch, even if they reside on the same cordgrass stem, represent independent replicates for the estimation of *A. columbi* density. Foraging female wasps almost invariably emigrate from a leaf by flying (*unpublished data*). Colonization of a subsequent leaf that is attached to the same or a different stem occurs with equal likelihood. The distance moved is on the order of decimeters and is comparable to the movement patterns of *A. sophiae* (Cronin and Strong 1993*a*, *b*, 1999).

For comparison with the 26 discrete cordgrass patches, I also established experimental host-egg clutches and parasitoid leaf traps on potted stems placed in four large cordgrass patches (hereafter denoted as mainland control patches). Because of the enormity of these patches (ranging in size from 3855 to 46 524 m$^2$), I made no attempt to eliminate old host embryos or parasitoid larvae in advanced developmental stages; thus, *A. columbi* sources in these patches were derived from both immigrant and resident individuals. A total of 20 pots, each bearing a stem with two host-egg clutches and a stem with two sticky trap leaves were placed in each patch. One-half of the pots were placed along the patch edge and the other half were placed 5 m in the interior. Pots were spaced 1 m apart.

Pots bearing host egg clutches and trap leaves were left out in the prairie for 5 d to accumulate parasitoid attacks and capture foraging *A. columbi*. Afterward, the potted plants were collected and returned to the laboratory. I then placed a 1/4 × 1/4 m sampling frame in three randomly chosen locations within the patch, counted the number of cordgrass stems, and collected all of the leaves that were naturally infested with planthopper eggs (in patches $<0.25$ m$^2$, all stems were counted). In the laboratory, the sticky leaves were examined under a dissecting microscope and the number of male and female *A. columbi* counted. After a 5-d incubation period, the leaves bearing experimental and natural host egg clutches were dissected to determine the number of healthy and parasitized hosts.

For each cordgrass patch and mainland control, I used the data obtained from the experimental host egg clutches and sticky leaves to compute the following patch means (on a per-leaf basis): (1) number of female *A. columbi* immigrants, (2) number of hosts parasitized per female parasitoid (mean number of hosts parasitized per leaf/mean number of wasps captured per leaf), and (3) proportion of hosts parasitized. Also, I computed ''within'' each cordgrass patch the aggregation of parasitism ($\mathrm{CV}^2$) among host-infested leaves and the aggregation of adult female *A. columbi* among sticky leaves using the procedures outlined in *Methods: Computing aggregation*. Based on the pooled number of healthy and parasitized hosts among the 16 host-egg clutches, and the number of *A. columbi* captured on the 16 sticky leaves, I also determined the $\mathrm{CV}^2$ and aggregation of parasitoids ''among'' the 26 cordgrass patches (plus four controls). Finally, separate measures of the mean number of hosts parasitized, mean proportion parasitized, and the aggregation of parasitism were determined for the naturally occurring planthopper-infested leaves.

### *Distance-dependent oviposition and aggregation*

In the previous experiment, patch isolation was by definition dependent upon the distance to, and size of, neighboring patches. To address the effect of isolation distance alone on the number of immigrant females, oviposition behavior, and aggregation of *A. columbi*, I performed the following experiment. In the summer of 1999, I selected three large (mainland) cordgrass patches that were bordered on one side by an expansive open mudflat (60–80 m wide). Mudflat is common in my research sites, accounting for ~47% of the prairie landscape (Cronin 2003*b*). Potted cordgrass plants containing either host-egg clutches on two leaves (host pots to accumulate ovipositions) or Tanglefoot on two leaves (trap pots to capture dispersing parasitoids) were placed within the mudflat at 2, 5, 10, and 25 m from the mainland source of *A. columbi*. For each distance, host pots alternated with trap pots in a line transect that paralleled the mainland patch. There were 12 of each pot type at each distance and all pots were spaced 1 m apart and sunk flush to the mud. In colonizing a potted cordgrass plant (a small experimental cordgrass patch), the parasitoid had to have dispersed, at a minimum, the distance separating the pot from the mainland source patch. A control transect, identical to the dispersal transects, was placed within the mainland patch, 3 m from the patch border.

A single experimental replicate consisted of four dispersal transects (2, 5, 10, and 25 m) and a control that were deployed simultaneously and in association with the same mainland patch. The transects were offset by at least 10 m from each other to reduce the likelihood that parasitoids would leapfrog between transects. Three experimental replicates were used in this study. In each of these replicates, the closest source of parasitoids, not counting the mainland, was at least 40–50 m away for the 25-m transects and even further for all other transects.

Host and trap plants were left in the marsh for 5 d to accumulate parasitoid attacks and capture searching parasitoids, respectively. I then returned the pots to the laboratory and determined the number of planthopper eggs parasitized in each of the 24 host-egg clutches per transect located at distance $d$ ($p_d$) and the number of adult female wasps captured on each of the 24 sticky leaves per transect at distance $d$ ($w_d$). Because individual *A. columbi* are roughly equally likely to disperse between leaves on the same plant, to the adjacent plant, and to a plant ~1 m away, even when other cordgrass plants are in between (*unpublished data*), I treated values of $p_d$ and $w_d$ from within each transect as independent measures of the number of hosts parasitized and number of wasps per leaf, respectively (see also Cronin and Strong 1993*a*, 1999). From these independent parameter estimates, I computed the mean number parasitized ($\bar{p}_d$) and mean wasps per leaf ($\bar{w}_d$) for each transect. I then computed an indirect estimate of the per capita number of hosts parasitized per host-egg clutch, $\bar{o}_d$, from the quotient $\bar{p}_d/\bar{w}_d$. For each transect, then, I obtained a measure of the mean number of colonizing *A. columbi*, per capita hosts parasitized, and proportion of hosts parasitized on a per-leaf basis. I also computed the aggregation of parasitism ($\mathrm{CV}^2$) and the aggregation of adult female parasitoids among leaves within each transect.

### *Parasitism in the laboratory*

For comparison with previous field experiments, I quantified the oviposition behavior of *A. columbi* under controlled laboratory conditions. Twenty-five host-egg clutches were established on separate potted cordgrass stems using the procedure outlined previously. These pots were placed on a laboratory bench with lighting provided from overhanging high pressure sodium vapor grow lights. *Anagrus columbi* used for this study were all newly eclosed female adults (<3 h old), having a full complement of eggs (mean = 54; *unpublished data*), and were in good physical condition. Between 0800 and 1000 hours, a single female parasitoid was gently released onto each host-egg clutch. I monitored the leaf continuously and terminated the trial after the parasitoid emigrated from the leaf (see also Cronin and Strong 1990*a*, 1993*a*, *b*, 1996). The leaves were dissected after a 5-d incubation period and I recorded the number of parasitized and unparasitized hosts.

### *Statistical analyses*

For the census data, the analyses of spatial or temporal density dependence were determined by regressing planthopper egg density against the proportion of hosts parasitized (both ln-transformed). In the experimental study of *A. columbi*'s response to patch geography, multiple least-squares regression was used to quantify the effect of two independent variables, patch size and isolation, on each of the parasitoid-response variables (female parasitoid density, per capita hosts parasitized, proportion parasitized, and aggregation of parasitism and female parasitoids). Paired *t* tests were also used to evaluate differences between the patch edge and interior, and between experimental and naturally occurring leaves for each response variable. For these tests, the pair was derived from the same cordgrass patch. Finally, separate one-way ANOVAs were used to determine the effect of isolation distance on the five parasitoid response variables. All possible pairwise comparisons among distance means were assessed using Tukey's HSD test (Sokal and Rohlf 1995). To homogenize variances and normalize distributions, patch size and isolation, as well as all response variables, were ln-transformed prior to analysis; the exception was the proportion of hosts parasitized, which was angular-transformed (arcsine-square root of the proportion). All tests were performed using SYSTAT 10.0 (SPSS 2000).

In the analyses outlined above, separate statistical tests were performed for each of the five parasitoid response variables. Because these variables were derived from the same experimental units (i.e., a cordgrass patch), the tests were not completely independent of each other. Therefore, a sequential Bonferroni correction based on the Dunn-Šidák method was used to maintain an experiment-wise error rate ($\alpha$) at the nominal level of 0.05 (Sokal and Rohlf 1995).

### *Computing aggregation of parasitism and parasitoids*

Parasitoid aggregation was estimated indirectly from the distribution of parasitized hosts among leaves or among cordgrass patches (see Pacala et al. 1990, Hassell et al. 1991, Pacala and Hassell 1991). Here, I used the maximum likelihood method of Reeve et al. (1994*b*), which assumes that parasitoids aggregate independently of host density. Density-independent patterns of parasitism appear to be widespread in the Mymaridae (Cronin and Strong 1993*c*), and *A. columbi* is no exception (see *Results*). The log-likelihood function of aggregation used is

$$L = \sum_{i=1}^{M} \ln\left[\binom{n_{2i}}{n_{1i}}\frac{k^{k}}{\Gamma(k)} \times \int_{0}^{\infty} (e^{-aPu})^{n_{2i}-n_{1i}}(1 - e^{-aPu})^{n_{1i}}u^{k-1}e^{-ku}\,du\right]$$

where $M$ is the number of patches, $n_{1\mathrm{i}}$ and $n_{2\mathrm{i}}$ are the number of individuals parasitized and hosts, respectively in the $i^{\mathrm{th}}$ patch, $P_i$ is the number of searching parasitoids in patch $i$, and $a$ is the attack rate of the parasitoid. $U_i$ is a gamma random variable with a mean $= 1$ and shape parameter $k$. Parasitoid aggregation is controlled by $k$; where $k < 1$ indicates a highly aggregated distribution of parasitoids across patches and $k > 1$ indicates a more even distribution. In this model, $1/k$ is equal to the coefficient of variation squared ($\mathrm{CV}^2$). The maximum likelihood estimates of $k$ and $aP$ (a measure of parasitoid density) were found by maximizing $L$ with respect to the above parameters.

For this model, the number of parasitoids visiting a patch was assumed large enough that their distribution can be approximated by a continuous (i.e., gamma) random variable. Low parasitoid densities can bias the estimates of $k$ to smaller values, and cause an overestimate of $\mathrm{CV}^2$ (Hassell et al. 1991, Reeve et al. 1994*b*, Olson et al. 2000). I quantified the magnitude of the bias in the $\mathrm{CV}^2$ using the formula $\mathrm{CV}_\mathrm{T}^2 = b/aP + \mathrm{CV}_\mathrm{Z}^2$; where $\mathrm{CV}_\mathrm{T}^2$ is the total aggregation estimated from above, $b$ is the bias in aggregation, and $\mathrm{CV}_\mathrm{Z}^2$ is the theoretically stabilizing form of aggregation (Hassell et al. 1991). Nonlinear regression was used to estimate mean $b$ and $\mathrm{CV}_\mathrm{Z}^2$ and their asymptotic 95% confidence intervals.

The aggregation of adult female *A. columbi* was estimated by fitting the distribution of captured wasps to a negative-binomial model and solving for $k_{\mathrm{nb}}$. In analogy with the $\mathrm{CV}^2$, the quantity $1/k_{\mathrm{nb}}$ represents a measure of the degree of aggregation, where small values of $1/k_{\mathrm{nb}}$ imply weakly aggregated distributions and large values a highly aggregated distribution. Whether the distribution of parasitoid adults differed significantly from the expectations of a random (Poisson) distribution was assessed using a one-sample Komolgorov-Smirnov test (Sokal and Rohlf 1995).

## RESULTS

### *Natural distribution of parasitism*

Among the six planthopper generations, the proportion of hosts parasitized per leaf ranged from 0 to 54% within a site (Fig. 2A), and averaged 21.5 ± 2.3% (mean ± 1 SE, $n = 39$). At the spatial scale of the leaf, parasitism within a site and generation was independent of host density in 35 out of 37 tests (Table 1). There was an approximately equal split between tests exhibiting a tendency toward positive and inverse density dependence, suggesting an overall tendency for density-independent parasitism at the leaf scale. Furthermore, for the eight prairie sites that were continuously censused for six generations, I could find no evidence of temporal density dependence in parasitism (Table 1). Considering the short time frame which these data span, this result must be viewed with some caution.

Among generations and prairie sites, there was no indication that the magnitude of the $\mathrm{CV}^2$ was influenced by $aP$ (Fig. 3A). Bias in the estimate of total aggregation, $\mathrm{CV}_\mathrm{T}^2$, was low and not significantly different

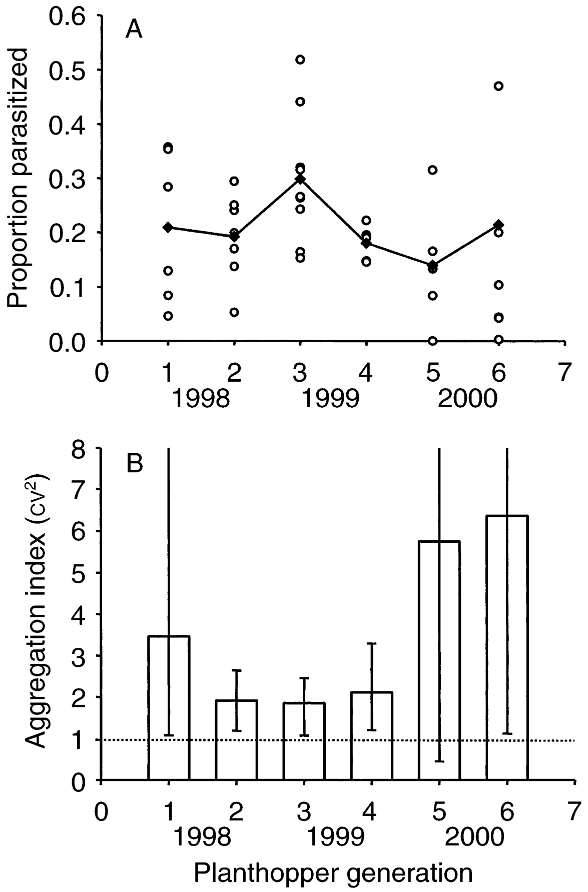

FIG. 2. The proportion of hosts parasitized and the aggregation of parasitism (CV$^2$) for six planthopper generations (1998–2000). (A) Proportion parasitism in different cordgrass sites (open circles) and the mean within each generation (closed diamonds). (B) Mean CV$^2$ among cordgrass sites with 95% confidence intervals. Confidence intervals were adjusted using a Bonferroni correction to account for an increased Type I error associated with multiple, nonindependent tests (Sokal and Rohlf 1995). To achieve an overall error rate ($\alpha$) of 5%, the CI for each generation was set at $100 \times 1 - (\alpha/6 \text{ generations}) = 99.2\%$. The dotted line represents the theoretical delineation between a stable (below) and unstable (above) host–parasitoid interaction.

TABLE 1. The relationship between the proportion of hosts parasitized (angular-transformed) and host density (ln-transformed) in space (among cordgrass leaves or cordgrass patches) and in time (six generations among leaves).

| | | Positive trend | | Negative trend | |
|---|---|---|---|---|---|
| Scale of test | Tests (no.) | Significant | Not significant | Significant | Not significant |
| Spatial | | | | | |
| Leaf | 37 | 1 | 15 | 1 | 20 |
| Patch | 3 | 0 | 3 | 0 | 0 |
| Temporal (leaf) | 8 | 1 | 2 | 1 | 4 |

*Note:* Separate least-squares regressions were used to determine the slope (positive or negative) and significance ($P \leq 0.05$) of the relationship.

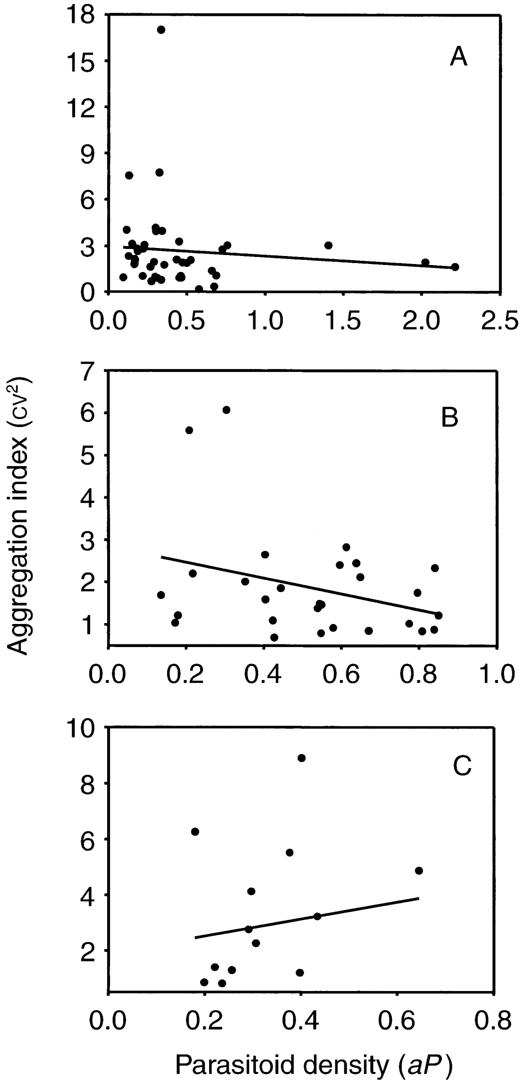

FIG. 3. The relationship between the CV$^2$ and an estimate of parasitoid density, *aP*, for (A) leaves collected from multiple generations and prairie sites ($y = 2.95 - 0.62x$, $R^2 = 0.02$, $P = 0.37$), (B) experimental leaves from the parasitoid response to patch structure study ($y = 2.84 - 1.87x$, $R^2 = 0.10$, $P = 0.10$), and (C) experimental leaves from the distance-dependent oviposition and aggregation study ($y = 6.30 + 0.48x$, $R^2 = 0.10$, $P = 0.26$).

from zero ($b = 0.087$; 95% CI: $-0.25$, 0.18). For five of six generations, the CV$^2$ based on the distribution of parasitism among leaves within a prairie site averaged significantly $>1$: 95% confidence intervals surrounding the mean did not overlap unity (Fig. 2B). Averaged among the six planthopper generations, CV$^2$ = 3.58 (95% CI: 1.46, 5.70).

At the cordgrass-patch scale, parasitism was also independent of host density (Table 1). In contrast to the strongly aggregated distribution of parasitism among leaves, the distribution of parasitism among cordgrass patches was very weakly aggregated. The CV$^2$ (and 95%

TABLE 2. Parasitoid response variables and their relationship with patch size (m$^2$) and isolation (based on the index of isolation, $I$) for experimental and naturally occurring planthopper-infested cordgrass leaves ($n$ = 26 cordgrass patches).

| Source | Parasitoid response variable (per-leaf basis) | Mean | 95% CI | Model $R^2$ | Area | | Isolation | |
|---|---|---|---|---|---|---|---|---|
| | | | | | Slope ± 1 SE | $P$ | Slope ± 1 SE | $P$ |
| Experimental leaves (discrete patches) | *A. columbi* density | 0.91 | 0.72, 1.09 | 0.49 | 0.21 ± 0.06 | 0.002† | −0.05 ± 0.01 | 0.001† |
| | hosts parasitized per female wasp | 17.07 | 13.57, 20.56 | 0.32 | −0.17 ± 0.10 | 0.109 | 0.07 ± 0.02 | 0.005† |
| | proportion parasitized | 0.28 | 0.22, 0.34 | 0.22 | 0.01 ± 0.02 | 0.747 | −0.02 ± 0.01 | 0.022† |
| | CV$^2$ | 1.63 | 1.30, 1.97 | 0.38 | −0.25 ± 0.09 | 0.009† | 0.10 ± 0.03 | 0.001† |
| Naturally occurring cordgrass leaves | *A. columbi* density | … | … | … | … | … | … | … |
| | hosts parasitized per female wasp | … | … | … | … | … | … | … |
| | proportion parasitized | 0.105 | 0.077, 0.133 | 0.07 | 0.002 ± 0.02 | 0.932 | −0.004 ± 0.004 | 0.267 |
| | CV$^2$ | 2.54 | 1.53, 3.85 | 0.81 | −0.48 ± 0.10 | 0.003† | 0.09 ± 0.02 | 0.021† |

*Notes:* All reported measurements are computed on a per-leaf basis. Separate multiple-regression analyses were performed for each parasitoid response variable. Because tests within leaf source were not independent, a sequential Bonferroni correction based on the Dunn-Šidák method (Sokal and Rohlf 1995) was used to achieve an experiment-wise error rate of $\alpha = 0.05$.

† Test was deemed significant after a sequential Bonferroni correction was applied.

confidence intervals based on bootstrap estimates) was 0.02 (0.002, 0.32; $n$ = 25) for generation 2 in 1999, 0.41 (0.17, 0.55; $n$ = 106) for generation 1 in 2000, and 1.32 (0.71, 1.50; $n$ = 106) for generation 2 in 2000. The mean aggregation for these three generations was 0.58 (−1.08, 2.24). Finally, with only three CV$^2$ estimates, it was impossible to evaluate the relationship between CV$^2$ and $aP$. However, even if reported values of CV$^2$ are inflated, correcting those values would not change the result: the distribution of parasitism among patches is not very heterogeneous.

### *Parasitoid response to patch structure*

Number of immigrants and attack rates by *A. columbi* were relatively high among the 26 experimental patches of cordgrass. During a 5-d period, an average of 0.9 female wasps discovered each experimentally infested cordgrass leaf, successfully parasitized 17.1 hosts per parasitoid (an estimated 36% of their total egg load) and resulted in 28% of the hosts being parasitized (Table 2). Every patch had immigrant parasitoids and parasitized hosts. The density of immigrant female *A. columbi* was strongly influenced by patch geography: numbers per leaf significantly increased with patch size and decreased with patch isolation based on multiple least-squares regression (Table 2, Fig. 4A). The per capita hosts parasitized and the proportion of hosts parasitized were both unaffected by patch size but were strongly affected in opposite ways by patch isolation. Female parasitoids colonizing the most isolated patches parasitized two times more hosts per capita than parasitoids colonizing the least isolated patches (28 vs. 14 hosts parasitized; Table 2, Fig. 4B). This oviposition response did not counteract the effect of a decrease in wasp density with isolation; the proportion of hosts parasitized per patch declined significantly with isolation ($P$ = 0.022; Table 2, Fig. 4C).

It is possible that the positive correlation between patch isolation and per capita parasitized is due to parasitoid interference: fewer females were searching for hosts within isolated than nearby cordgrass patches. Indeed, the highly significant negative correlation between female *A. columbi* density per leaf and per capita parasitized (Fig. 5) is suggestive of parasitoid interference. However, this correlation is strongly confounded by patch isolation. I therefore performed a stepwise multiple regression to determine whether isolation or parasitoid density independently influenced the per capita parasitized (Sokal and Rohlf 1995). Despite the presence of multicolinearity between the two independent variables (Montgomery and Peck 1982), changing the order in which these variables were entered into the model did not affect the outcome. Hosts parasitized per parasitoid was dependent only on parasitoid density (model $R^2$ = 0.544; significance for parasitoid density: $P$ = 0.001) supporting the possibility that parasitoid interference was important. As a result of this negative relationship, the total number of hosts parasitized per leaf increased only modestly with increasing parasitoid density ($y$ = 0.33[ln parasitoid density] + 2.63; $R^2$ = 0.14, $P$ = 0.042).

The aggregation of parasitism among the 16 experimental leaves within a patch was quite variable with respect to $aP$ (Fig. 3B), and no significant bias was detected in the estimates of the CV$^2$ ($b$ = 0.176; 95% CI: −0.13, 0.49). Mean CV$^2$ for the 26 patches was significantly greater than unity ($\bar{X}$ = 1.63; 95% CI: 1.30, 1.97). The CV$^2$ was also strongly influenced by patch geography: the degree of aggregation declined with increasing patch size and increased with increasing

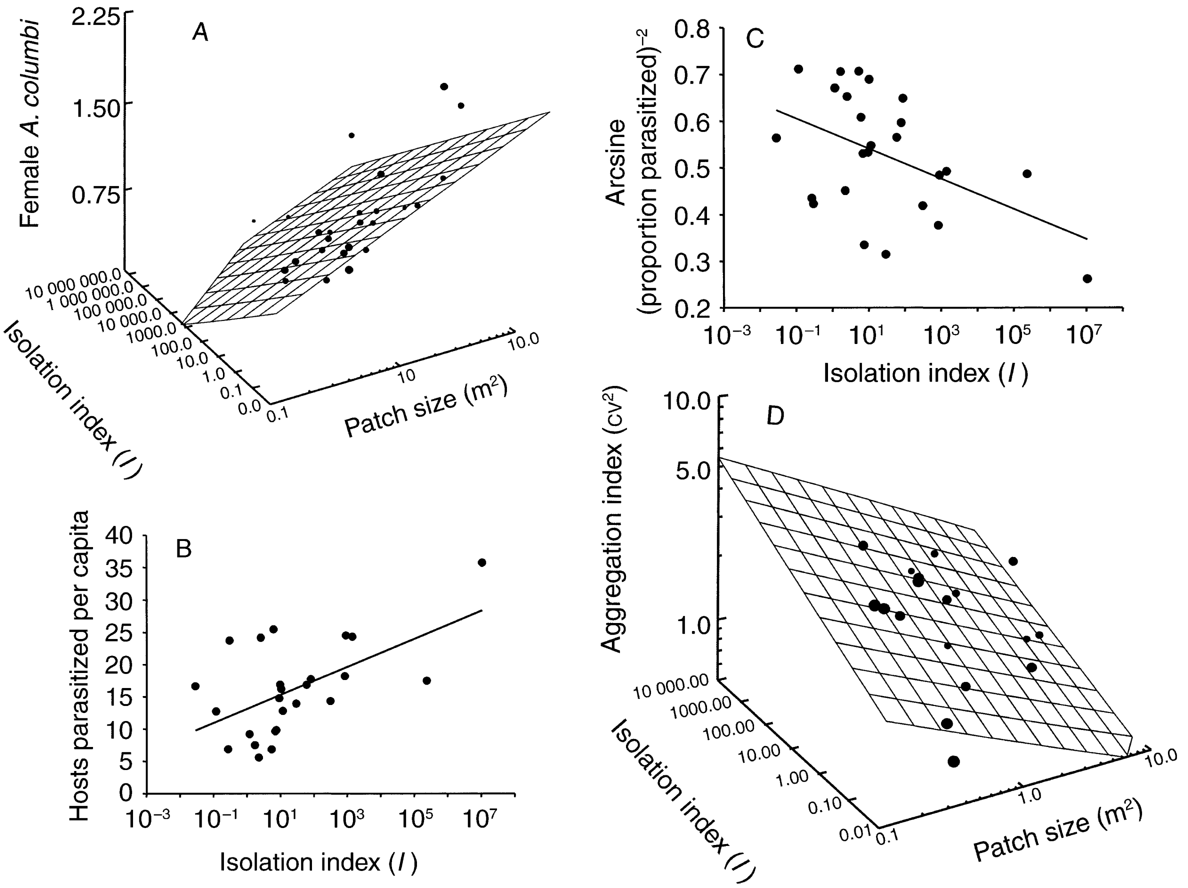

FIG. 4. The relationship between cordgrass patch geography (size and isolation) and various parasitoid-response variables based on the results from multiple regression (see Table 1). Only statistically significant relationships are displayed along with their corresponding coefficients of determination, $R^2$. (A) Number of female parasitoid immigrants ($R^2 = 0.49$), (B) hosts parasitized per female wasp ($R^2 = 0.32$), (C) proportion of hosts parasitized ($R^2 = 0.22$), and (D) aggregation of parasitism (CV$^2$) ($R^2 = 0.52$). Data points represent the mean (on a per-leaf basis) for each of 26 discrete cordgrass patches.

patch isolation (Table 2, Fig. 4D). Based on a comparison of the absolute values of the standardized regression coefficients, the effect of isolation was ~17% stronger than the effect of patch size on the CV$^2$ (coefficients are 0.61 and 0.54 for isolation and size, respectively). The CV$^2$ was uncorrelated with *A. columbi* density ($R = -0.296$, $P = 0.218$) and proportion parasitized ($R = -0.270$, $P = 0.263$), but positively correlated with the per capita parasitized ($R = 0.78$ and $P < 0.001$) per patch.

The strongly aggregated distribution of parasitism was not related to the distribution of adult female *A. columbi*. In fitting the distribution of parasitoids to a negative-binomial model, I found that $1/k_{\mathrm{nb}}$ (analogous to the CV$^2$) was less than unity in 22 out of 26 cases. In 15 of those 22 cases, the value of $1/k_{\mathrm{nb}}$ approached $1/\infty$, indicating that the mean and the variance were equal and the distribution very close to Poisson (random). Based on separate one-sample Komolgorov-Smirnov tests, the distribution of female *A. columbi* among leaves within a patch differed significantly from a Poisson distribution in only 1 of 26 tests. Because

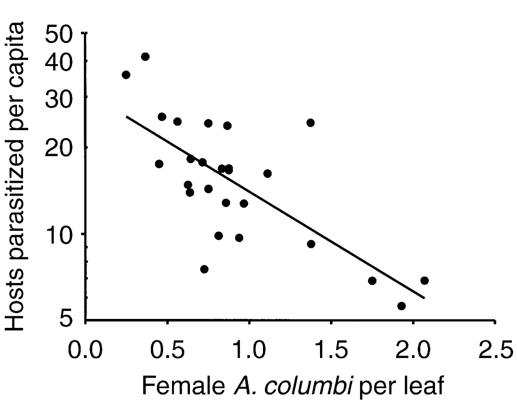

FIG. 5. Correlation between mean *A. columbi* density per cordgrass leaf per patch and the mean number of ovipositions per female parasitoid per leaf per patch ($R = -0.719$, $P < 0.001$).

TABLE 3. The influence of the patch edge and interior on *A. columbi* response variables.

| Variable | Interior mean ± 1 SE | Edge mean ± 1 SE | Interior edge | 95% CI of difference | *n* |
|---|---|---|---|---|---|
| Female *A. columbi* density | 0.705 ± 0.09 | 0.826 ± 0.07 | 0.121 | −0.01, 0.36 | 23 |
| Hosts parasitized per female wasp | 24.50 ± 2.83 | 15.50 ± 2.76 | 9.00 | 2.34, 15.67 | 21 |
| Proportion parasitized | 0.28 ± 0.03 | 0.24 ± 0.03 | 0.04 | −0.12, 0.05 | 23 |
| $CV^2$ (paired for size) | 1.56 ± 0.21 | 2.30 ± 0.30 | 0.74 | 0.17, 1.30 | 12 |
| $CV^2$ (paired for isolation) | 1.51 ± 0.24 | 2.66 ± 0.39 | 1.16 | 0.34, 1.98 | 11 |

*Notes:* Data were obtained from experimentally established host-infested leaves and sticky leaf traps that were positioned at the edge or interior of 26 discrete cordgrass patches. Separate multiple-regression analyses were performed to determine the effect of patch size ($m^2$) and isolation ($I$) on the interior-edge differential for each parasitoid response variable. A sequential Bonferroni correction was used to achieve an experiment-wise error rate of $\alpha = 0.05$ (applied separately to the $t$ tests and regression analyses).

† Test was deemed significant after a sequential Bonferroni correction was applied.

the majority of the $1/k_{nb}$ values were undefined ($1/\infty$), it was impossible to evaluate whether the within-patch distribution of parasitoids was influenced by patch size or isolation.

The inclusion of the four mainland control patches did not alter the results described previously. It is noteworthy that with a much broader range of patch sizes, the response of parasitoid density and the $CV^2$ were still positively (slope: 0.251 ± 0.069, $P = 0.002$) and negatively (slope: −0.252 ± 0.103, $P = 0.001$) correlated with patch size, respectively. Per capita hosts parasitized and the parasitism rate remained unaffected by patch size. In addition, mean $CV^2$ was 1.57 (95% CI: 1.27, 1.87) and mean $1/k_{nb}$ was 0.50 (0.03, 0.96) for the four mainland control plots. As before, the distribution of adult parasitoids in these large patches did not differ from Poisson (Komolgorov-Smirnov, $P > 0.50$).

Twenty-three of the 26 cordgrass patches bore leaves naturally infested with hosts (range: 1–20 leaves/patch; mean = 12.1). Each infested leaf had an average of 12.3 ± 0.7 eggs ($n = 302$). Mean number of planthopper eggs per stem per cordgrass patch was independent of patch size and isolation (multiple regression, $R^2 = 0.20$, $P = 0.196$), indicating that the response by *A. columbi* to both experimentally and naturally infested leaves was also independent of host distribution.

The distributions of *A. columbi* attacks among experimentally infested leaves generally matched the distributions observed for naturally infested leaves from the same patches. Although the proportion of hosts parasitized in the naturally infested leaves was less than one-half as much as the proportion in the experimental leaves (11% vs. 28%; paired $t$ test, $t = 5.66$, df = 22, $P < 0.001$; Table 2), for both types of leaves the proportions parasitized were unaffected by patch size and isolation (Table 2). Similarly, the mean $CV^2$ per patch was higher in the natural, relative to the experimental, leaves (2.54 vs. 1.63; paired $t$ test, $t = 7.54$, df = 9, $P < 0.001$; Table 2). The relatively high $CV^2$ among naturally infested leaves did not appear to be a consequence of bias associated with low parasitoid densities: the $CV^2$ was independent of $aP$ ($b = 0.075$; 95% CI: −0.50, 0.65). As with experimental leaves, the $CV^2$ for natural leaves decreased significantly with patch size and increased significantly with patch isolation (Table 2). Between the experimental and natural infested leaves, there was no correlation in the mean proportion of hosts parasitized per leaf per patch ($R = 0.22$, $n = 23$, $P = 0.319$), but there was a significant positive correlation in $CV^2$ per patch ($R = 0.64$, $n = 13$, $P = 0.019$).

At the spatial scale of cordgrass patches, parasitism was not strongly aggregated. Among the 26 cordgrass patches, the $CV^2$ was 0.13 (95% CI from bootstrapped estimates: 0.03, 0.52) based on the experimental leaves and 0.29 (95% CI: 0.05, 0.78) based on naturally infested leaves. These estimates of the $CV^2$ were not significantly different from one another (95% CIs overlap; $P > 0.05$), nor were they different from the estimates obtained among the 7–12 prairie sites surveyed in Fig. 2. The distribution of wasps among cordgrass patches was not strongly aggregated, $1/k_{nb} = 1/\infty$ (bootstrapped 95% CI: $1/\infty$, 0.30), and did not differ significantly from a Poisson distribution (Komolgorov-Smirnov, $P = 0.144$).

### *Edge effects and parasitism*

In addition to the pervasive effects of patch isolation and size on the interaction between *P. crocea* and *A. columbi*, I also found that location of host-infested leaves within a patch influenced this interaction. Based on the 26 experimental cordgrass patches, I found that on average there was 17% more female parasitoids captured per sticky trap leaf on the patch edge than on the patch interior (Table 3). However, this difference in parasitoid density was not quite statistically significant ($P = 0.06$). Interestingly, the interior–edge differential per patch was unaffected by patch size but decreased significantly with increasing patch isolation (Table 3). Coincident with the generally lower female wasp density on the patch interiors, I found that the per capita number of hosts parasitized per leaf was almost 60%

TABLE 3. Extended.

| Paired $t$ test | $P$ | Model $R^2$ | Regression analysis: Area, Slope ± 1 SE | Area, $P$ | Slope, Slope ± 1 SE | Slope, $P$ |
|---|---|---|---|---|---|---|
| 1.98 | 0.061 | 0.53 | −0.110 ± 0.089 | 0.235 | −0.049 ± 0.013 | 0.003† |
| 3.60 | 0.002† | 0.21 | 5.802 ± 3.388 | 0.109 | 0.209 ± 0.686 | 0.766 |
| 0.88 | 0.388 | 0.05 | 0.045 ± 0.050 | 0.381 | −0.004 ± 0.010 | 0.693 |
| 2.88 | 0.015† | 0.03 | 0.029 ± 0.052 | 0.584 | ··· | ··· |
| 3.14 | 0.010† | 0.01 | ··· | ··· | 0.020 ± 0.078 | 0.802 |

higher (24.5 vs. 15.5) for leaves in the interior than along the edge of the patch (Table 3). This significant difference did not vary with patch size or isolation (Table 3).

There were insufficient numbers of leaf samples to quantify the aggregation of parasitism or parasitoids at both the edge ($n = 8$ leaves) and interior ($n = 8$ leaves) of a single patch. I therefore pooled data from pairs of patches that were most similar in terms of either patch size or patch isolation; separate analyses were performed for each basis of pairing. When patches were paired according to size, I found that the $\mathrm{CV}^2$ was higher on the edge than interior in 10 of 12 comparisons; a significant difference (Table 3). Overall, the aggregation of parasitism averaged 47% higher on the edge than interior of a patch (Table 3). The interior–edge differential in $\mathrm{CV}^2$ did not vary significantly with the mean size of the pair ($R^2 = 0.03$, $P = 0.584$; Table 3). For the distribution of adult parasitoids along the edge relative to the interior of patches paired for size, almost one-half of all cases at each position had $1/k_{\mathrm{nb}} = 1/\infty$. A sign test (nonparametric equivalent to the paired $t$ test; Sokal and Rohlf 1995) was consequently used. In six of nine nontied cases, $1/k_{\mathrm{nb}}$ was greater for the interior, but this difference was not significant ($P = 0.298$).

For cordgrass patches that were paired according to similarity in isolation, I found the same basic results. The $\mathrm{CV}^2$ was higher on the patch edge than interior for 11 of 12 possible comparisons; the 77% mean increase in $\mathrm{CV}^2$ from the interior to the edge was statistically significant (Table 3). Furthermore, isolation (midpoint for the patch-pair) was unrelated to the $\mathrm{CV}^2$ interior–edge differential ($R^2 = 0.01$, $P = 0.802$; Table 3). Finally, $1/k_{\mathrm{nb}}$ approached $1/\infty$ in one-half of cases and no difference between the patch interior or edge could be detected ($P > 0.99$).

It is possible that the above reported edge effects developed in response to differences in the accessibility or availability of hosts along the patch edge relative to the patch interior. Indeed, stem densities in the patch interior were 21% higher than on the patch edge (371.2 ± 30.4 stems/m$^2$ vs. 305.6 ± 27.2 stems/m$^2$, respectively; paired $t$ test, $t = 2.56$, df = 24, $P = 0.017$). However, the number of stems per square meter that had at least one host-infested leaf (46.1 ± 8.6 and 49.2 ± 7.2 stems/m$^2$ on the interior and edge, respectively; $t = 0.52$, df = 24, $P = 0.611$), the proportion of stems infested by planthopper eggs (0.124 ± 0.020 vs. 0.135 ± 0.020; $t = 1.71$, df = 24, $P = 0.100$), and the number of host eggs per infested leaf (12.5 ± 1.1 vs. 14.2 ± 1.6 eggs/infested leaf; $t = 1.33$, df = 24, $P = 0.122$) were indistinguishable between the two patch locations.

### *Distance-dependent oviposition and aggregation*

By standardizing the size of the source (large mainland) and target (one 16-cm pot of 3–4 stems) patches while varying isolation distance of patches, I was able to assess directly the effects of dispersal distance on the distribution, oviposition behavior, and aggregation of *A. columbi*. An isolation distance of ≤25 m was sufficient to influence all parasitoid response variables. First, the number of immigrant female parasitoids declined significantly with increasing distance from the mainland patch (Fig. 6A). This decline, however, leveled off beyond a distance of 2 m from the mainland patch. Second, isolation distance had a significant impact on the hosts parasitized per capita: on average 14.1 hosts were parasitized per wasp within and to a distance of 5 m from the mainland (30% of *A. columbi*'s egg load), but this number doubled (to 28.1 eggs or 60% of the egg load) at more distant transects (Fig. 6B). This increase in per capita hosts parasitized with distance was independent of the concomitant decline in parasitoid density with distance. Based on a stepwise multiple regression, only distance was found to affect the number of hosts parasitized per parasitoid (model $R^2 = 0.90$; significance for parasitoid density: $P < 0.001$), suggesting that parasitoid interference was not responsible for this pattern. Third, the proportion of hosts parasitized declined only modestly with isolation distance (Fig. 6C). In fact, I could detect no significant difference in parasitism with increasing distance for transects positioned outside of the mainland patch. This result may be attributable to the elevated per capita attacks in more distant transects. Fourth, the distribution of parasitism was weakly aggregated in the mainland ($\mathrm{CV}^2 = 0.55 \pm 0.13$), but became increasingly more aggregated with distance from the mainland. There was no indication that bias existed in the estimates of $\mathrm{CV}^2$ (Fig. 3C; $b = -0.244$; 95% CI: −1.53,

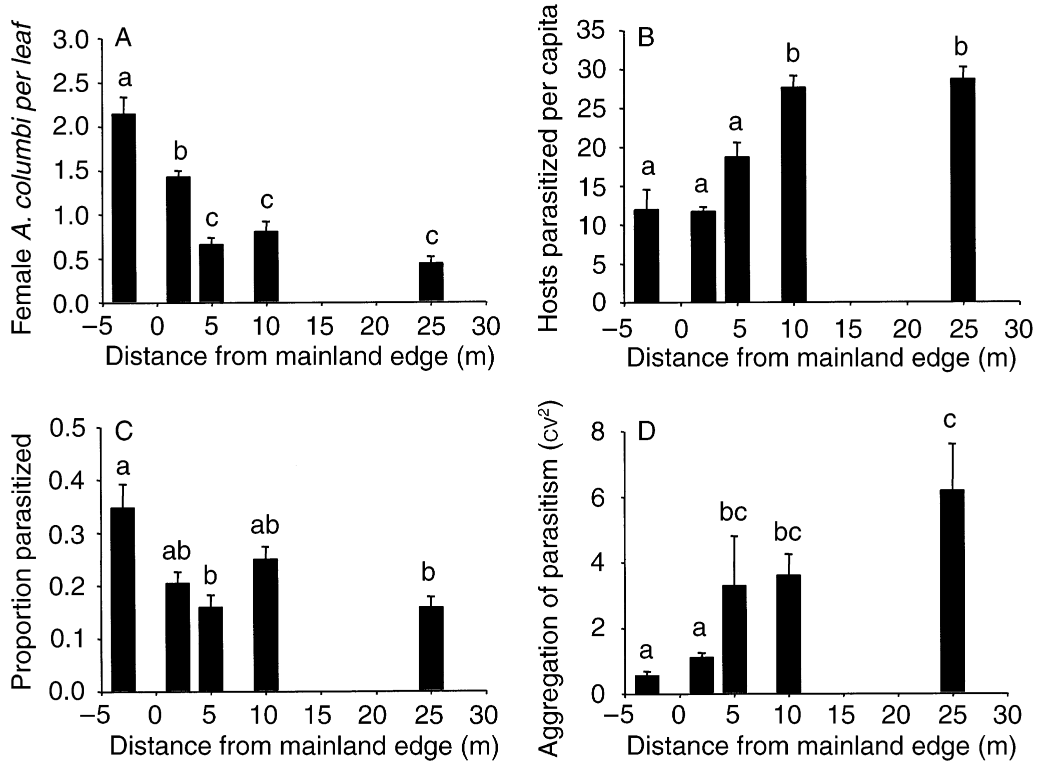

FIG. 6. Patch isolation distance and its effect on (A) mean density of immigrant *A. columbi* (based on a one-way ANOVA; $F_{4,10} = 36.81$, $P < 0.001$), (B) mean number of hosts parasitized per capita ($F_{4,10} = 22.32$, $P < 0.001$), (C) mean proportion of hosts parasitized ($F_{4,10} = 8.14$, $P = 0.004$), and (D) the aggregation of parasitism, CV$^2$ ($F_{4,10} = 13.64$, $P < 0.001$). Separate one-way ANOVAs were performed on each parasitoid response variable. Means + 1 SE with different letters denote significant differences at $P < 0.01$ using Tukey's HSD test. The cutoff for significance was set at 0.0125 to adjust for an inflated Type I error associated with performing four ANOVA tests with the same data (Bonferroni correction = 0.05/4 = 0.0125; Sokal and Rohlf 1995).

1.05). Finally, the distribution of adult *A. columbi* was weakly aggregated. While parasitoid densities were too low in the 25-m transects to estimate $1/k_{\text{nb}}$, in all other transects, the median value of $1/k_{\text{nb}}$ was 0.200 with a range of $1/\infty - 0.75$. Because of the extreme values for $1/k_{\text{nb}}$, the effects of isolation distance on the aggregation of adult parasitoids were assessed with the nonparametric Kruskal-Wallis test (Sokal and Rohlf 1995). Although the mean rankings of $1/k_{\text{nb}}$ were greatest within the mainland (9.33) and lowest at 5 and 10 m (4.17 for both distances combined), the difference among distances was not significant ($H = 5.54$, df = 3, $P = 0.136$).

### *Parasitism in the laboratory*

In the laboratory, a young inexperienced *A. columbi* spent 77.5 ± 16.0 min ($n = 22$) on a single leaf bearing host eggs (75.5 ± 8.0 eggs, mean ± 1 SE; range: 14–151) and successfully parasitized 18.6 ± 3.4 hosts (~39% of its potential fecundity). The number of hosts parasitized per leaf was variable but increased linearly with host density (number parasitized = 0.21host density + 5.20; $R^2 = 0.24$, $P = 0.030$). The addition of a quadratic term did not improve the model fit, suggesting that the functional response of *A. columbi* across this range of host densities is approximately linear (a type I functional response). Finally, the distribution of parasitized hosts among these laboratory leaves was quite aggregated. The CV$^2$ was 1.32 (bootstrapped 95% CI: 0.92, 1.60).

## DISCUSSION

*Anagrus columbi* and its planthopper host, *P. crocea*, coexist together in a highly subdivided habitat consisting of discrete patches of the host plant, prairie cordgrass. In the tallgrass prairies where this work was conducted, the maximum linear distance between a cordgrass patch and its nearest neighbor was 46 m (Cronin 2003*a*). For both *A. columbi* (see *Results*) and its host (Cronin 2003*a*), recolonization of even the most isolated patches occurred within 1–2 generations; connectivity among patches is high. Therefore, categorization of the subdivision of each population is somewhere between a patchy population and a true metapopulation (sensu latto Harrison and Taylor 1997). Within this spatial framework, a high degree of aggregation in the distribution of the risk of parasitism among host patches has been widely regarded as a stabilizing force in the dynamics of discrete-time host–parasitoid interactions (e.g., Chesson and Murdoch 1986, Pacala et al. 1990, Hassell et al. 1991). This study is among the first to report that patch structure significantly impacts a parasitoid's density distribution, oviposition behavior, and distribution of parasitism risk.

### *Distribution of parasitism risk in nature*

Both temporally and spatially, the distribution of parasitism risk by *A. columbi* among cordgrass leaves was highly aggregated (mean $\mathrm{CV}^2$ among generations = 3.58). Because I could detect no evidence of density dependence in the proportion of hosts parasitized, either in space or time, this aggregation can be attributable to host density-independent processes. To date, the majority of studies reporting high $\mathrm{CV}^2$ have come to similar conclusions (Hassell and Pacala 1990, Pacala et al. 1990, Driessen and Hemerik 1991, Redfern et al. 1992, Reeve et al. 1994*b*; but see Jones et al. 1993). In contrast to the highly aggregated distribution of parasitism risk among cordgrass leaves, the distribution of risk among cordgrass patches was quite random. As I will discuss, the summation of parasitism among leaves within a patch likely obscures important within-patch sources of heterogeneity such as variation in host age among leaves and location effects (patch edge–interior differences). Regardless of the spatial scale of study (the leaf or cordgrass patch), the distribution of parasitism risk in this study may be sufficient in theory to stabilize a host–parasitoid interaction. As Comins et al. (1992) have demonstrated, if parasitism within a patch is sufficiently aggregated (e.g., among leaves within a cordgrass patch), stability is possible even though parasitism is randomly distributed among patches (see also Hassell 2000).

### *Experimental analysis of the distribution of parasitism risk*

As in the census study, the distribution of parasitism in the *Parasitoid response to patch structure* experiment was highly aggregated within, but not among, patches. At the scale of the leaf within a cordgrass patch, the proportion of hosts parasitized was unaffected by the size of the patch or proximity to the patch edge, but declined significantly as patches became more isolated. The drop in parasitism with isolation corresponded to the decline in numbers of female *A. columbi* immigrating into isolated patches, suggesting that the connectivity of cordgrass patches to *A. columbi* is limited at least to some extent by dispersal. This result is somewhat surprising given the generally high dispersal capabilities of the genus *Anagrus* (e.g., Doutt et al. 1966, Ôtake 1976, Antolin and Strong 1987, Corbett and Rosenheim 1996, Cronin and Strong 1999). Parasitism risk was more aggregated on the patch edge than the interior and became increasingly more aggregated in smaller and more isolated patches. From my analyses, isolation had a greater impact on the $\mathrm{CV}^2$ than patch size (~17% stronger effect), but within a patch the aggregation of parasitism was almost 60% greater on the edge than the interior. Clearly, these data suggest that the distribution of parasitism risk is strongly influenced by patch geography and the within-patch distribution of hosts. The cause for the high within-patch $\mathrm{CV}^2$ and how patch structure influences its magnitude are examined below.

A commonly held view is that the distribution of parasitism risk is a consequence of the distribution of searching adult parasitoids (Pacala et al. 1990, Hassell et al. 1991, Taylor 1993). This prediction is derived from the assumption that parasitoids have a type I functional response; as such, an aggregated distribution of parasitoids should translate into an aggregated distribution of parasitism. In spite of evidence that *A. columbi* has a type I response (see *Results*), the distributions of parasitoids and parasitism appear to be uncoupled within patches. *Anagrus columbi* were approximately randomly distributed while parasitism was strongly aggregated. Similar patterns were found for *A. sophiae* (Reeve et al. 1994*b*) and a eucoilid parasitoid of *Drosophila* (Driessen and Hemerik 1991). This uncoupling of searching parasitoids from parasitism can be due to the differential vulnerability of hosts to parasitoid attack or suitability of hosts to larval parasitoid development (Bailey et al. 1962, Taylor 1993, Reeve et al. 1994*b*). Under these scenarios, parasitoids can be randomly distributed but their successful attacks limited to a subset of the host-infested leaves, thus generating aggregated distributions of parasitism.

To a degree, my experimental data can be used to evaluate the possibility that differential vulnerability of hosts contributes to the aggregated distribution of parasitism among cordgrass leaves within a patch. The experimental host-infested leaves represented a very uniform source of hosts. Host eggs were even in age (≤48 h difference), positioned at the base of the leaf blade, located on the highest two open leaves of the stem, and at approximately the same height from the ground. Leaves naturally infested with hosts were much more variable with regard to these characters. If differential vulnerability of hosts is important, the natural-infested leaves should have had a significantly higher degree of aggregation than the experimental-infested leaves within the same patch. This was precisely the result I found; the $\mathrm{CV}^2$ was 56% higher among the natural, than the experimental, leaves.

The cause for differential vulnerability of leaves bearing hosts to searching *A. columbi* is unknown, but a possible candidate is host age. In nature, the egg-laying period of the *P. crocea* population is long relative to the period of adult activity of the *A. columbi* population (*unpublished data*). Furthermore, the age distribution of planthopper eggs within a leaf is relatively uniform (planthoppers tend to spend 1–2 d laying a cluster of eggs on a leaf before they disperse to a new leaf), and only young embryos, those that have completed $<40\%$ of the egg-development period (total duration $= 14$–$20$ d), are preferred as hosts and allow for the successful development of parasitoid offspring (*unpublished data*; similar age effects were also found with *A. sophiae* [Cronin and Strong 1990*a*]). As a consequence, leaves receiving ovipositions early in the season may be invulnerable to attack to the majority of the *A. columbi* population. Old age, therefore, may represent a refuge from parasitoid attack.

Location of host-infested leaves within a patch does appear to influence the distribution of parasitism. Aggregation was 60% greater among host-infested leaves on the patch edge than in the patch interior and was independent of patch size and isolation. Based on my quadrat samples from discrete cordgrass patches, approximately equal densities of hosts were found within the edge and interior, suggesting that this edge effect was not trivial to the *A. columbi* population. Significant differences have been found between patch edges and interiors in terms of insect growth, fecundity, density, and survivorship (e.g., Roland and Kaupp 1995, Cappuccino and Martin 1997, McGeoch and Gaston 2000), and effects on herbivores are known to be transmitted to higher trophic levels (e.g., Lovejoy et al. 1989, Bolger et al. 2000). However, no studies have ever reported edge effects in the aggregation of parasitism, a natural-enemy response so directly linked to host–parasitoid stability. The cause for higher aggregation on the patch edge is currently unknown, but my data suggest that it is not due to differences in host density, parasitoid density, per capita hosts parasitized (the higher per capita attacks found in the interior than edge would be expected to favor higher interior $\mathrm{CV}^2$ values; see *Discussion: Aggregation*), or parasitism. Possible explanations include greater disturbances on the edge (due to greater fluctuations in winds, temperature, moisture, density of other natural enemies) that increase heterogeneity in *A. columbi* attacks, or a more variable fraction of leaves on the edge that bear invulnerable host stages (old eggs).

### *Oviposition behavior and patch isolation*

The random distribution of parasitoids, the differential vulnerability of hosts, and the presence of edge effects cannot explain the effect of patch geography on the distribution of parasitism. One factor that can is the oviposition behavior of *A. columbi*. In both field experiments (*Results: Parasitoid response* and *Results: Distance-dependent oviposition*), the aggregation of parasitism was strongly and positively correlated with the per capita number of hosts parasitized per cordgrass leaf ($R = 0.78$ and $P < 0.001$ for the former experiment, and $R = 0.73$ and $P = 0.002$ for the latter experiment). This association between the $\mathrm{CV}^2$ and per capita parasitized is not surprising because if parasitoids concentrate their attacks in fewer host-infested leaves, parasitism will be more aggregated. It is therefore likely that the oviposition behavior of *A. columbi* (parasitizing more hosts per capita in small and isolated patches) is largely responsible for the increased aggregation of parasitism in those same patches. A similar conclusion was drawn by Cronin and Strong (1999) for parasitism by *A. sophiae* (with regard to isolation only). The low $\mathrm{CV}^2$ for patches could be explained by the effects of averaging the concentrated attacks per leaf across the whole cordgrass patch.

In the *Parasitoid response to patch structure* experiment, the correlation between per capita hosts parasitized and patch isolation was largely attributable to parasitoid density: patches colonized by few female *A. columbi* (isolated patches) had more hosts parasitized per capita per leaf than those patches colonized by many female *A. columbi* (less isolated patches) (Fig. 5). This pattern would be expected if parasitoid interference were occurring in nature (Hassell 1978, Visser and Driessen 1991). The cause for this interference could be direct interactions among searching adults that lead to reduced patch time or hosts attacked (direct or indirect mutual interference; Visser and Driessen 1991) or the loss of fitness due to superparasitism (Free et al. 1977, van Alphen and Visser 1990). Mutual interference, through the disruption of oviposition behavior, has been reported to occur in the congeneric *A. sophiae* (Cronin and Strong 1993*b*), and observations suggest that similar behavior occurs in *A. columbi* (*unpublished data*). Increased superparasitism at high parasitoid density (leading to pseudointerference) is also a possibility with *A. columbi*. This species exhibits little ability to discriminate between parasitized and unparasitized hosts when caged on a cordgrass leaf (*unpublished data*).

For this experimental study, the density of searching female *A. columbi* was generally low, averaging just $1 \cdot \mathrm{leaf}^{-1} \cdot 5\text{-d period}^{-1}$ (range: 0–8). Few direct interactions among parasitoids likely would have taken place at these densities. However, parasitoids may have left markers behind on the leaf that deterred subsequent parasitoids from either alighting on the leaf or remaining there to oviposit. As yet, no studies have addressed whether mymarids employ patch markers, but such markers are known to exist for other parasitoids (e.g., Price 1970, Galis and van Alphen 1981, van Dijken et al. 1992). Because *A. columbi* appears to be time-limited (females are very short-lived and have never been captured in the field with $<6\%$ of their estimated egg complement; *unpublished data*), time lost in detecting and rejecting marked leaves could lead to mutual interference (Visser and Driessen 1991). Pseudointerference resulting from superparasitism may have also contributed to the negative correlation between parasitoid density and per capita hosts parasitized, but could not be solely responsible for it. If we assume that ovipositions among hosts within a leaf occurred at random, the total number of eggs laid per parasitoid per leaf can be predicted using the Poisson frequency distribution. Even after correcting for parasitoid eggs lost to superparasitism, there was a strong negative correlation between *A. columbi* density and per capita number of ovipositions ($R = 0.62$, $P < 0.001$).

In the *Distance-dependent oviposition and aggregation* experiment, my analyses suggested that isolation distance, and not parasitoid interference, was responsible for variation in per capita parasitism among patches. This difference between the two experiments was not due to lower parasitoid densities in the *Distance-dependent oviposition and aggregation,* relative to the *Parasitoid response to patch structure* experiment. The density of female *A. columbi* was 1.1 individuals/leaf (mean proportion parasitized per leaf was 22.4%) and 0.9 individuals/leaf (28%) in the former and latter experiments, respectively. The difference in conclusions between the two experiments may stem from the widely divergent cordgrass patch sizes used in each experiment: 3–5 stems in the *Distance-dependent oviposition and aggregation* experiment and 12–3956 stems in the *Parasitoid response to patch structure* experiment. If, for example, marker chemical effects carry over to other leaves in the same cordgrass patch, or parasitoids remember and count encounters with marked leaves within a patch, larger patches with more total parasitoids may exhibit stronger parasitoid-density effects than smaller patches. Regardless of the cause for the difference between the two studies, there is a very strong effect of isolation distance on the per capita number of hosts parasitized. Below, I evaluate three hypotheses to explain these results.

The first hypothesis is that the *A. columbi* population is heterogeneous in terms of oviposition rates, and that individuals with a high propensity to lay eggs are also the same individuals that have a high propensity to disperse long distances (i.e., egg-laying rates and dispersal are correlated traits). I currently have no evidence as to whether those individuals laying many eggs in the laboratory are the most dispersive. The second hypothesis involves a change in oviposition behavior of *A. columbi* that is in direct response to dispersal distance, isolation that is indirectly brought about by dispersal, or some combination of both factors. An increase in the per capita number of hosts parasitized with dispersal distance is consistent with the predictions from a diverse array of optimal foraging models (reviewed in Cronin and Strong 1999). Whether parasitoids are seeking to maximize the time rate of ovipositions or their lifetime reproductive success (egg-limited individuals), models predict the same outcome; foraging or oviposition rates should increase with dispersal distance.

In the third hypothesis, *A. columbi* may not be responding behaviorally to dispersal distance per se, but to the habitat conditions associated with those patches that are colonized by long-distance dispersers. In this study, patches with the highest per capita number of hosts parasitized were the patches most isolated from any other cordgrass patches. A parasitoid that has immigrated into an isolated patch may be subsequently reluctant to disperse from that patch (e.g., Roitberg and Prokopy 1982) or more likely to return to that patch after a foray into the surrounding matrix (Cronin and Strong 1999). Thus, the effects of isolation may favor increased patch residence times and greater per capita ovipositions. This seems not to be a possibility for *A. columbi* because isolation does not promote increased patch philopatry or increased visitations (*unpublished data*). In conclusion, the distance-dependent oviposition response by *A. columbi* appears to be driven by either heterogeneity in individual oviposition rates that are correlated with dispersal ability or an optimal foraging response to dispersal distance.

The distance-dependent oviposition response by *A. columbi* can have a tremendous impact on the spatial dynamics of a host–parasitoid system (Cronin and Strong 1999). For isolated cordgrass patches, fewer immigrant wasps will be necessary to initiate a local population. Female *A. columbi* appear to be mated quickly upon emergence from a host egg (*unpublished data*), obviating the need to find mates following dispersal. In addition, mates are often derived from the same host-infested leaf (*unpublished data*), suggesting that the offspring from the same mother do not refrain from inbreeding. Therefore, a new population can be initiated by a single female immigrant. A high oviposition rate in those isolated patches would serve to improve a parasitoid's colonization success by increasing mate availability for its offspring, thus ameliorating the Allee effect associated with the colonization of vacant patches (Hanski 1994, Amarasekare 1998, Kuussaari et al. 1998). With this dispersal-dependent oviposition response by *A. columbi* facilitating colonization of isolated vacant patches, we would expect a greater rate of patch occupancy and more rapid spatial spread of the parasitoid population than in the absence of this oviposition response (Hanski 1994, Kot et al. 1996, Amarasekare 1998, Kuussaari et al. 1998).

### *Aggregation of risk and stability*

Explanations for the persistence of host–parasitoid interactions have long focused on heterogeneity, with much recent emphasis on heterogeneity in the risk of parasitism (for review, see Hassell 2000). The $\mathrm{CV}^2 > 1$ rule as a general criterion for stability in theoretical host–parasitoid models (Pacala et al. 1990, Hassell et al. 1991) is questionable; many factors can invalidate this rule (e.g., Ives 1992*b*, Murdoch et al. 1992, Taylor 1993, Reeve et al. 1994*a, b,* Gross and Ives 1999, Olson et al. 2000). However, if assumptions underlying the criterion are met, the $\mathrm{CV}^2$ can serve as a useful tool in identifying aspects of host and parasitoid biology or landscape features that influence heterogeneity in parasitism risk and may contribute to the stability of the host–parasitoid interaction (Taylor 1993). To my knowledge, very few field studies have attempted to describe the effects of the landscape on parasitism risk (but see Sheehan and Shelton 1989, Lei and Hanski 1997, Lei and Camara 1999, Doak 2000), and only one has sought to quantify the aggregation of this risk (Cronin and Strong 1999). *Anagrus columbi* and *P. crocea* fit well the assumptions associated with the negative-binomial model that underlie the $\mathrm{CV}^2 > 1$ rule. Both species have discrete generations and parasitism, as reported in this study, represented the integrated effect of the parasitoid population on the planthopper population. Also, *A. columbi* is locally a specialist of its host, searches at random within a leaf, and displays a type I functional response.

The distribution of *A. columbi* parasitism risk among cordgrass leaves in nature was quite aggregated (mean $\mathrm{CV}^2 = 3.58$). However, this high $\mathrm{CV}^2$ value incorporates a significant component of aggregation that is neutral in its effect on stability—multiple ovipositions by an individual parasitoid within a single patch of hosts (in this case a leaf) (‘‘within-parasitoid aggregation,’’ Gross and Ives 1999). Within-parasitoid aggregation does not generate pseudointerference among parasitoids, the source of stability from highly aggregated distributions of parasitism (Free et al. 1977, Chesson and Murdoch 1986, Pacala et al. 1990, Hassell et al. 1991). In this study system, within-parasitoid aggregation can be attributed to two related factors: the intrinsic capacity of the parasitoid to oviposit within a patch (i.e., number of hosts parasitized) and the effects of patch geography in modifying the parasitoid’s oviposition behavior. In the laboratory, individual *A. columbi* oviposited multiple times per host-infested leaf (mean = 18.6 parasitized hosts), but that number was quite variable among leaves. The $\mathrm{CV}^2$ was 1.32 and represents an estimate of the pure within-parasitoid aggregation under ideal conditions. In nature, the number of ovipositions by *A. columbi* also rises with increasing dispersal distance and decreasing patch size. The overall contribution of within-parasitoid aggregation to the total aggregation estimated from the census data cannot be determined without knowing the distribution of *A. columbi* dispersal distances and patch sizes in nature. I would therefore echo the cautionary note by Gross and Ives (1999) that without some knowledge of the parasitoid’s foraging behavior and the magnitude of the within-parasitoid contribution, the $\mathrm{CV}^2 > 1$ rule cannot be evaluated using field data.

My experiments revealed one aspect of patch geography that influences the magnitude of the theoretically stabilizing component of the aggregation of parasitism risk (the among-parasitoid aggregation; Gross and Ives 1999). The $\mathrm{CV}^2$ was 60% greater on the patch edge than the interior (Table 3). Because the per capita number of hosts parasitized did not differ between the edge and interior, this patch-geographic effect is not due to within-parasitoid aggregation. Thus, edge effects may contribute to the stability of the host–parasitoid interaction (in the form of increased among-parasitoid aggregation).

### *Conclusions*

This study is one of the first to quantify how features of the landscape (patch size, isolation, and edges) influence parasitoid movement, oviposition behavior, and the distribution of parasitism risk. In nature, parasitism of the planthopper *P. crocea* by the egg parasitoid *A. columbi* was spatially density independent and very heterogeneous in its distribution among host-infested cordgrass leaves. Aggregation in parasitism risk was strongly landscape dependent. Small and isolated cordgrass patches received fewer immigrant *A. columbi* and had more highly aggregated within-patch distributions of parasitism (as measured by the $\mathrm{CV}^2$) than larger and less isolated patches. The high $\mathrm{CV}^2$ within isolated patches was likely a consequence of an increase in the per capita number of hosts parasitized per leaf as patch isolation increased. A release from competition with conspecifics (parasitoid interference) or an optimal oviposition response to dispersing long distances to a cordgrass patch were likely explanations for this isolation-dependent oviposition response by *A. columbi*. Another landscape feature that influenced the distribution of parasitism was the patch edge. Parasitism risk was 60% more heterogeneous at the edge than in the interior of a patch, and the effect was patch-size independent. Finally, adult female *A. columbi* were randomly distributed among cordgrass patches. The uncoupled distribution of parasitoids and their attacks may have been an indication that hosts were not all equally vulnerable to attack or suitable for parasitoid larval development.

Results from this study suggest some possible consequences for the host–parasitoid interaction as a result of changes to prairie landscape structure. For example, increased fragmentation of the cordgrass habitat, resulting in smaller and more isolated patches, is expected to cause the distribution of parasitism risk to become dramatically more aggregated. Two reasons explain this predicted response: (1) ovipositions should increase and become more concentrated on fewer leaves in smaller and isolated patches, and (2) the increased patch perimeter-to-area ratio (i.e., more edge habitat) in a more fragmented habitat should favor increased aggregation of parasitism. The latter source of heterogeneity may in theory promote host–parasitoid stability.

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