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The spatio-temporal distribution dynamics of the cabbage seedpod weevil, *Ceutorhynchus obstrictus* (Coleoptera: Curculionidae), and its larval parasitoids in canola in western Canada

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Abstract
Distribution patterns of the cabbage seedpod weevil, *Ceutorhynchus obstrictus* (Marsham) (Coleoptera: Curculionidae), and its larval parasitoids were investigated in commercial fields of spring canola (*Brassica rapa* L. and *Brassica napus* L.) in southern Alberta, Canada, from 2002 to 2004 in relation to developmental stages of its host plants. Adult weevils invaded fields along one or more fronts when crops were in bud to early flower. Significant clustering of adults along field edges in early stages of invasion was followed by more homogeneous distributions as canola reached the mid to late flowering and pod enlargement stages. Larval weevil distributions, as indicated by exit holes in siliques at the end of the season, were often aligned spatially with adult distributions, but they did not coincide in all regions of the fields. The primary ectoparasitoid species attacking weevil larvae comprised *Necremnus tidius* (Walker) (Hymenoptera: Eulophidae), and *Trichomalus lucidus* (Walker), *Chlorocytus* sp., and *Pteromalus* sp. (Hymenoptera: Pteromalidae). Parasitism rates increased from 0.1 to 5.0% over the three years of study. Parasitoid distributions were often, but not consistently, spatially associated with high densities of *C. obstrictus* larvae. Lack of close spatial alignment of parasitoids and their hosts probably reflects low parasitoid numbers in comparison with an abundant resource of weevil larvae, and a lack of co-evolutionary history between host and parasitoids. Some parasitoids invaded fields early in host plant development, at the same time that weevils invaded. Unfortunately the synchronous invasions of host and parasitoids indicate that insecticidal applications to reduce adult weevil infestations may be detrimental to these beneficial species.

Keywords: Ceutorhynchus obstrictus, Necremnus tidius, Trichomalus lucidus, Chlorocytus *sp.*, Pteromalus *sp., endemic parasitoids, integrated pest management, spatio-temporal distributions*

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Introduction

The cabbage seedpod weevil, *Ceutorhynchus obstrictus* (Marsham) (Coleoptera: Curculionidae), is a serious pest of canola or oilseed rape, *Brassica napus* L. and *Brassica rapa* L. (Brassicaceae), in Europe and North America (Dmoch 1965; McCaffrey 1992; Buntin et al. 1995; Cárcamo et al. 2001). The weevil is native to Europe (Dmoch 1965), and was first reported in North America in 1931 (McLeod 1962). It was discovered infesting canola in southern Alberta in 1995 (Butts & Byers 1996), and since then the species has dispersed extensively so its range now extends over hundreds of thousands of hectares throughout southern and central Alberta and Saskatchewan. Its range is predicted to eventually encompass the entire region of canola production in western Canada (Dosdall et al. 2002).

The cabbage seedpod weevil is univoltine and oligophagous on Brassicaceae (Dmoch 1965). Adults overwinter primarily in soil beneath leaf litter in shelterbelts (Dmoch 1965), and emerge from these sites in spring when soil temperatures warm to approximately 15°C (Ulmer & Dosdall 2006). In southern Alberta *C. obstrictus* migrates from its overwintering sites to feed on early-flowering weeds like hoary cress (*Lepidium* spp.), flixweed (*Descurainia sophia* (L.) Webb), and wild mustard (*Sinapis arvensis* L.) before they are attracted to canola crops in the bud to early flowering stages (Fox & Dosdall 2003; Dosdall & Moisey 2004). Mated females oviposit into siliques, and larvae feed on developing seeds. After a larval developmental period spanning 2–4 weeks, the mature final-instar larva chews an opening through the pod wall, drops to the soil surface, burrows down, and pupates within an earthen cell. The new generation adult emerges about 14 days later and feeds on maturing canola seeds before migrating to overwintering sites (Dosdall & Moisey 2004).

Weevil damage is inflicted on the crop by adult feeding on developing flower buds causing buds to desiccate and racemes to bear fewer pods, by larval feeding on seeds within siliques, and by premature shattering of infested pods (Dosdall et al. 2001). Feeding by new generation adults through the pod walls can further reduce yield and crop quality (Buntin et al. 1995; Dosdall et al. 2001).

Previous studies in winter canola in Europe determined that weevil immigration to the crop occurs initially along crop edges, but weevil densities later become more uniform as crop development proceeds (Free & Williams 1979). Subsequent invasions of *Trichomalus perfectus* (Walker) (Hymenoptera: Pteromalidae), the primary European parasitoid of *C. obstrictus* larvae, occurred later than immigration of its host, and parasitoids were also initially distributed along crop edges (Murchie et al. 1999). Close spatial association was observed between *C. obstrictus* and *T. perfectus* in canola crops, indicating that the parasitoid was effective both in its dispersal and host location capabilities (Ferguson et al. 1999, 2000).

Understanding the spatial and temporal ecologies of insect pests and their natural enemies is an important prerequisite for targeting insecticidal treatments to maximize their impact on pests while conserving populations of natural enemies. The spatio-temporal population dynamics of the cabbage seedpod weevil and its parasitoids have not been investigated previously in canola in North America. North American canola agroecosystems have important differences compared with European systems. In contrast to the fall-seeded, slow maturing 'winter' cultivars of *B. napus* grown commonly in Europe, most North American production consists of spring-seeded, rapidly maturing cultivars of both *B. napus* and *B. rapa*. Climatic differences also exist, and although European weevils are parasitized principally by *T. perfectus*, which

evidently co-evolved with its host, the North American parasitoid fauna is comprised of endemic and Holarctic species of Chalcidoidea that would have attacked other hosts before *C. obstrictus* became abundant and widespread (Gibson et al. 2005). The objectives of this study were to investigate the distribution patterns of *C. obstrictus* in spring canola in western Canada in relation to host plant phenology, and to compare spatio-temporal distributions of the weevil with its larvae and with distributions of its parasitoids. The study was undertaken to develop the required background information needed for better targeting of insecticide applications in space and time, and so enhance integrated management of the weevil.

Materials and methods

2002 studies

In 2002, an area comprising 250 × 75 m along the southern and eastern edges of an irrigated commercial field of *B. napus* near Coaldale, Alberta (112°37′W; 49°44′N) was subdivided in a grid pattern to form 375 plots, each measuring 10 × 5 m. The dimensions of the commercial crop were ca. 300 × 350 m. Each 50-m^2 plot was sampled on three dates: 4, 18, and 30 July when the crop was in bud to early flower (Growth Stages 3.1–3.2 of Harper and Berkenkamp 1975), mid flower (Growth Stages 4.3–4.4), and early pod (Growth Stage 5.1), respectively. Sampling consisted of taking ten, 180° sweep net samples from each grid plot, placing each sample in a labeled plastic bag, and storing samples temporarily in a freezer until adult weevils could later be identified, counted, and recorded.

When seeds in the lower pods were fully enlarged but still green (Growth Stage 5.2), a sample of 100 randomly selected pods was collected from the plots and the samples were returned to the laboratory where they were placed in cardboard boxes (18 × 18 cm and 16 cm tall), and the boxes were sealed with tape. Each box had a small cylindrical plastic vial attached over a 4-cm diameter opening in the side of the box for collecting parasitoids as they emerged. Boxes were maintained under continuous light at room temperature for 6 weeks until all parasitoids had emerged. The boxes were then opened and any additional parasitoid adults were collected that had not moved to the plastic collecting vials. Pods of each box were examined and counts made of larval and parasitoid exit holes, which could be distinguished because exit holes of *C. obstrictus* larvae are circular but irregular along their margins whereas those of weevil parasitoids are smaller and rounded along their margins (Dosdall, unpublished data).

2003 studies

In 2003, an area comprising 160 × 160 m along the eastern edge of a commercial crop of *B. rapa* ca. 10 km south of Lethbridge, Alberta (112°39′W; 49°38′N) was subdivided in a grid pattern to form 256 plots, each measuring 10 × 10 m. The dimensions of the commercial *B. rapa* crop were ca. 450 × 350 m. A grid of identical dimensions was also established along the southern and eastern edges of a commercial crop of *B. napus* near Macgrath, Alberta (112°39′W; 49°33′N). The dimensions of the commercial *B. napus* crop were ca. 800 × 400 m.

The sampling method was altered in 2003 and in subsequent years so that the plots could be sampled more frequently (i.e. weekly for ca. 6 weeks instead of three times per season), to better document changes in spatial and temporal distributions of

C. obstrictus. Sweep net sampling was found to remove large numbers of adults from the population, and was damaging to canola plants, which could affect weevil distribution patterns. Consequently, yellow bowl trap samplers were used that were elevated to the height of the crop canopy. Traps followed the design of Murchie et al. (1999) who found that they effectively sampled both *C. obstrictus* and its European parasitoid, *T. perfectus*, in canola in the UK.

In 2003, yellow bowl traps (15 cm diameter, 9 cm depth) were placed in the centre of every other plot within each grid in a checkerboard pattern so that a total of 128 samplers were installed per site. Bowl traps were attached with a metal bracket to a metal post driven into the ground so its height above ground was at least 1.5 m. The height of each bracket was adjusted on the post so the trap could be maintained at the level of the top of the crop canopy throughout the study. Each bowl trap was filled with a 1:1 mixture of water:propylene glycol and refilled as needed. The bowl traps were installed at each site when the majority of plants were in bud (Growth Stage 3.1), and samples were collected at weekly intervals until the crop matured (Growth Stage 5.3). Sampling involved straining bowl trap contents through a fine mesh net and preserving the filtered insect specimens in jars of 70% ethanol. Samples were sorted in the laboratory, and adults of *C. obstrictus* and its larval ectoparasitoids were counted and recorded.

Late in the season when most of the larval population of *C. obstrictus* was in the final instar, a collection was made of 250 randomly selected pods from each of the grid plots that contained a bowl trap sampler. The pods were stored temporarily in sealed plastic bags and labeled as to their locations within the grid. The samples were then returned to the laboratory where they were placed in cardboard emergence boxes as described above, and the boxes were sealed with tape. The boxes were opened after being held at room temperature for 6 weeks and all ectoparasitoid adults were counted and identified to species. Pods of each box were examined for exit holes and counts were made to determine numbers *C. obstrictus* larval and parasitoid exit holes per pod.

2004 studies

In 2004 a single grid was established in the southwest corner of a commercial crop of *B. napus* located near Lethbridge, Alberta (112°47′W; 49°40′N). One hundred plots were established in this section of the field, each measuring 10 × 10 m, and a bowl trap sampler was placed in the centre of each plot (Figure 1). Bowl trap samplers were also placed 200, 300, and 400 m from the corner of the primary grid, and extended at right angles into the crop. Bowl trap samplers were placed 20 m apart on the 200 m transect, 30 m apart on the 300 m transect, and 40 m apart on the 400 m transect. The corner of the 400 m transect reached the geographic centre of the crop (Figure 1). A total of 163 bowl traps were installed over the entire grid. Bowl traps were set in position on 16 June 2004 when the crop was in bud (Growth Stage 3.1) and samples were collected at approximately weekly intervals for 5 weeks until the end of flowering. When most of the *C. obstrictus* larval population was in the final instar, collections were made of 250 randomly selected pods from each of the grid plots. The pods were placed in cardboard rearing boxes, as described above, and approximately 6 weeks later all parasitoid adults were removed from the collecting vials, identified to species, and all exit holes were counted for the pod samples.

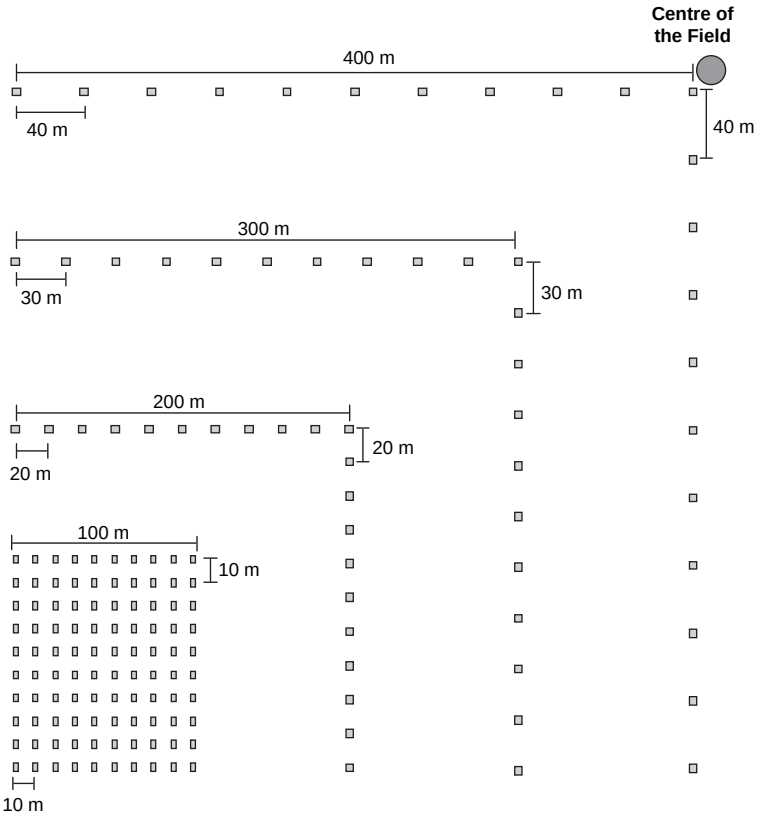

Figure 1. The arrangement of bowl trap samplers used in 2004 to sample intensively in one corner of the *B. napus* crop with additional samplers extending along transects at varying distances at right angles to the corner grid.

Parasitoids were identified using published taxonomic keys and by comparison with type material or other authoritatively identified specimens. Voucher specimens of parasitoids have been deposited in the Canadian National Collection of Insects and Arachnids, Ottawa, Ontario, Canada.

Spatial analyses

Numbers of *C. obstrictus* adults collected using sweep net or bowl trap samples on each sampling date, and weevil larvae and their ectoparasitoids reared from pods at the end of the season, were restructured to create separate ascii grid matrices by date using SAS statistical software (SAS Institute 1999). The ascii files were then imported into ArcInfo Geographical Information Systems software (ESRI Services, Redlands, CA) to create GRIDS using the ASCIIGRID function. Grid size was set to 100 units, and the grid data were then converted to point functions using the GRIDPOINT function of ArcInfo. The point coverages were then interpolated back to GRIDS using the POINTINTERP command. Interpolation was done by resampling the grid size to 10 units and interpolating to a radius of 200 units using exponential distance weighted interpolation with a smoothing factor applied to the point values. The process

examines point data in relation to values from its nearest neighbor to estimate how values decline (decay) with distance from the point in question. On each sampling date, the spatial distributions of weevil adults, weevil larval exit holes, and larval ectoparasitoids were presented as contour maps of density as interpolated using the ArcInfo software.

Grid sizes, and consequently the distances between samples, were identical within the experiments for the grid designs used in 2002 and 2003. In 2004, however, grid distances varied within the study site because sampling units (input points) were spaced comparatively close together in the southwest corner of the field, but became progressively further apart toward the outer limits of the grid. Therefore the inverse distance weighted interpolation was used to conduct the 2004 analysis. Inverse distance weighting was considered more appropriate than exponential distance weighting because of the assumption in inverse distance weighting that nearby points are more closely related than distant points to the value at the interpolated location. Inverse distance weighting applies stronger weights to nearby points. This approach was considered appropriate, therefore, because data points were more abundant and closely spaced in the corner of the field sampled intensively than at more distant locations in the field. The weight assigned to each data point then diminished as the distance from the interpolation point to the scatter point increased, with the sample data closest to the unmeasured point contributing more to the calculated average (Burrough & McDonnell 1998).

Spatial Analysis by Distance IndicEs (SADIE) software (Perry 1998) was used to analyze spatial distributions of *C. obstrictus* adults for each of the sampling dates, as well as distributions of weevil larvae and their ectoparasitoids at the end of the season (based on larval exit hole frequencies and emergence of parasitoids from rearing containers). SADIE performs permutations of observed insect counts among sampling units and assesses observed arrangements in species count data by tests of randomization. The technique identifies areas of clustering or gaps by assigning an index that quantifies the degree to which a sampled count at a particular location contributes toward clustering of the population. SADIE estimates the total distance that individuals must be moved between sampling units so that data are as regular as possible (Perry 1998).

Spatial patterns of single sets of sweep net counts of weevil adults on a given date, larval exit holes at the end of the season, and ectoparasitoids emerging from the different locations within the grid were determined using the main SADIE index, I_a, the subsidiary index, $\mathcal{J}_a$, and the distance, δ. Values of index I_a that approximate 1.0 indicate random distributions in a data set, but values that exceed 1.0 indicate aggregated arrangements. The index of aggregation, I_a, measures pattern over the entire sample area (Perry & Klukowski 1997), and is defined as $I_a = D/E_a$ where E_a is the arithmetic mean distance to regularity for the randomized samples, and D is the minimum total distance that individuals in the sample would need to move so that all units would have an identical number of individuals (Perry 1998). The index, $\mathcal{J}_a$, distinguishes among patterns. When the value of $\mathcal{J}_a$ is greater than 1.0, it indicates a single major cluster, but values less than 1.0 indicate two or more clusters. Finally, δ refers to the distance between two centroids, P and C. The computation determines the distance from the centroid of the counts to the centroid of the sample units. The spatial analysis computes the location P from the x and y co-ordinates of sample units as the 'middle' of the sample, and location C, as the centroid of the counts. The value of δ is then the distance between these

two centroids, P and C. This is a means of quantifying the degree to which an observed set of counts of individuals in a population occupies the edge or the centre of the area defined by the sample units (Perry & Klukowski 1997).

The degree of clustering or non-randomness is estimated, in part, in the SADIE program by the distance to regularity in rearrangements of the observed data (Perry 1998). Our analyses used the maximum number of randomizations possible within the SADIE program (5,967).

Spatial associations among distinct but related data sets of insect distributions within the grids were also assessed within the SADIE system. The method, described by Winder et al. (2001) and Perry and Dixon (2002), calculates similarities in clustering indices of two sets of data, in this case between the occurrence of weevil larvae and their ectoparasitoids. The method assigns individual sample units to specific aggregation measures, thereby quantifying the extent that a particular unit contributed toward aggregation. The associations were evaluated by correlating the specific aggregation measures and the results were expressed as Pearson Correlation Coefficient statistics.

Results

2002 studies

A total of 1590, 620, and 248 *C. obstrictus* adults were collected in the sweep net samples at the study site in 2002 when plants were in the bud to early flower, mid flower, and pod enlargement stages, respectively. When the *B. napus* plants were in bud to early flower, weevil adults were most abundant along the southern edge of the crop (Figure 2a). However, in mid flower overall densities had declined and populations were more uniformly dispersed, although the region of greatest density remained at the southern section of the grid (Figure 2b). By pod ripening, adult abundance had declined in all areas previously colonized (Figure 2c).

The SADIE index, I_a, and its associated P values indicated that adult weevils were significantly aggregated on all dates with the aggregation patterns particularly strong when plants were in bud to mid flower (Table I). The index, $\mathcal{J}_a$, exceeded unity on all dates, indicating invasion along a single front. The value of δ became progressively smaller over the season suggesting that the distribution patterns during the phase when insect numbers declined did not repeat in reverse the patterns observed in the initial weevil invasion. Larvae of *C. obstrictus* occurred in approximately 8% of pods, and larval populations were significantly aggregated ($P < 0.009$) (Table I).

Larval chalcidoid parasitoids were low in abundance at the study site in 2002, with only 24 reared from 37,500 pods collected. Most specimens were comprised of *Trichomalus lucidus* (Walker) (50.0% of specimens reared) and *Pteromalus* sp. (25.0%) (Pteromalidae), but small numbers of *Necremnus tidius* (Walker) (Eulophidae) (12.5%), and *Chlorocytus* sp. (8.3%) and *Lyrcus maculatus* (Gahan) (Pteromalidae) (4.2%) also were collected. The low densities of larval parasitoids precluded further analysis of these data.

2003 studies

A total of 3592, 3963, 338, 759, and 3078 adults of *C. obstrictus* were collected in the 128 bowl trap samplers in the *B. rapa* field in 2003 on the five weekly sampling dates

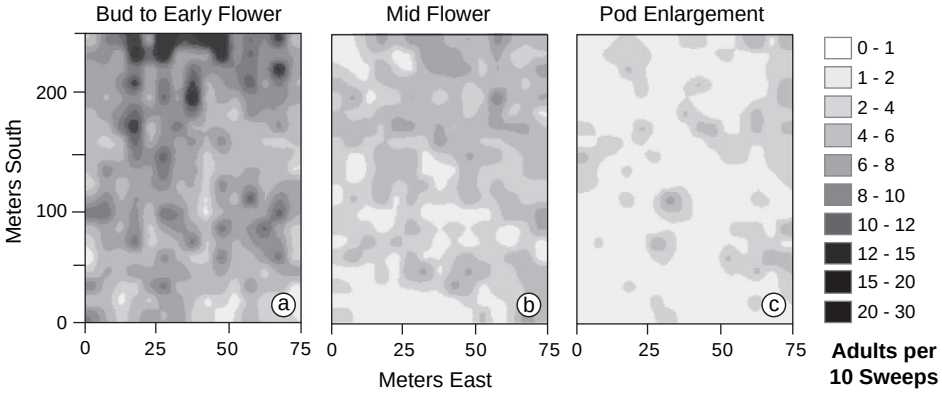

Figure 2. Distributions of *C. obstrictus* adults interpolated from sweep net samples collected in 2002 at 375 locations within an area comprising 18 750 m^2 of a commercial crop of *B. napus* near Lethbridge, Alberta, when most plants were in bud to early flower, mid flower, and pod enlargement developmental stages. The legend gives weevil adults per ten 180° sweep net samples.

spanning crop development from bud to pod maturity. Mean adults per trap ranged from 2.6 when plants were in mid flower to 31.0 when plants were in early flower (Table II). On the earliest sampling date when plants were in bud to early flower, adult numbers were high, averaging 28 per bowl trap, and abundance was greatest along the western margin of the grid (Figure 3a). Later when most plants were in the pod enlargement stage, adult weevil numbers were still comparatively high throughout the field (mean = 24 per trap), but densities were more homogeneously distributed (Figure 3b).

Adult weevil trap numbers were significantly aggregated in early flower as indicated by I_a values substantially greater than unity ($P < 0.001$) (Table II). However, in mid flower, the I_a value only slightly exceeded unity, and adult densities were not significantly aggregated ($P < 0.25$). For the remainder of the season, when *B. rapa* plants were in late flower and pod enlargement, weevil populations were again significantly aggregated ($P < 0.009$). The greatest degree of aggregation occurred in early flower, and the most homogeneous distributions were observed during mid flower (Table II).

Table I. Mean adults of *C. obstrictus* per ten sweep net samples collected from each of 375–50-m^2 plots on 4, 18, and 30 July 2002 when the *B. napus* crop was in bud to early flower, full flower, and early pod, respectively, and mean weevil larval exit holes per pod at the end of the season. Spatial distribution indices are presented for the sampling dates based on calculations with the SADIE procedure.

Sample date (2002)	Canola growth stage	Mean *C. obstrictus* per 10 sweeps (S.E.)	δ (m)	I_a^1	*P*	$\mathcal{J}_a^2$
4 July	Bud to early flower	5.30 (0.27)	1.93	3.10	<0.009	1.02
18 July	Early flower	2.07 (0.11)	1.71	2.75	<0.009	1.04
30 July	Pod enlargement	0.83 (0.06)	1.19	1.49	<0.026	9.94
		Mean *C. obstrictus* exit holes per pod (S.E.)				
20 Aug.	Pod enlargement	0.08 (0.31)	1.68	3.660	<0.009	1.02

[1]Values of $I_a > 1$ indicate aggregation within the sample area. [2]Values of $\mathcal{J}_a \leq 1$ indicate the presence of multiple clusters when $I_a > 1$.

Table II. Mean adults of *C. obstrictus* per bowl trap sample from a total of 128 traps sampled weekly in 2003 in a grid pattern within a commercial field of *B. rapa*. Mean larval exit holes and mean chalcidoid parasitoids per pod are from a single collection made in the same field at the end of the season in 64 sites within the grid. Spatial distribution indices, calculated with the SADIE procedure, are presented for weevil adults, larval exit holes, total larval parasitoids and for the chalcidoid species *N. tidius* and *T. lucidus*.

Sample period (2003)	Canola growth stage	Mean *C. obstrictus* adults per trap (S.E.)	δ (m)	I_a^1	P	ν_a^2
19–26 June	Early Flower	28.06 (1.605)	1.69	2.80	<0.009	1.01
26 June–3 July	Early Flower	30.96 (1.108)	1.18	3.04	<0.009	1.01
3–10 July	Mid Flower	2.64 (0.171)	0.53	1.07	<0.248	1.04
10–16 July	Late Flower	5.93 (0.296)	1.19	2.26	<0.009	1.05
16–24 July	Pod Enlargement	24.05 (0.825)	0.67	1.91	<0.009	1.01
Sample date (2003)		Mean *C. obstrictus* exit holes per pod (S.E.)				
24 July	Pod Enlargement	0.144 (0.005)	0.35	1.34	<0.009	1.04
Sample date (2003)		Mean ctoparasitoids per pod (S.E.)				
24 July	Pod Enlargement	0.003 (0.000)	1.91	1.57	<0.009	1.05
Sample date (2003)		Mean *Trichomalus lucidus* per pod (S.E.)				
24 July	Pod Enlargement	0.001 (0.000)	2.33	1.27	<0.060	1.04
Sample date (2003)		Mean *Necremnus tidius* per pod (S.E.)				
24 July	Pod Enlargement	0.001 (0.001)	2.33	1.26	<0.060	1.15

[1]Values of $I_a > 1$ indicate aggregation within the sample area. [2]Values of $\nu_a < 1$ indicate the presence of multiple clusters when $I_a > 1$.

Larvae of *C. obstrictus* emerged from approximately 14% of *B. rapa* pods and their distribution was significantly aggregated ($P < 0.009$) (Table II). Development of *C. obstrictus* larvae occurred most abundantly in the central region of the grid and along its western perimeter (Figure 3c).

Twenty-seven adult specimens of weevil larval parasitoids were collected during 5 weeks of bowl trap sampling spanning crop development from early flower to pod enlargement (Table III). *Necremnus tidius*, *Mesopolobus* spp., and *Pteromalus* sp. (Pteromalidae) comprised 78% of all parasitoids collected, with the remaining specimens comprising *Chlorocytus* sp., *T. lucidus*, and *Eurytoma* sp. (Eurytomidae).

A total of 83 larval ectoparasitoids emerged from 0.3% of pods over the entire grid (Table II). The predominant ectoparasitoid species consisted of *N. tidius* (47.0% of all parasitoids reared), *T. lucidus* (21.7%), *Chlorocytus* sp. (15.7%), and *Pteromalus* sp. (9.6%). Small numbers of *Conura albifrons* (Walsh) (Chalcididae) (2.4% of all parasitoids reared), *Mesopolobus moryoides* Gibson (Pteromalidae) (2.4%), and *Euderus albitarsus* (Zetterstedt) (Eulophidae) (1.2%) also were present. Greatest ectoparasitoid densities were observed along the southern perimeter of the grid, which corresponded with some areas that also had high larval densities (Figure 3d,e). However, several regions of the grid with high larval densities of *C. obstrictus* were not associated with correspondingly high numbers of parasitoids. Distributions of total parasitoids were significantly aggregated ($P < 0.009$) (Table II). The two dominant parasitoid species, *T. lucidus* and *N. tidius*, each occurred in approximately 1% of pods

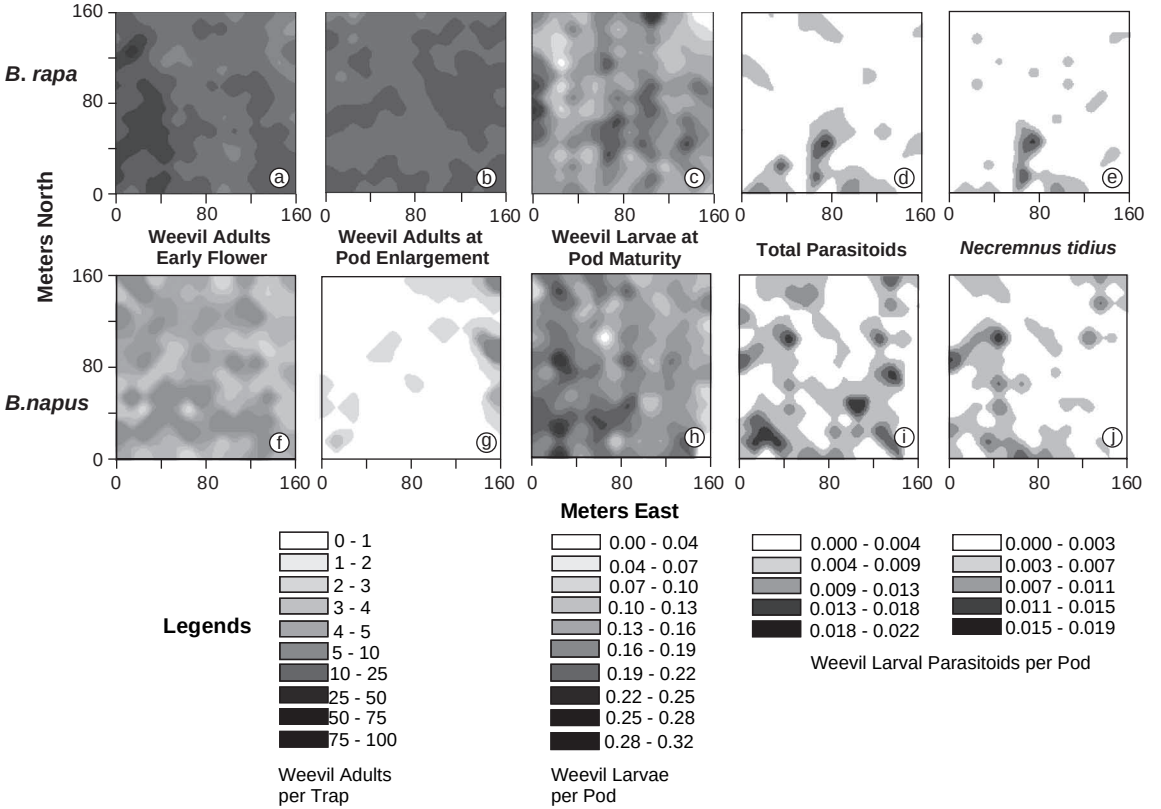

Figure 3. Distributions of *C. obstrictus* and its larval parasitoids interpolated from samples collected in 2003 at 256 locations within grid areas each comprising 25 600 m^2 of commercial crops of *B. rapa* and *B. napus* near Lethbridge, Alberta. The legends give weevil adults per bowl trap sample, and weevil larvae and parasitoids per pod.

Table III. Adult parasitoids of *C. obstrictus* larvae collected in bowl trap samplers in fields of *B. rapa* and *B. napus* during 2003 and 2004.

Sample period	Crop species	Crop stage	*Necremnus tidius*	*Pteromalus* sp.	*Chlorocytus* sp.	*Trichomalus lucidus*	*Mesopolobus* spp.	*Conura* spp.	*Eurytoma* sp.
2003									
19–26 June	*B. rapa*	Early flower	2	1	0	0	1	0	0
26 June–3 July	*B. rapa*	Early flower	0	1	1	0	4	0	1
3–10 July	*B. rapa*	Mid flower	1	1	1	1	1	0	0
10–16 July	*B. rapa*	Late flower	0	0	0	0	1	0	1
16–24 July	*B. rapa*	Pod	5	3	0	1	0	0	0
18–25 June	*B. napus*	Bud	11	1	0	0	0	0	0
25 June–2 July	*B. napus*	Early flower	0	0	0	0	0	0	0
2–9 July	*B. napus*	Early flower	0	0	0	0	0	0	0
9–17 July	*B. napus*	Mid flower	1	1	0	1	1	0	0
17–23 July	*B. napus*	Late flower	1	0	1	1	1	1	0
23–31 July	*B. napus*	Pod	6	1	0	0	0	3	0
2004									
16–23 June	*B. napus*	Bud	1	0	0	0	1	0	0
24–30 June	*B. napus*	Early flower	0	0	0	0	0	0	0
1–7 July	*B. napus*	Early flower	0	0	0	0	0	0	0
8–14 July	*B. napus*	Mid flower	9	0	0	0	0	1	1
15–21 July	*B. napus*	Late flower	0	0	0	0	0	0	1

throughout the entire grid, and although their I_a values exceeded unity and indicated aggregation, these were marginally nonsignificant ($P < 0.06$) (Table II).

Some, but not all, of the parasitoids were correlated with larval populations of the cabbage seedpod weevil. Populations of *Chlorocytus* sp. were significantly correlated with *C. obstrictus* larvae ($F = 4.95$; df = 46.55; $P < 0.03$; $r = 0.31$), but not populations of total parasitoids ($F = 3.26$; df = 70.90; $P < 0.08$; $r = 0.21$), *N. tidius* ($F = 0.38$; df = 79.11; $P < 0.54$; $r = 0.07$), or *T. lucidus* ($F = 0.73$; df = 60.42; $P < 0.40$; $r = 0.11$).

A total of 458, 1140, 54, 4442, 7211, and 97 *C. obstrictus* adults were collected in bowl traps in the *B. napus* field in 2003 during the 6-week period spanning crop development from bud to pod maturity. Mean adults per trap ranged from 0.4 when plants were in early flower, to 56.3 when plants were in late flower (Table IV). When *B. napus* was in early flower, weevil adults were relatively uniformly distributed across the field with greatest densities occurring along the southern and northern sections of the grid, and lowest densities along the eastern perimeter (Figure 3f). By the time of pod enlargement, however, adult densities had declined dramatically to zero throughout most of the field, with most specimens occurring along the eastern margin of the grid (Figure 3g).

Table IV. Mean adults of *C. obstrictus* per bowl trap sample from a total of 128 traps sampled weekly in 2003 in a grid pattern within a commercial field of *B. napus*. Mean larval exit holes and mean chalcidoid parasitoids per pod are from a single collection made in the same field at the end of the season in 64 sites within the grid. Spatial distribution indices, calculated with the SADIE procedure, are presented for weevil adults, larval exit holes, and larval parasitoids.

Sample period (2003)	Canola growth stage	Mean *C. obstrictus* adults per trap (S.E.)	δ (m)	I_a^1	P	$\mathcal{J}_a^2$
18–25 June	Bud	3.58 (0.21)	0.67	1.27	<0.077	1.02
25 June – 2 July	Early Flower	8.91 (0.53)	1.20	1.99	<0.009	1.02
2–9 July	Early Flower	0.42 (0.05)	0.92	0.99	<0.458	9.88
9–17 July	Mid Flower	34.70 (1.41)	0.83	2.39	<0.009	1.08
17–23 July	Late Flower	56.34 (1.78)	0.83	2.46	<0.009	1.02
23–31 July	Pod Enlargement	0.76 (0.11)	2.57	1.90	<0.009	9.77
Sample date (2003)		Mean *C. obstrictus* exit holes per pod (S.E.)				
31 July	Pod Enlargement	0.161 (0.005)	0.92	2.62	<0.009	1.02
Sample date (2003)		Mean ectoparasitoids per pod (S.E.)				
31 July	Pod Enlargement	0.005 (0.000)	1.07	1.23	<0.068	9.82
Sample date (2003)		Mean *Necremnus tidius* per pod (S.E.)				
31 July	Pod Enlargement	0.003 (0.000)	1.75	1.40	<0.009	1.02
Sample date (2003)		Mean *Chlorocytus* sp. per pod (S.E.)				
31 July	Pod Enlargement	0.001 (0.001)	1.35	1.07	<0.265	9.62
Sample date (2003)		Mean *Trichomalus lucidus* per pod (S.E.)				
31 July	Pod Enlargement	0.001 (0.000)	2.35	1.11	<0.248	9.74

[1]Values of $I_a > 1$ indicate aggregation within the sample area. [2]Values of $\mathcal{J}_a < 1$ indicate the presence of multiple clusters when $I_a > 1$.

The distribution of adult weevils was significantly aggregated during four of the six sampling dates (Table IV). When plants were in bud, the SADIE I_a index exceeded unity, but no significant aggregation was evident ($P < 0.08$). Similarly, during early flower (2–9 July), weevil distributions were not aggregated ($P = 0.46$). During all other sampling periods, however, weevil distributions were significantly aggregated ($P < 0.009$). The greatest degree of aggregation occurred during mid to late flower, and the most homogeneous distributions were observed during early flower (2–9 July) (Table IV).

When the *B. napus* plants were mature, larval exit holes occurred in approximately 16% of pods throughout the field. Larval distributions were significantly aggregated ($P < 0.009$) (Table IV), with greatest larval densities occurring along the western half of the grid (Figure 3h).

Thirty-one adult specimens of weevil larval ectoparasitoids were collected during 6 weeks of bowl trap sampling spanning crop development from bud to pod enlargement (Table III). *Necremnus tidius* comprised 61% of total adult parasitoids collected, and 58% of all *N. tidius* were from bowl trap collections made during the 1-week period when most plants were in bud. Other adult ectoparasitoids collected included *Pteromalus* sp., *Chlorocytus* sp., *T. lucidus*, *Mesopolobus* spp., and *Conura* spp.

A total of 172 larval parasitoids emerged from 0.5% of pods collected throughout the grid (Table IV). The dominant parasitoid species consisted of *N. tidius* (46.5% of all parasitoids reared), *Chlorocytus* sp. (19.8%), *T. lucidus* (16.9%), and *Pteromalus* sp. (9.8%). Small numbers of *Conura torvina* (Cresson) (Chalcididae) (2.3% of all parasitoids reared), *C. albifrons* (2.3%), *Mesopolobus bruchophagi* Gahan (Pteromalidae) (1.2%), *M. moryoides* (0.6%), and *E. albitarsis* (0.6%) also were reared. Greatest parasitoid densities occurred along the southern half of the grid, but other areas of high parasitoid densities occurred throughout the field (Figure 3i). The area along the southern region of the grid generally corresponded with sites that also had high larval densities, but there were several areas of high larval densities that did not correspond with high ectoparasitoid densities. Some sites with high parasitoid densities corresponded to areas of low larval weevil densities (Figure 3i). Although the value of I_a exceeded unity, clustering of total parasitoids was marginally nonsignificant ($P < 0.07$) (Table IV). Distributions of *N. tidius*, which comprised approximately one-half of all parasitoids reared, were aggregated ($P < 0.009$) with several clusters evident along the western and southern regions of the grid (Figure 3j), but no significant aggregation patterns were observed for *Chlorocytus* sp. and *T. lucidus* ($P > 0.05$) (Table IV). Populations of *C. obstrictus* larvae were not significantly correlated with those of total parasitoids ($F = 1.40$; df = 48.23; $P < 0.24$; $r = 0.17$), *N. tidius* ($F = 2.53$; df = 26.78; $P < 0.12$; $r = 0.29$), *Chlorocytus* sp. ($F = 1.18$; df = 23.83; $P < 0.29$; $r = 0.22$), or *T. lucidus* ($F = 1.72$; df = 26.78; $P < 0.20$; $r = 0.25$).

2004 studies

A total of 7934, 1582, 150, 3468, and 155 adults of *C. obstrictus* were collected in the 163 bowl trap samplers in the *B. napus* field in 2004 on the five weekly sampling dates spanning crop development from bud to pod maturity. Mean adults ranged from 0.9 per bowl trap during early (1–7 July) and late flower, to 48.7 per trap during bud (Table V). On the earliest sampling date when plants were in bud, adult abundance was greatest in the southern region of the grid along a front that extended for

Table V. Mean adults of *C. obstrictus* per bowl trap sample from a total of 163 traps sampled weekly in 2004 in a grid pattern within a commercial field of *B. napus*. Mean larval exit holes and mean chalcidoid parasitoids per pod are from a single collection made in the same field at the end of the season in 163 sites within the grid. Spatial distribution indices, calculated with the SADIE procedure, are presented for weevil adults, larval exit holes, and larval parasitoids.

Sample period (2003)	Canola growth stage	Mean *C. obstrictus* adults per trap (S.E.)	δ (m)	I_a^1	P	$\mathfrak{J}_a^2$
16–23 June	Bud	48.67 (2.33)	3.98	4.06	<0.009	1.40
24–30 June	Early Flower	9.71 (0.91)	4.87	2.56	<0.009	1.40
1–7 July	Early Flower	0.93 (0.12)	2.83	1.15	<0.248	1.12
8–14 July	Mid Flower	21.28 (0.74)	1.39	2.11	<0.009	9.34
15–21 July	Late Flower	0.95 (0.09)	1.83	1.28	<0.145	1.06
Sample date (2003)		Mean *C. obstrictus* exit holes per pod (S.E.)				
30 July	Pod Enlargement	0. 62 (0.12)	1.07	2.73	<0.009	1.08
Sample date (2003)		Mean ectoparasitoids per pod (S.E.)				
30 July	Pod Enlargement	0.05 (0.01)	2.97	2.30	<0.009	1.25
Sample date (2003)		Mean *Necremnus tidius* per pod (S.E.)				
30 July	Pod Enlargement	0.03 (0.24)	3.66	2.53	<0.009	1.36

[1]Values of $I_a > 1$ indicate aggregation within the sample area. [2]Values of $\mathfrak{J}_a \leq 1$ indicate the presence of multiple clusters when $I_a > 1$.

approximately one-third of the distance into the grid (Figure 4a). A week later during early flower, weevil densities in all regions of the field had declined dramatically, but were still greatest in the southern region of the grid (Figure 4b). By the time of pod enlargement, adult weevil numbers were low, but remained most abundant near the southern perimeter of the grid (data not shown).

The distribution of weevil adults from traps were significantly aggregated during three of the five sampling dates ($P < 0.009$) (Table V). The value of δ increased to a maximum during early flower, then became progressively smaller over the season suggesting that the distribution patterns during the phase when insect numbers declined did not repeat, in reverse, the patterns of the initial weevil invasion. The greatest degree of aggregation occurred in bud, and the most homogeneous distribution was observed in early flower (1–7 July) (Table V).

When the *B. napus* plants were mature, larval exit holes occurred in approximately 62% of pods sampled throughout the field. Larval distributions were significantly aggregated ($P < 0.009$) (Table V), with greatest larval densities occurring along the western half of the grid (Figure 4c).

Fourteen adult specimens of weevil larval parasitoids were collected during 5 weeks of bowl trap sampling spanning crop development from bud to late flowering (Table III). *Necremnus tidius* comprised 71% of total adult parasitoids collected. Other adult parasitoids collected included *C. torvina* and *Eurytoma* sp.

A total of 728 larval parasitoids emerged from 4.6% of pods throughout the entire grid (Table V). The dominant parasitoid species consisted of *N. tidius* (67.3% of all parasitoids reared), *Chlorocytus* sp. (12.5%), and *Pteromalus* sp. (12.2%); *T. lucidus* (3.9%), *L. maculatus* (3.3%), *Lyrcus perdubius* (Girault)

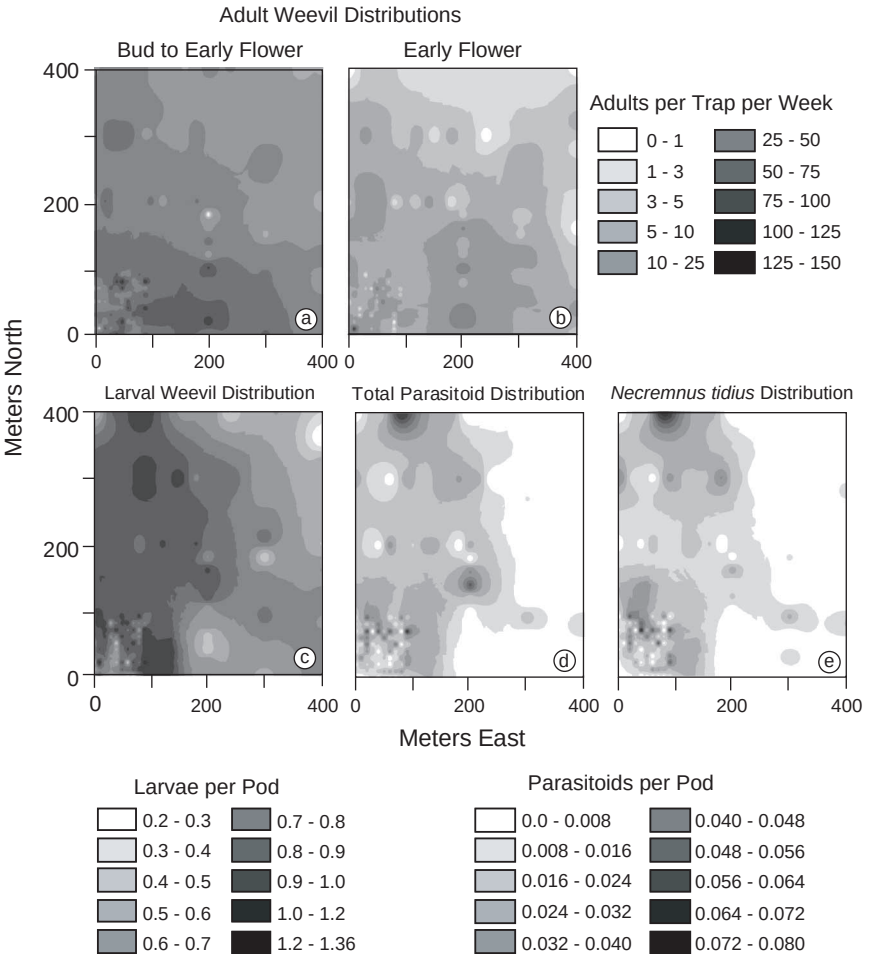

Figure 4. Distributions of *C. obstrictus* and its larval ectoparasitoids interpolated from samples collected in 2004 at 160 locations within a grid area comprising 160 000 m^2 of a commercial crop of *B. napus* near Lethbridge, Alberta. The legends give weevil adults per bowl trap sample, and weevil larvae and parasitoids per pod.

(Pteromalidae) (0.4%), and *E. albitarsus* (0.4%) also occurred in small numbers. Greatest ectoparasitoid densities were observed along the western half of the grid, which also corresponded with sites that had highest larval densities, but there were areas of high ectoparasitoid densities that did not correspond with high weevil larval densities (Figure 4d). Significant clustering was observed for both total parasitoids and the principal parasitoid, *N. tidius* ($P < 0.009$). Distributions of *N. tidius* were closely aligned spatially with those of *C. obstrictus* larvae (Figure 4c, e). Distributions of *C. obstrictus* larvae were significantly correlated with those of total parasitoids ($F = 41.59$; df $= 49.57$; $P < 0.001$; $r = 0.68$), *N. tidius* ($F = 43.85$; df $= 36.77$; $P < 0.001$; $r = 0.74$), *Chlorocytus* sp. ($F = 7.95$; df $= 110.6$; $P < 0.01$; $r = 0.26$), and *T. lucidus* ($F = 3.76$; df $= 75.32$; $P < 0.05$; $r = 0.22$), but not *Pteromalus* sp. ($F = 0.23$; df $= 122.73$; $P < 0.62$; $r = 0.04$).

Discussion

Analysis and mapping of *C. obstrictus* populations that were sampled from sites in a grid pattern over portions of commercial crops of spring canola indicated invasions along one or more fronts, most commonly during the early stages of crop development when plants were in bud to early flowering. The complex invasion patterns of cabbage seedpod weevil adults involved aggregations along field edges on different scales during colonization followed by a decline in population density throughout the crop toward the end of flowering. Patterns of weevil invasions of spring canola in western Canada were similar to those observed in winter canola in Europe, where Risbec (1952), Free and Williams (1979), and Ferguson et al. (2000) reported that crop edges tended to be more densely populated by *C. obstrictus* adults than crop centers early in weevil migrations, and that the proportion of the population at the edges diminished later in crop development as adults dispersed to form more homogeneous distributions.

In 2003 and 2004, we found that adult weevil numbers were highest early in the season, when host plants were in bud to early flower, but numbers then declined dramatically usually when canola was in mid flower. However, adult numbers often rebounded in late flower, but decreased again later in the season (Tables II, IV and V). These changes are likely a reflection of both weevil migrations and sampling bias of the bowl traps. Our bowl containers were yellow, and appeared to be quite attractive to adults early in the season, but their attractiveness may have diminished when the crop plants flowered. With the disappearance of canola petals during pod formation, the bowl samplers appeared to regain their attractiveness to weevil adults. Sweep net sampling, as used in 2002 (Table I), would not be subjected to this bias and may have more accurately reflected actual weevil densities at all stages of crop development.

In 2003 when distributions of *C. obstrictus* were compared in different canola crops, it was evident that adults were more abundant in the *B. rapa* crop than in *B. napus* (Figure 3). Plants of *B. rapa* are preferred by weevils to a greater extent than *B. napus* (Kalischuk & Dosdall 2004), which would explain these differences in weevil population densities between canola species.

The weevil distribution patterns described here are based on combined data for both sexes; however, it is possible that males and females differed in their distributions. Fox and Dosdall (2003) found that males tended to be more abundant on host plants early in the season, but that relatively equal proportions of the sexes were present later. It is unlikely, however, that sex-related differences strongly affected the distribution patterns we describe because Ferguson et al. (2000) found no evidence for differential distributions of males and females in canola in the UK.

The sampling regime used in 2002 and 2003 enabled description of distribution patterns of *C. obstrictus* and its parasitoids in comparatively small portions of the large commercial fields that are typical of western Canadian canola production systems. The primary reason for expanding the sampling regime in 2004 to encompass sampling over both small and larger scales was to determine whether distributions found in the small grids were mirrored throughout a larger portion of the field. The larger-scale sampling did not uncover major new distribution patterns not found in the smaller-scale sampling: no areas of population densities of adults, larvae, and parasitoids that were substantially greater or lower than those found in the small grid occurred in more distant regions of the crop (Figure 4). However, the larger-scale sampling showed how widespread different population densities could be. For

example, larval densities of 0.9–1.0 per pod occurred throughout approximately 30% of the area of the small grid, but analysis over the larger portion of the field indicated that this density level occurred more extensively throughout the field. The most accurate determinations of population distributions will of course be achieved by sampling over larger than smaller areas, but it is also necessary to balance the desire for extensive geographical coverage with the availability of resources for collecting, processing, and analyzing the samples.

Percentages of weevil larvae parasitized by Chalcidoidea increased over the three years of our study from only 0.1% in 2002 to 0.3% (*B. rapa*) and 0.5% (*B. napus*) in 2003, to 5.0% in 2004. Eleven larval ectoparasitoid species were collected during the three years of our study, of which *C. albifrons*, *C. torvina*, *Chlorocytus* sp., *E. albitarsis*, *L. perdubius*, and *M. bruchophagi* represent new parasitoid records for *C. obstrictus*. Most of the parasitism was attributable to only four species: *N. tidius*, *T. lucidus*, *Chlorocytus* sp., and *Pteromalus* sp., and of these, *N. tidius* was most frequently the dominant parasitoid. This differs from previous parasitoid surveys in western USA, in which *T. lucidus* and *M. moryoides* were the dominant species (Gibson et al. 2005). These levels of parasitism are considerably lower than those commonly recorded in Europe where parasitism rates typically reach about 50% (Alford et al. 1996; Ulber & Vidal 1998), but can reach 90% and can be high even when larval densities are low (Murchie & Williams 1998). The situation in western Canada appears to reflect parasitoid populations that are building over time, because no parasitism of weevil larvae was found in southern Alberta from 1998 to 2001 (Dosdall & Dolinski 2001), and incidence of parasitism in this study increased approximately 50-fold from 2002 to 2004.

Although distributions of *C. obstrictus* adults were often spatially aligned with those of their larvae, they were not coincident in all regions of the crop. Free & Williams (1979) and Ferguson et al. (2000) reported similar inconsistencies in spatial association that can be attributable to the relationship between collecting methods and female weevil oviposition behavior. Sweep net collections of adult weevils sampled along line transects (Free & Williams 1979), and specimens collected in flight intercept traps (Ferguson et al. 2000) or elevated bowl traps (present study), likely reflected weevil flight activities rather than abundance of ovipositing females. Movements of ovipositing females within the crop canopy may differ from those of males or nonovipositing females, sometimes causing distributions of adults and larvae to lack close spatial association.

Distributions of larval parasitoids were often spatially associated with high densities of *C. obstrictus* larvae; however, highest densities of parasitoids were not always coincident with high densities of weevil larvae, and some areas of high weevil larval densities were not exploited by parasitoids (Figures 3 and 4). In contrast, Ferguson et al. (1999, 2000) found a close spatial association between *C. obstrictus* and its principal parasitoid, *T. perfectus*, in European fields of *B. napus*, and concluded that the parasitoid was quite effective in dispersing throughout the crop and locating hosts. There are two possible explanations for the differences in host–parasitoid spatial alignments in Europe versus western Canada. First, from 99.5 to 95.0% of weevil larvae were nonparasitized in our studies in 2003 and 2004, respectively (Tables II, IV and V). With such an abundant resource of nonparasitized weevil larvae in the system, and comparatively few parasitoids, weevils were not likely sufficiently limiting for parasitoid distributions to be influenced by weevil larvae in a density-dependent

manner. A second possible explanation for the lack of close and consistent spatial alignment of weevil ectoparasitoids with distributions of their hosts relates to coevolution of host and parasitoids. *Ceutorhynchus obstrictus* is an invasive alien species in North America, and the parasitoid fauna recorded in our study is composed of endemic species or species, such as *N. tidius* and *T. lucidus*, that appear to be Holarctic in their distributions but not principal parasitoids of *C. obstrictus* in Europe (Gibson et al. 2005). Because host and parasitoids lack a long history of co-evolution under North American environmental conditions, host-seeking and other parasitoid behaviors would not be as well adapted as in Europe where co-occurrence of *C. obstrictus* and *T. perfectus* has been known for many years (Dmoch 1975; Lerin 1987) and likely represents a long-evolved host–parasitoid relationship.

The elevated bowl traps used in this study were not very effective for capturing adult specimens of weevil larval parasitoids because comparatively few were captured throughout the studies compared with the numbers of individuals reared from weevil hosts in pod collections (Table III). Nevertheless, it was evident that specimens of *N. tidius*, one of the dominant ectoparasitoid species in our study, invaded canola in bud and early flowering, at a time coincident with invasion of weevil adults. The synchronous invasion pattern of *C. obstrictus* and *N. tidius* in our study differs from the relationship observed between *C. obstrictus* and *T. perfectus* in crops of winter canola in Europe. Murchie et al. (1999) found that immigration of *T. perfectus* occurred approximately 4 weeks later than that of *C. obstrictus* and was synchronized with the appearance of host larvae in siliques. The comparatively early invasion of *N. tidius* in canola in bud or early flowering may indicate that the crop provides an important nutrient source for sustaining parasitoids until mating and host parasitization can occur later in the season. Early invasion could also indicate that *N. tidius* has a native host with larval development that occurs earlier in the season than that of *C. obstrictus*. However, the temporal alignment of invasions of *C. obstrictus* and *N. tidius* poses difficulties in developing an integrated management strategy for cabbage seedpod weevil in canola. Currently the recommended application time for insecticidal treatments to control *C. obstrictus* infestations in canola is at 10% flowering (Dosdall et al. 2001; Cárcamo et al. 2005), timing that would also kill some parasitoids like *N. tidius*.

The invasion pattern of *C. obstrictus* from field edges to more central regions of crops has led to investigations of trap cropping for minimizing insecticide use, but to date this approach has met with limited success in experimental plot studies (Buntin 1998; Cook et al. 2003). Trap crops in larger commercial fields have been more effective (Dosdall et al. 2004). However, the aggregated distributions of *C. obstrictus* adults later in crop development can also afford opportunities to reduce insecticide use. Our study and those of Ferguson et al. (1999, 2000) have shown that areas of high weevil densities may not occupy large portions of crops, so applying insecticide to entire fields could be environmentally and economically inappropriate. However, further studies are needed to identify the environmental and behavioral factors associated with aggregation to better predict sites most attractive to *C. obstrictus* in canola.

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