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Spatial distributions of *Cephus cinctus* Norton (Hymenoptera: Cephidae) and its braconid parasitoids in Montana wheat fields

David K. Weaver [a,*], Christian Nansen [a,1], Justin B. Runyon [a,2], Sharlene E. Sing [b,3], Wendell L. Morrill [a]

[a] *Department of Entomology, 333 Leon Johnson Hall, Montana State University, Bozeman, MT 59717, USA*
[b] *Department of Land Resources and Environmental Sciences, 334 Leon Johnson Hall, Montana State University, Bozeman, MT 59717, USA*

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Abstract

Bracon cephi and *Bracon lissogaster* are native parasitoids of the wheat stem sawfly, *Cephus cinctus*, an important pest of dryland wheat production. This spatial distribution study, using survey data from seven dryland wheat fields at four locations in north-central Montana over two years, examined: (1) the spatial distribution and spatial association of *C. cinctus* infestation and parasitism, and (2) parasitism in response to the level of *C. cinctus* infestation. Spatial distribution analyses revealed that *C. cinctus* infestations were significantly aggregated along field edges in three of five fields, while parasitism followed a random spatial distribution in all five fields. We demonstrate that the level of parasitism is highest for lower levels of *C. cinctus* infestation, in fields where parasitoids are either scarce or abundant. The combination of (1) a spatial aggregation of *C. cinctus* infestations along field edges, and (2) a potential negative interaction between parasitism and *C. cinctus* infestation may lower the level of parasitism at high host densities. This outcome can be viewed as beneficial to the insect pest, because parasitized *C. cinctus* larvae are at a greater risk of being cannibalized by conspecifics. An equally plausible hypothesis for this negative interaction is a limitation on the successful location of unparasitized hosts at higher host densities, which is also compelling because of the cryptic location of hosts within wheat stems that belie little visible evidence of infestation. Supporting data from other heavily infested fields that were sampled in 1999–2000 are used to illustrate the recurrence of this pattern. These findings are discussed in the context of developing redistribution strategies for introducing these parasitoids at sawfly infested locations where they are currently present at negligible levels.

Keywords: *Cephus cinctus*; *Bracon cephi*; *Bracon lissogaster*; Wheat; Integrated pest management; Biological control; Tritrophic interactions

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1. Introduction

The earliest record of the wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae) dates back to 1872 in Colorado (Norton, 1872), and the current geographical distribution includes twenty-nine states in the western US and the southern portions of seven provinces in Canada (Ainslie, 1920; Ivie, 2001; Morrill, 1997). Preferred hosts for *C. cinctus* are tall, hollow-stemmed grasses, and in Montana the wheat stem sawfly is the most important insect pest of dryland wheat (Morrill and Kushnak, 1999). A total of 10 parasitoid species have been reported to parasitize *C. cinctus* in native or feral grasses (Marsh, 1979), but only two species, *Bracon cephi* (Gahan) and *Bracon lissogaster* Muesebeck (Hymenoptera: Braconidae), are known to parasitize *C. cinctus* larvae in wheat

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[*] Corresponding author. Fax: +1 406 994 6029.
E-mail address: weaver@montana.edu (D.K. Weaver).

[1] Present address: The Steritech Group Incorporated, 7600 Little Avenue, Charlotte NC 28226, USA.

[2] Present address: Department of Entomology, The Pennsylvania State University, 501 ASI Building, University Park, PA 16802, USA.

[3] Present address: USDA Forest Service, Rocky Mountain Research Station, Forestry Sciences Laboratory, 1648 South Seventh Avenue, Bozeman, MT 59717, USA.

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stems (Davis et al., 1955; Morrill et al., 1994; Somsen and Luginbill, 1956). *B. cephi* and *B. lissogaster* are sympatric idiobont ectoparasitoids with similar life histories and phenologies (Runyon et al., 2001), although *B. cephi* is a solitary ectoparasitoid, while *B. lissogaster* can be either solitary or gregarious (Nelson and Farstad, 1953; Somsen and Luginbill, 1956). There are two generations of each species per year on the univoltine wheat stem sawfly (Nelson and Farstad, 1953; Somsen and Luginbill, 1956), although the second generation may be incomplete due to drought or excessive heat causing early maturity of the host crop (Holmes, 1963). Female braconids and female *C. cinctus* will both oviposit repeatedly in wheat stems in fields affected by high densities of *C. cinctus* (Holmes, 1963). *C. cinctus* oviposits in wheat stems after the initiation of stem elongation (Ainslie, 1920), and developing larvae feed on the parenchyma throughout the interior length of the stems. The braconid eggs are inserted into the wheat stems on or near late-instar *C. cinctus* larvae. The hosts are paralyzed at the time of attack, ending their consumption of wheat tissue. Host paralysis by ectoparasitoids prevents moulting or defence reactions from the host from interfering with the externally feeding parasitoid larva (Beckage and Gelman, 2004). The braconid larvae feed externally on the *C. cinctus* larvae for about 10 days before pupation (Holmes, 1963), killing the host. The mechanisms of long- and short range host-finding behavior of *B. cephi* and *B. lissogaster* are not known in detail, but preliminary laboratory studies suggest that both parasitoid species respond positively to specific volatiles that are produced by *C. cinctus*-infested wheat plants (Peck, 2004, Weaver, unpublished data).

Cephus cinctus larvae are highly cannibalistic (Holmes, 1963) with only one individual surviving to maturity per stem. When several *C. cinctus* larvae are present in a wheat stem, a parasitized *C. cinctus* larva that has become paralyzed is more likely to be encountered and consumed by conspecifics than if it were active. Thus, although many parasitism events can occur in wheat during the growing season, the level of protection afforded by parasitism may be fairly low unless all of the *C. cinctus* larvae in each affected wheat stem are parasitized. This relationship is different from many other parasitoid-host systems, because the cannibalistic behavior of the host suppresses the potential population density of the associated parasitoids. An alternative, but equally plausible explanation for decreased parasitism at greater host numbers is inefficient host discovery. Because the larvae of the *C. cinctus* are cryptically located inside wheat stems, one would expect that host location would become easier at higher densities. This will be true, but only to a certain point, after which clear reception of host-finding cues is lost and it becomes increasingly more difficult to locate unparasitized hosts. A parallel to this inefficiency in the discovery of hosts at high densities has been studied for several internal feeding stored-product insects and their associated parasitoids (Flinn and Hagstrum, 2002; Smith, 2004; Smith and Press, 1992).

Using field-collected data from 1998 and 1999 from multiple wheat fields in north central Montana, we: (1) used the statistical freeware package SADIE (Spatial Analysis of Distance IndicEs—http://www.rothamsted.bbsrc.ac.uk/pie/sadie/SADIE_home_page_1.htm) to characterize the spatial distribution and the level of spatial association between *C. cinctus* infestation and parasitism, and (2) analyzed the relationship between parasitism and the level of *C. cinctus* infestation, also including additional sampling data from Runyon (2001). This study supports ongoing research efforts in Montana to develop methods for measuring the impact of redistributing *B. cephi* and *B. lissogaster* from fields where parasitism is high to augment infested fields where parasitism levels are negligible. In particular, we ultimately wish to design a sampling strategy for effectively monitoring parasitoid population growth from future inoculative releases. Therefore, the initial challenge is to determine if the fine structure of the association between infestation and parasitism tracks aggregation of the host at the low and intermediate parasitoid densities that would occur from inoculative redistribution.

2. Material and methods

2.1. Field sites and wheat stem samples

All field sites were located in the dryland wheat production area in north central Montana within a 150 km range. One large field was sampled at three sites in both 1998 and 1999 and another field was sampled only in 1998. These fields are described in detail in Nansen et al. (2005) and summarized in Table 1. Briefly, either the entire field (Ledger, Pendroy, and Chester) or a section of a field (Loma) was divided into a regular grid with grid points at every 50 m and a reference point (0,0) in

Table 1
Summary of wheat stem samples collected from six fields in north central Montana in 1998 and 1999

Field site	Year	Stem type	Variety	Planting date	Stem density
Loma	1998	Hollow	Rocky	Winter	45.1(1.6)
Loma	1999	Hollow	Rocky	Winter	75.1(1.9)
Ledger	1998	Solid	Lew	Spring	40.3(1.2)
Ledger	1999	Solid	Rambo	Spring	48.5(1.2)
Pendroy	1998	Hollow	Rocky	Winter	87.5(3.4)
Pendroy	1999	Solid	Rambo	Spring	40.2(1.4)
Chester	1998	Solid	Ernest	Spring	33.5(0.9)

Wheat fields were sampled at each location in 1998 and 1999, except for Chester, and both hollow stem and solid stem varieties were sampled. Stem density is the mean (standard error) number of stems per 30 cm row-length sample.

the southwestern corner of each sampled area. In 1998, the sampled section of the Loma field was located along the eastern edge of a large field, while the sampled section in 1999 was located along the western field in the adjacent field. Due to yearly alternation between wheat and fallow, adjacent fields were sampled in subsequent years. For a description of the wheat-fallow dryland production system in Montana, see Morrill et al. (2001). Wheat stems were collected 72 h before harvest to allow maximum second-generation parasitism, and a sample represented all wheat stems in 30 cm of row at each grid point. Wheat stem samples were brought to the laboratory, where stems were dissected lengthwise with a fine-bladed scalpel to determine presence or absence of *C. cinctus* larvae. Field samples were incubated at room temperature for 21 days to allow the parasitoids to spin characteristic cocoons for ease in enumeration, and on rare occasions, microscopy was used to differentiate between sawfly larvae and larval braconids that had not yet become pre-pupae within coccons. The level of parasitism of *C. cinctus* is usually determined from observations of *C. cinctus* overwintering prepupae in cocoons in the wheat stems, but *B. cephi* and *B. lissogaster* can only be distinguished as adults. Thus, throughout this article, parasitism refers to the presence of *B. cephi* and/or *B. lissogaster* cocoons or larvae and is equal to the number of stems with a parasitized *C. cinctus* larva divided by the total number of *C. cinctus* infested stems, per sample. Infestation denotes the number of *C. cinctus* infested stems divided by the total number stems per sample.

2.2. Spatial distributions for parasitism and infestation

SADIE (Spatial Analysis of Distance IndicEs) software for MS-DOS (Perry, 1995; Perry and Hewitt, 1991; Perry et al., 1996) was used to examine whether the spatial distribution patterns of *C. cinctus* infestation and parasitism were significantly aggregated or random. The SADIE procedures are described at the website—http://www.rothamsted.bbsrc.ac.uk/pie/sadie/SADIE_home_page_1.htm. SADIE calculates an index of aggregation, I_a, which is a measurement of effort to stretch the data set to either a completely even or an aggregated distribution, and this index is compared with that obtained from repeated random permutations. For each data set, we ran 5000 permutations. Cluster indices of *C. cinctus* infestation and parasitism were also calculated using SADIE, and they represent the weightings of the actual counts so that, for instance, a wheat stem sample with a large number of *C. cinctus* infested stems gets a large positive cluster index (i.e., >1.5), denoted patch cluster, if the adjacent samples also have large numbers of *C. cinctus* infested stems, while a sample with a large number of *C. cinctus* infested stems will get low positive cluster index, if the adjacent samples have low numbers of *C. cinctus* infested stems. Similarly, a wheat stem sample with a low number of *C. cinctus* infested stems gets a low negative cluster index (i.e., <−1.5), denoted gap cluster, if the adjacent samples also have low numbers of *C. cinctus* infested stems, while a sample with a low number of *C. cinctus* infested stems will get a less negative cluster index, if the adjacent samples have larger numbers of *C. cinctus* infested stems. For wheat fields in which *C. cinctus* infestation was significantly aggregated, the cluster index scores are visualized as bubble plots using Sigma plot 8.0 for Windows (SPSS, Chicago, IL, USA). Using the SADIE procedure for analysis of spatial association between two data sets, cluster indices for paired *C. cinctus* infestation and parasitism values at each grid point were analyzed for spatial association and the overall measure of association, χ, was determined.

2.3. Overall relationship between parasitism and infestation

The data from five of these seven fields were also plotted with parasitism as a function of infestation without any spatial reference. Additional individual sample data from Runyon (2001) is also plotted, providing a larger survey data set in which to view the same relationship. These samples were also taken as 30 cm of row and processed identically to the samples described above, and were collected along the edge and in the interior of a number of solid and hollow stem wheat fields of varying sizes in 1999 and 2000. In these two years, a large number of fields were planted with solid stem winter wheat in response to favorable fall moisture and widespread lodging of crops infested with *C. cinctus*. In 1999, nine winter wheat fields were sampled, and only one was planted with a hollow stem variety. In 2000, four other winter wheat fields were sampled, with only one planted to a hollow stem variety. A solid-stem spring wheat field was also sampled in 2000.

3. Results

3.1. Spatial distribution and spatial association analyses

The data are first summarized by focusing on crop agronomic parameters (Table 1) and on categorical summaries of infestation and parasitism (Table 2), especially for parasitism when infestation levels exceeded 0.05. The significant aggregation of *C. cinctus* infestation observed at Chester in 1998 (Table 3) was mainly due to patch clustering along the western and northern edges of the field, while *C. cinctus* infestation in the eastern part of the field was clearly gap clustered (Fig. 1A). Parasitism in the same field was random (Table 3), with the map of cluster indices showing a scatter of moderate gap clusters with no clear patch clusters (Fig. 1B). However, the spatial association between *C. cinctus* infestation and

Table 2
Cephus cinctus infestation and parasitism in wheat fields in Montana

Field	Year	Wheat stem samples					
		Samples collected	Samples with *C. cinctus*	Average (SE) infestation[a]	Samples with parasitism[b]	Maximum parasitism when infestation > 0.05	Average (SE) parasitism when infestation > 0.05
Solid stem varieties							
Ledger	1998	112	80	0.07(0.01)	14	0.50	0.06(0.02)
Chester	1998	120	116	0.33(0.03)	22	0.75	0.03(0.01)
Ledger[c]	1999	107	11	0.01(<0.01)	3	0.67	0.33(0.33)
Pendroy[c]	1999	96	9	0.01(<0.01)	3	0.50	0.17(0.17)
Hollow stem varieties							
Loma	1998	120	103	0.20(0.02)	92	1.0	0.47(0.02)
Pendroy	1998	79	67	0.04(<0.01)	25	0.50	0.11(0.04)
Loma	1999	120	36	0.01(<0.01)	11	0.50	0.32(0.09)

[a] The number of stems infested by *C. cinctus* divided by the total number stems in a sample.

[b] Parasitism denotes parasitism by either *B. cephi* and *B. lissogaster* and equals the number of stems with a parasitized *C. cinctus* larva divided by the total number of *C. cinctus* infested stems in a sample.

[c] Data from Ledger and Pendroy in 1999 were not analyzed further due to low numbers of samples with infestation or parasitism.

Table 3
Spatial distribution and spatial association of *C. cinctus* infestation and parasitism in individual wheat fields

Field	Year	*C. cinctus* infestation		Parasitism of *C. cinctus*		Overall association between infestation and parasitism	
		I_a[a]	P_a[b]	I_a[a]	P_a[b]	χ[c]	P_χ[d]
Solid stem varieties							
Ledger	1998	1.25	0.09	0.98	0.45	0.07	0.29
Chester	1998	2.30	<0.01	0.96	0.45	0.27	0.02
Hollow stem varieties							
Loma	1998	1.62	0.04	1.51	0.06	0.91	<0.01
Pendroy	1998	1.71	<0.01	1.17	0.14	0.04	0.47
Loma	1999	1.32	0.12	1.06	0.34	0.62	<0.01

[a] The index of overall association for either infestation or parasitism.

[b] The probability associated with I_a.

[c] The correlation coefficient for the overall association between infestation and parasitism.

[d] The probability associated with χ.

parasitism was highly significant (Table 3), with association strongest in the northwestern part of the field (Fig. 1C). The significant aggregation of *C. cinctus* infestation in the hollow stem wheat crop at Loma in 1998 (Table 3) was mainly due to patch clustering along the eastern edge of the field, while infestation in the western part of the field was clearly gap clustered (Fig. 2A). The spatial distribution of parasitism at Loma in 1998 was random (Table 3), but the spatial pattern of the parasitism cluster indices was very similar to those for infestation (Fig. 2B). Thus, there was a very strong spatial association between the level of infestation and parasitism (Table 3) with the greatest associations occurring along the western edge (both low-occurrence gap clusters) and along the eastern edge (both high occurrence patch clusters) of the field (Fig. 2C). The significant aggregation of *C. cinctus* infestation in the hollow stem wheat crop at Loma in 1999 (Table 3) was mainly due to patch clustering along the western edge of the field, while *C. cinctus* infestation in the eastern part of the field was clearly gap clustered (Fig. 3A). The spatial distribution pattern of parasitism in Loma 1999 was found to be random (Table 3), but the pattern of these cluster indices was very similar to that for infestation (Fig. 3B). As in the previous year, there was a very strong spatial association between infestation and parasitism (Table 3) with positive associations in the northeastern corner (both low occurrence gap clusters) and along the western edge of the field (both high occurrence patch clusters) (Fig. 3C).

3.2. *Cephus cinctus infestation and parasitism*

In 1998 a total of 112 and 120 samples from fields with solid stem spring wheat varieties were collected from Ledger and Chester, respectively (Table 1), and most of the samples in both fields contained stems that were infested by *C. cinctus* larvae (Table 2). Average *C. cinctus* infestation was considerably greater in Chester compared to Ledger (Table 2). In the Ledger field the highest level of parasitism in individual samples for infestation levels greater than 0.05 was 0.50, while it was 0.75 in the Chester field (Table 2). In 1999, 107 and 96 solid stem wheat samples were collected from Ledger and Pendroy, respectively (Table 1). The *C. cinctus* infes-

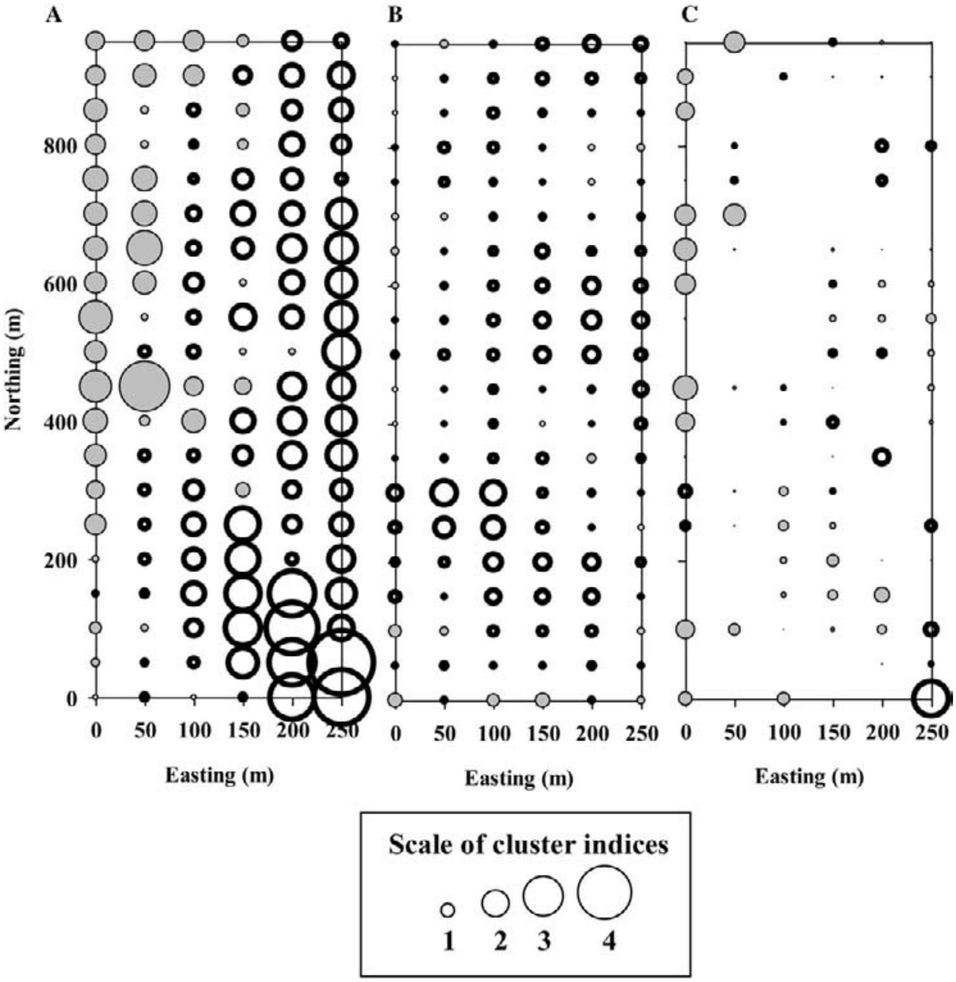

Fig. 1. Spatial pattern of *C. cinctus* infestation (A), parasitism of *C. cinctus* (B), and the spatial association of parasitism and *C. cinctus* infestation (C) at the Chester field in 1998. Statistical results are presented in Table 3. Gray filled circles denote patch clustering, while bold open circles denote gap clustering.

tation level was considerably lower in 1999 compared to 1998, and only three samples from each of the fields contained parasitized *C. cinctus* larvae (Table 2). Due to the low level of *C. cinctus* infestation and parasitism, the data from Ledger and Pendroy in 1999 were not analyzed further. A total of 112 and 79 samples from fields with hollow wheat stems were collected from Loma and Pendroy, respectively in 1998 (Table 1), and many samples in both fields contained stems with parasitized *C. cinctus* larvae (Table 2). The average *C. cinctus* infestation level was about five times higher in Loma compared to Pendroy (Table 2), and the maximum level of parasitism was also considerably higher in the Loma field compared to the Pendroy field (Table 2). Samples of hollow wheat stems were only collected from a single field in 1999 (Loma, 120 samples), and the average *C. cinctus* infestation level was about 20 times lower in 1999 compared to the previous year. At Loma in 1999, about 30% of the *C. cinctus* infested wheat stem samples contained parasitized *C. cinctus* larvae, and maximum level of parasitism, when infestation was greater than 0.05, was 0.50, with an average parasitism of 0.32 at the higher levels of infestation (Table 2). This contrasts with a maximum level of parasitism of 1.0, occurring at infestation level 0.08, and an average parasitism of 0.47 across the higher levels of infestation, for the same wheat variety grown on immediately adjacent land in Loma in the previous year (Table 2).

In all five extensively sampled fields with adequate levels of parasitism (omitting Ledger and Pendroy 1999 from consideration), we found that for samples with low levels of infestation, trends in the level of parasitism tended to be predominantly 0 or 1.0, and that the highest levels of parasitism occurred in wheat samples with a only a few infested stems (Fig. 4). The same trend occurs for fields that were survey sampled (Fig. 5). In Chester, Ledger, and Pendroy (Fig. 4A–C), the relationship between *C. cinctus* infestation and parasitism declined as infestation increased, while in Loma 1998 and 1999 (Fig. 4D–E), parasitism occurred at levels ranging from 0.4 to 0.7 at higher levels of *C. cinctus* infestation. For the survey samples from 1999 and 2000, the level of parasitism did not exceed 0.40 at higher levels of infestation (Fig. 5).

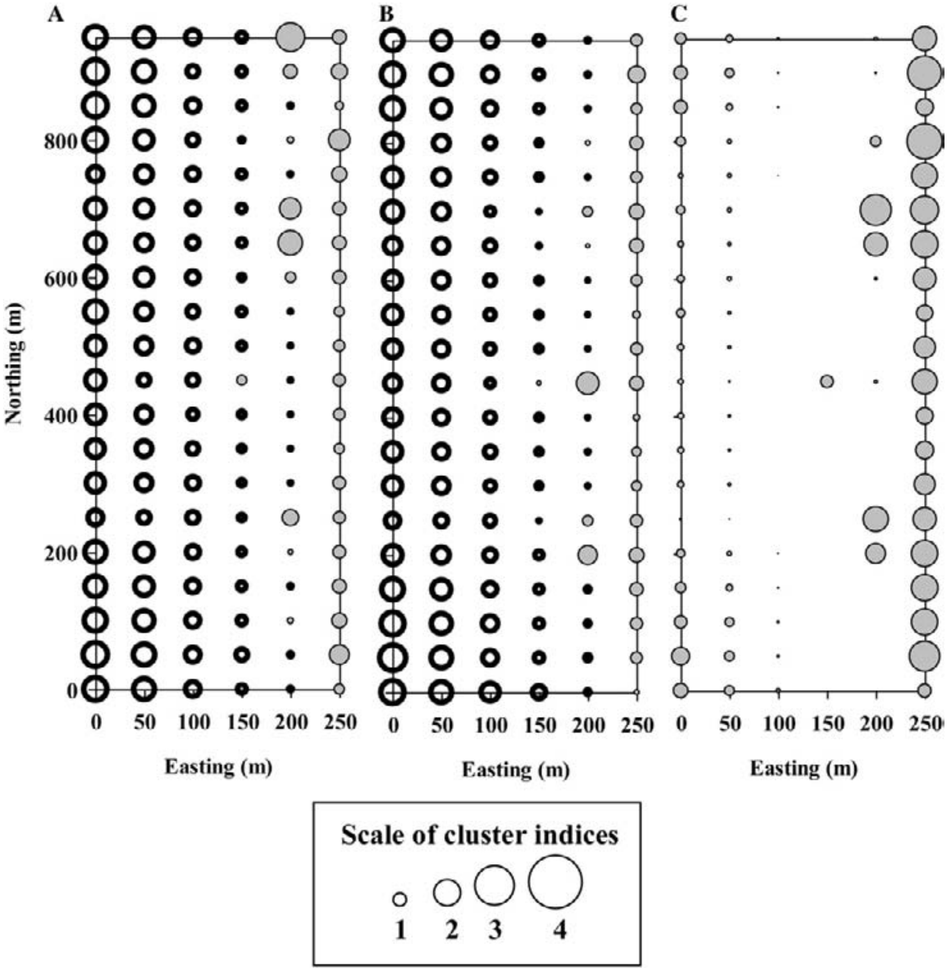

Fig. 2. Spatial pattern of *C. cinctus* infestation (A), parasitism of *C. cinctus* (B), and the spatial association of parasitism and *C. cinctus* infestation (C) at the Loma field in 1998. Statistical results are presented in Table 3. Gray filled circles denote patch clustering, while bold open circles denote gap clustering.

4. Discussion

4.1. Interpretation of the spatial distribution patterns of the host

In three out of five fields, we found a significant spatial association between *C. cinctus* infestation and parasitism, while this interaction was random in the fields at Pendroy and Ledger in 1998. Additionally, at these Pendroy and Ledger fields, no significant aggregation of *C. cinctus* infestation along field edges was observed, and inconsistent occurrence of infestation edge effects has been shown in other field surveys as well (Runyon, 2001; Sing, 2002). Figs. 1–3 show a clear edge effect for *C. cinctus* infestation with the highest infestation levels occurring along the western (Chester, 1998; and Loma, 1999) or eastern (Loma, 1998) edges with a gradual decline in infestation levels inwards to the field interior. Edge effects in many *C. cinctus* infested fields have been previously documented (Holmes, 1982; Morrill et al., 2001; Pesho et al., 1971; Runyon, 2001; Sing, 2002). In these yearly dryland alternations between wheat and fallow cropland, the newly emerged adult *C. cinctus* disperse from overwintering sites to the standing crop and begin to oviposit as soon as suitable wheat plants are encountered. As a result, larval infestations are concentrated in field edges, especially in winter wheat fields and early planted spring wheat fields where stem elongation has already occurred, and where these are located bordering overwintering sites such as fallow wheat and grassland. While aggregation of *C. cinctus* infestations along field edges surely reduces time and energy consumption in ovipositing *C. cinctus* females advancing into susceptible wheat fields, we speculate that resulting high density concentrations of available hosts may also reduce the overall risk by cannibalism or by decreasing successful host location, and ultimately, parasitism.

4.2. Cannibalism in the host/parasitoid system

Deposition of multiple *C. cinctus* eggs per stem appears to occur more frequently in high density reproductive populations (Holmes, 1963). The incidence of cannibalism within individual wheat stems should be considered a key

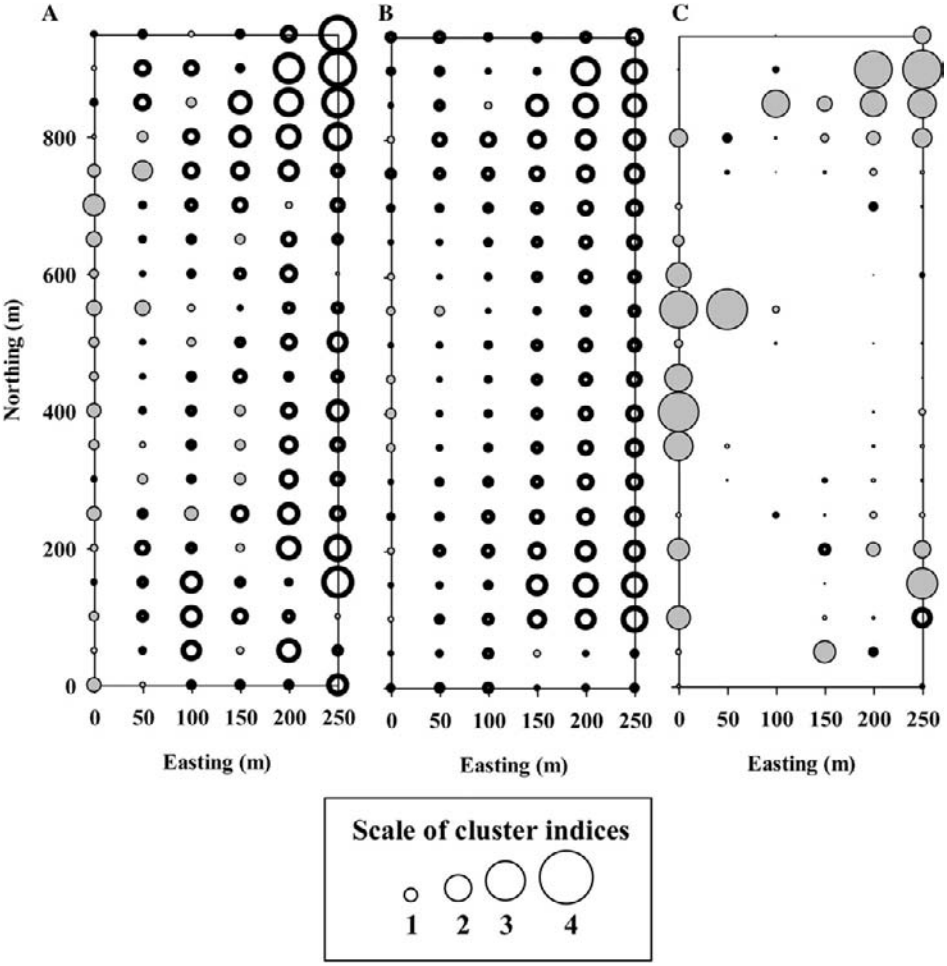

Fig. 3. Spatial pattern of *C. cinctus* infestation (A), parasitism of *C. cinctus* (B), and the spatial association of parasitism and *C. cinctus* infestation (C) at the Loma field in 1999. Statistical results are presented in Table 3. Gray filled circles denote patch clustering, while bold open circles denote gap clustering.

factor in the overall population dynamics. Parasitized *C. cinctus* larvae inside a wheat stem are likely to be more susceptible to cannibalism and are of potentially advantageous nutritional value to non-parasitized conspecifics. Cannibalism has been reported for other sawfly/parasitoid systems. Two egg parasitoids, *Collyria calcitrator* Grav. (Hymenoptera: Ichneumonidae) and *Pediobius beneficus* (Gahan) (Hymenoptera: Eulophidae) were released as parasites of the European wheat stem sawfly, *Cephus pygmaeus* (L.), but in this system parasitized and unparasitized eggs were reported to be at equal risk of cannibalism (Smith, 1959). However, parasitized larvae of *Plodia interpunctella* (Hübner) were more likely to be cannibalized than unparasitized ones (Reed et al., 1996), which is a parallel to the current study. In addition, the nutritional importance of cannibalism has also been described for armyworms (Chapman et al., 1999). Thus, if the number of larvae per stem is high enough to allow at least one *C. cinctus* larva to escape parasitism, then laying multiple eggs in one stem may be an advantageous strategy. This advantage is most likely to occur in areas where infestation is highly aggregated.

4.3. Host location inefficiency at greater numbers

It is equally plausible that at higher numbers of infested stems, successful location of remaining unparasitized larvae becomes increasingly difficult, especially if plant volatile signaling is important in cryptic host location by *B. cephi* and *B. lissogaster*. Ovipositing primarily in spatially aggregated clusters along field edges may be advantageous because it may increase the parasaitoid host search complexity when most plants are infested, and cues distinguishing between infested and uninfested plants that facilitate host location are confused or obscured. Finally, the probability of encountering a previously parasitized cryptic host becomes greater as the number of parasitized hosts increases. This situation with cryptic hosts is similar to that in stored products, where parasitoids of internally seed-feeding immatures must locate the infested kernels (Flinn and Hagstrum, 2002; Smith, 2004; Smith and Press, 1992), and then also must distinguish between parasitized cryptic hosts and unparasitized cryptic hosts to be maximally effective.

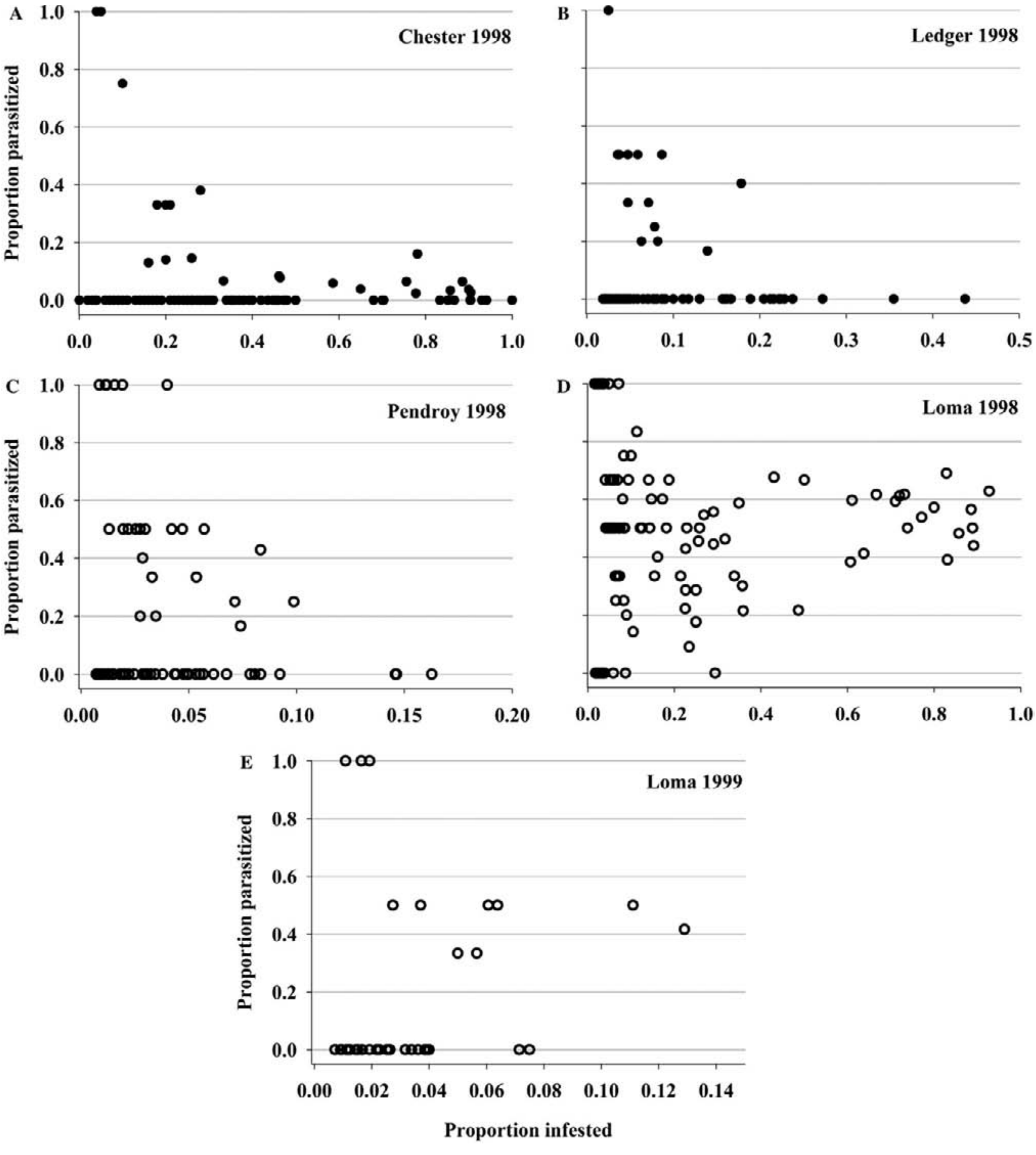

Fig. 4. Relationship between parasitism and infestation by *C. cinctus* for five wheat fields with the number of points equal to the number of samples with confirmed *C. cinctus* infestation (A–E). Proportion parasitized is the number of stems with a parasitized larva divided by the total number of stems infested by *C. cinctus* for each sample. Proportion infested is the number of stems infested by *C. cinctus* divided by the total number stems for each sample. The open circles represent hollow-stem wheat and the filled circles represent solid stem wheat.

Smith and Press (1992) reported that the inefficiency of *Sitophilus oryzae* (L.) larval parasitism, with the larvae developing hidden inside wheat kernels, was a function of the number of hosts available, irrespective of the amount of uninfested kernels that infested kernels were diluted in. Females of *Anisopteromalus calandrae* (Howard) missed approximately 44% of the *S. oryzae* hosts at 700 hosts per container, diluted in volumes ranging from 200 ml to 3 L of uninfested grain, while they failed to detect only approximately 32% of these cryptic hosts at 200 per container over the same range of dilutions (Smith and Press, 1992). Thus, it may be that

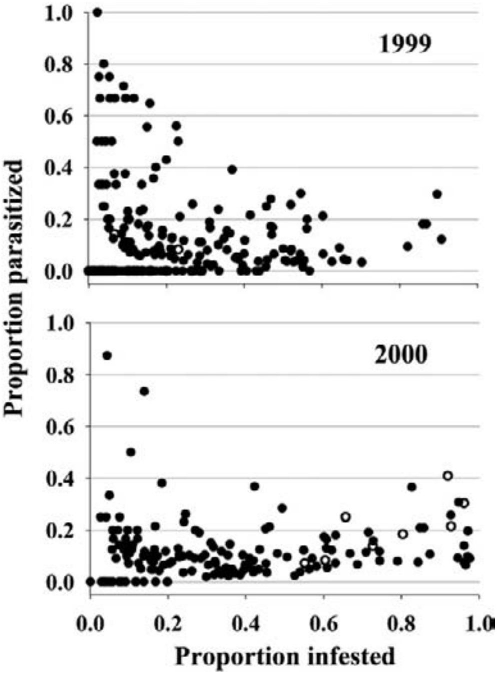

Fig. 5. Relationship between parasitism and infestation by *C. cinctus* for wheat fields that were survey sampled in 1999 and 2000, with the number of points equal to the number of samples with confirmed *C. cinctus* infestation. Proportion parasitized is the number of stems with a parasitized larva divided by the total number of stems infested by *C. cinctus* for each sample. Proportion infested is the number of stems infested by *C. cinctus* divided by the total number stems for each sample. For 1999, nine winter wheat fields were sampled for a total of 240 samples. For 2000, four winter wheat fields and a spring wheat field were sampled for a total of 160 samples. The open circles represent hollow-stem wheat and the filled circles represent solid stem wheat.

with an abundance of wheat stems infested with *C. cinctus*, locating the remaining unparasitized larvae is the greatest challenge to parasitoid females.

4.4. Spatial distribution patterns of host and parasitoids

This study is part of ongoing research on the potential use of redistributed parasitoids for improved management of *C. cinctus* in dryland wheat fields in Montana. The spatial distribution analyses we conducted revealed that infestations were significantly aggregated along field edges in three of five fields, while parasitism was spatially random in all five fields. Interestingly, all fields with spatial aggregations of infestation also showed significant spatial association between infestation and parasitism, although close scrutiny of the pattern suggests that parasitism is most strongly associated with intermediate aggregations of *C. cinctus*. For example, at Chester in 1998, the highest levels of association between parasitism and infestation (Fig. 1C) are found where aggregations of infestation are uniformly intermediate in size (Fig. 1A). The same is true for the field at Loma in 1999, where the largest aggregations of *C. cinctus* (Fig. 3A) are not where the strongest associations of parasitism and infestation (Fig. 3C) occur. However, the difference between these two fields is that in Chester in 1998, parasitoids were relatively rare, although there were many *C. cinctus* infested stems (Table 2), while at Loma in 1999, the opposite was true (Table 2). For the field at Loma in 1998, where both parasitoids and *C. cinctus* are relatively abundant (Table 2), the spatial association (Fig. 2C) closely tracks the pattern of *C. cinctus* infestation (Fig. 2A). However, even in this field, the largest aggregation of hosts, in the northeast corner (Fig. 2A) does not have a strong spatial association with parasitism (Fig. 2C).

4.5. Parasitoid efficacy and agronomic considerations

We have also illustrated that the level of parasitism either declined or is bounded at an intermediate level as the level of *C. cinctus* infestation increased (Figs. 4 and 5). The highest level of parasitism that occurred at higher host densities averaged only 60% (Fig. 4D) in the fields sampled from 1998 to 2000. However, it is important to consider the potential role of changes that happened from 1998 to 1999 in the adjacent Loma field sites. The eastern edge of the 1998 field and the western edge of the 1999 field share a common boundary. Since the hosts and parasitoids simply move to the growing crop from the fallow residue they overwintered in, which can be accomplished in a flight of as little as a few centimeters, it is reasonable to assume that the populations in 1999 represent the overwintered next generations of the 1998 populations. Thus, careful consideration should be given to the potential role of parasitoids in greatly reducing the level of infestation by *C. cinctus* observed in 1999, especially since the same susceptible, hollow-stem wheat variety was used in both years (Table 1).

These levels of parasitism are not as high as some that have been reported previously. Morrill et al. (1994) found that, on average, the level of parasitism ranged from 70 to 80% in trials with three wheat varieties. Morrill et al. (1998) reported levels of parasitism of *C. cinctus* larvae during four consecutive years at two locations in Pondera County in northwestern Montana, and they found that the level of parasitism varied from 23 to 98% with no clear relationship between *C. cinctus* infestation and parasitism between sites or among years.

Traditional pest management methods, such as insecticide application or tillage, do not adequately suppress *C. cinctus* (Morrill and Kushnak, 1999). Solid stem wheat cultivars experience lower yield losses as a result of reduced stem lodging caused by larvae (Holmes, 1977; Morrill et al., 1992a,b, 1994), and this study confirmed results from an earlier study (Morrill et al., 1994) indicating that solidness of the stem probably has little detrimental effect on the efficacy of *B. cephi* and *B. lissogaster* in suppressing *C. cinctus* (Fig. 5). In addition, cultural practices may play an important role in suppressing sawfly populations and reducing crop loss. For example, chemical fallow and minimum tillage practices for weed control promote survival of parasitoids, while heavy tillage is detrimental (Morrill et al., 1998; Runyon et al., 2002).

4.6. Considerations for inoculative parasitoid redistributions into infested fields

If we are planning to introduce *B. cephi* and *B. lissogaster* into moderately to heavily infested fields where they are currently present at negligible levels, we can now consider three key points. The most important is that it is likely that there may be negative interactions between the parasitoids and hosts at high host numbers, from either cannibalism or inefficient host seeking. Therefore, we can use the edge effect of the host to our advantage and release the parasitoids further into the field, where host numbers are lower. Doing this accurately would require minimal sampling of the growing stems to determine host numbers at the end of the *C. cinctus* oviposition period, when the larvae from the earliest deposited eggs are first of a sufficient size for parasitism. Second, when monitoring the initial establishment of these parasitoids we need to consider focusing our sampling over a moderate-sized area near the initial release point, within the area we have previously determined to be moderately infested. Finally, as part of this ongoing effort, we will accumulate additional data to determine approximate levels of parasitism required to sufficiently suppress *C. cinctus* in wheat fields, as well as determine the number of years that are required to reach this level.

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