

Responses of Chalcidoidea (Hymenoptera) parasitoids to invasion of the cabbage seedpod weevil (Coleoptera: Curculionidae) in western Canada

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Abstract Invasion of the European weevil, *Ceutorhynchus obstrictus* (Marsham), was investigated through surveys of its range and population densities in Alberta and Saskatchewan from 2001 to 2005. After it was first reported in southern Alberta, *C. obstrictus* rapidly expanded its range and abundance. Our more recent surveys indicate that its northward expansion has slowed, but that it has continued to extend its range eastward to southcentral Saskatchewan. The distribution and abundance of parasitoids of *C. obstrictus* in Alberta and Saskatchewan were investigated from 2003 to 2005 by mass rearing canola pods infested with *C. obstrictus* larvae. Although weevil populations were not parasitized for several years immediately following its introduction to southern Alberta, a surprisingly diverse assemblage of Chalcidoidea parasitoids, comprising 12 species from four families, were recently reared from weevil-infested canola siliques in Alberta and Saskatchewan. The

Chalcidoidea fauna of *C. obstrictus* include species with both Nearctic and Holarctic distributions, with some species having restricted host ranges and others that are more niche than taxon-specific. These Chalcidoidea species appear to have expanded their host ranges to parasitize *C. obstrictus* in the region. Most parasitism is attributable to *Trichomalus lucidus* (Walker), *Chlorocytus* sp., and *Pteromalus* sp. (Pteromalidae), and *Necremnus tidius* (Walker) (Eulophidae). Parasitism levels varied considerably over the three years of this study. From 2003 to 2005 increases in parasitism occurred among all four of the species dominating the parasitoid fauna of *C. obstrictus*, but greater increases were observed for *Chlorocytus* sp. and *Pteromalus* sp. than for *T. lucidus*. Parasitoid species have sometimes caused substantial levels of host mortality, although current levels are usually less than 15% for all species combined and so are not sufficient to control weevil populations. Implementing a classical biological control program for *C. obstrictus* by reconstructing its European natural enemy complex is being considered, but it is still uncertain whether parasitism levels by native Chalcidoidea will increase over time since considerable year-to-year variation has been found. Parasitism levels of *C. obstrictus* should therefore continue to be monitored to assess whether a classical biological control program should be implemented.

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Introduction

The cabbage seedpod weevil, *Ceutorhynchus obstrictus* (Marsham) (Coleoptera: Curculionidae), is native to Europe and is a serious pest of brassicaceous seed crops, especially canola (*Brassica napus* L. and *Brassica rapa* L.) and brown mustard (*Brassica juncea* (L.) Czern). It was first discovered in North America in the southwestern coastal region of British Columbia in 1931 (McLeod 1962). During the next 25 years it was recorded from several additional localities in the Pacific Northwest including Washington (Baker 1936), Idaho (Walz 1957), Oregon (Crowell 1952), and California (Hagen 1946), but it was not discovered in Alberta until 1995 (Dosdall et al. 2001). It has also been found in eastern North America, in Maryland (Anonymous 1977), Tennessee (Boyd and Lentz 1994), and Georgia (Buntin et al. 1995), and most recently in Québec (Brodeur et al. 2001) and Ontario (Mason et al. 2004). Based on analysis of variations in the mitochondrial DNA COI gene among geographically distinct populations, Laffin et al. (2005) concluded that North American populations of *C. obstrictus* likely resulted from at least two separate introductions. An introduction to western North America appears to have occurred from source populations in western or northern Europe, and a second introduction was made to northeastern North America in Québec from source populations in northern Europe.

The cabbage seedpod weevil is univoltine. Sexually immature adults diapause during winter in protected areas such as beneath leaf litter in shelterbelts, and emerge in spring when soil temperatures increase to approximately 15°C (Ulmer and Dosdall 2006). After feeding on early-flowering brassicaceous plants, adults invade canola crops in the bud to early flowering stages where mating and additional feeding occur (Fox and Dosdall 2003; Dosdall and Moisey 2004). After flowering and as soon as pistil enlargement occurs on canola racemes, a mated female can excavate a cavity in an immature pod with her mouthparts, and may deposit a white, cylindrical egg into the puncture. Eggs hatch in approximately one week, and each larva consumes about 5–6 seeds during three instars (Dmoch 1965; Dosdall and McFarlane 2004). Mature larvae chew exit holes in the walls of the siliques, drop to the soil surface, burrow in, and pupate. New generation adults emerge

approximately 10 days later, and feed on canola or other brassicaceous plants until late in the season when temperatures decline and they migrate to overwintering sites (Bonnemaison 1957; Dmoch 1965; Dosdall and Moisey 2004).

The invasion of western Canada by the cabbage seedpod weevil has garnered considerable attention within the agricultural community because of its economic impact on canola crops. *Ceutorhynchus obstrictus* can cause severe economic losses in canola at several stages of crop development. When overwintered adults invade crops primarily in the bud to early-flowering stages, they feed on buds and often destroy their vascular tissue causing “bud-blasting” (Dosdall et al. 2001). Plants with severe bud-blasting produce racemes with few pods, and may even fail to flower when weevil densities are high. Feeding by larvae within siliques causes seed losses of approximately 18–20% (Dmoch 1965). If environmental conditions are humid after larvae bore exit holes, the pods can be invaded by fungal pathogens that damage additional seeds within the pods. When new generation adults emerge late in the season, they feed upon seeds within green pods to build up fat stores for overwintering, causing further reductions in crop yield and quality (Buntin et al. 1995; Dosdall et al. 2001).

The rapid range expansions that have occurred historically in North America indicate that *C. obstrictus* has a remarkable ability to disperse and establish new populations. Surveys conducted in western Canada from 1997 to 2000 inclusive to monitor geographical changes in its distribution and abundance indicated rapid dispersal of *C. obstrictus* from southern Alberta to the north and east at a rate of approximately 55 km per year (Dosdall et al. 2002). When meteorological data from 193 sites across Alberta, Saskatchewan, and Manitoba were analyzed with data on the biological requirements of *C. obstrictus* using the CLIMEX[®] model, it was predicted that the distribution of the species would eventually encompass the entire region of canola production in western Canada (Dosdall et al. 2002). However, several species of Chalcidoidea parasitoids were recently found to attack larval populations of the weevil (Gibson et al. 2005; Dosdall et al. 2006). The current study was undertaken to monitor the distribution and abundance of the cabbage seedpod weevil in western Canada since earlier surveys established its initial dispersal patterns, and to

determine its ecological impact on populations of the Chalcidoidea parasitoids.

Materials and methods

Weevil geographical distribution patterns, 2001–2005

In 2001–2005, respectively, 258, 167, 419, 420, and 396 canola fields were sampled from 25 June to 10 July, when most canola crops in southern and central Alberta and Saskatchewan were in full flower (Growth Stages 4.2–4.3 of Harper and Berkenkamp 1975). A single sample, consisting of 25, 180° sweeps with a standard insect sweep net, was collected from each field. Sampling commenced at the field edge and progressed inward over a distance of about 30 m. Fields were sampled in an area extending from Edmonton, AB (53°34' N; 113°31' W) and North Battleford, SK (52°46' N; 108°15' W) south to the United States border, east to Swift Current (50°17' N; 107°41' W) in southcentral Saskatchewan, and west to the limits of canola production in the foothills of the Rocky Mountains in Alberta. The geographical location of each field was determined using high resolution maps or hand-held global positioning system units (Magellan Trailblazer XL[®] Personal Satellite Navigation System). Entire sweep net contents were either stored in plastic bags and frozen, or were preserved in jars containing 70% ethanol until they were sorted, and *C. obstrictus* specimens counted and recorded.

The numbers of *C. obstrictus* adults collected at each site were used to generate surface maps of cabbage seedpod weevil abundance with the Potential Mapping routine in SPANS GIS[™] v. 5.31 for OS/2 (PCI Geomatics). This procedure calculates a value for square cells which form the map as a weighted average of the values of the point data from the survey. A classification scheme was used to group cells according to the calculated weighted averages.

Geographical distribution and abundance of Chalcidoidea parasitoids

The distribution of Chalcidoidea parasitoids and their levels of parasitism of *C. obstrictus* larvae were assessed within infested areas of southern Alberta and Saskatchewan from 2003–2005. Commercial canola

crops were sampled from late July to mid August each year when the majority of plants in the fields were in the pod ripening stage of development and seeds in the lower pods were translucent to green (Growth Stages 5.1–5.2 of Harper and Berkenkamp [1975]). A total of 147, 202, and 165 fields were sampled in 2003–2005, respectively. A single sample of approximately 450–850 canola siliques was collected from each field. Pods were collected randomly from canola racemes by sampling plants first at the field edges, and progressing inward over a distance of about 35–50 m. The geographical location of each field was determined using high resolution maps or hand-held global positioning system units as described previously.

Pod samples were taken to the laboratory and placed into cardboard rearing containers, as described by Dodsall et al. (2006). Boxes were sealed with tape to prevent escape of *C. obstrictus* larvae or parasitoids, and were maintained under continuous light at room temperature for six weeks until all parasitoids had emerged. The boxes were then opened, and pod samples were examined under a stereoscopic microscope for the presence of any additional parasitoid adults that had not moved to the plastic collecting vials.

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 (CNC), Ottawa, ON, Canada.

Pods from 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 uniformly rounded along their margins (Dodsall et al. 2006). Although it is possible that some weevil and parasitoid larvae died before producing exit holes, our determinations of parasitism levels assumed no larval mortality. For each site, the level of parasitism was determined by dividing the number of weevil larvae parasitized by a particular species of Chalcidoidea by the total number of weevil hosts in the sample. The total number of specimens of a particular parasitoid species was determined by subtracting the number of individuals of that species in the sample from the total number of parasitoids that emerged, including both the species in question and other species. Samples were discarded when total numbers of emerged adult

parasitoids did not equal total parasitoid exit holes from the pods.

Parasitism levels of Chalcidoidea at each site were used to generate surface maps of abundance using ArcMap[®] Geographical Information Systems software with Spatial Analyst Extension (ESRI Services, Redlands, CA). The process examines point (site) data in relation to values from its nearest neighbor to estimate how values decline (decay) with distance from the point in question. The “interpolate to raster function” was used with the “inverse distance weighted option”. A fixed search radius of 500 km and an output cell size of 1 km were set. For each year, the spatial distributions of Chalcidoidea adults were presented as contour maps of parasitism levels of *C. obstrictus* larvae.

Results

Weevil geographical distribution patterns

In 2001, *C. obstrictus* was widespread throughout fields of flowering canola in southern Alberta but uncommon in southern Saskatchewan (Fig. 1). The northern limit of its range was near Red Deer, AB (52°11' N; 113°54' W) where densities averaged only about 0.1 adult per sweep; however, further south near Calgary densities increased to nearly 0.4 per sweep. Greatest population densities were recorded in fields between Lethbridge (49°38' N; 112°48' W) and Medicine Hat, AB (50°1' N; 110°43' W), where mean densities exceeded 3.6 per sweep and in some fields exceeded 11.0 weevils per sweep.

In 2002, adult weevil densities in southern Alberta declined somewhat to the east of Calgary; however, mean densities throughout large areas of canola cropland from Calgary to Lethbridge and east to the Saskatchewan border remained at approximately 1.0–4.0 adults per sweep (Fig. 1). Greatest densities of 8.4 per sweep were observed near Lethbridge. In Saskatchewan, weevil densities increased relative to those observed in 2001, with as many as 1.0 per sweep found in some fields west of Swift Current.

Infestations of *C. obstrictus* declined substantially in Alberta from 2002 to 2003, with few adults collected in fields from Red Deer south to Lethbridge (Fig. 1). The most densely populated fields spanned an area extending from Lethbridge to Medicine Hat where populations were occasionally as high as 1.0 per sweep, but often

only 0.2 per sweep. In Saskatchewan, the most densely populated fields were near its western border, with densities as high as 3.0 per sweep recorded.

In 2004, infestations of the cabbage seedpod weevil in canola fields from Lethbridge north to Calgary increased relative to those found in 2003, with most fields having densities of approximately 0.3 per sweep (Fig. 1). As in previous years, the highest densities occurred from Lethbridge to Medicine Hat where mean densities ranged from 0.4 to 1.0 per sweep. In Saskatchewan, weevil abundance in 2004 was similar to that observed in 2003.

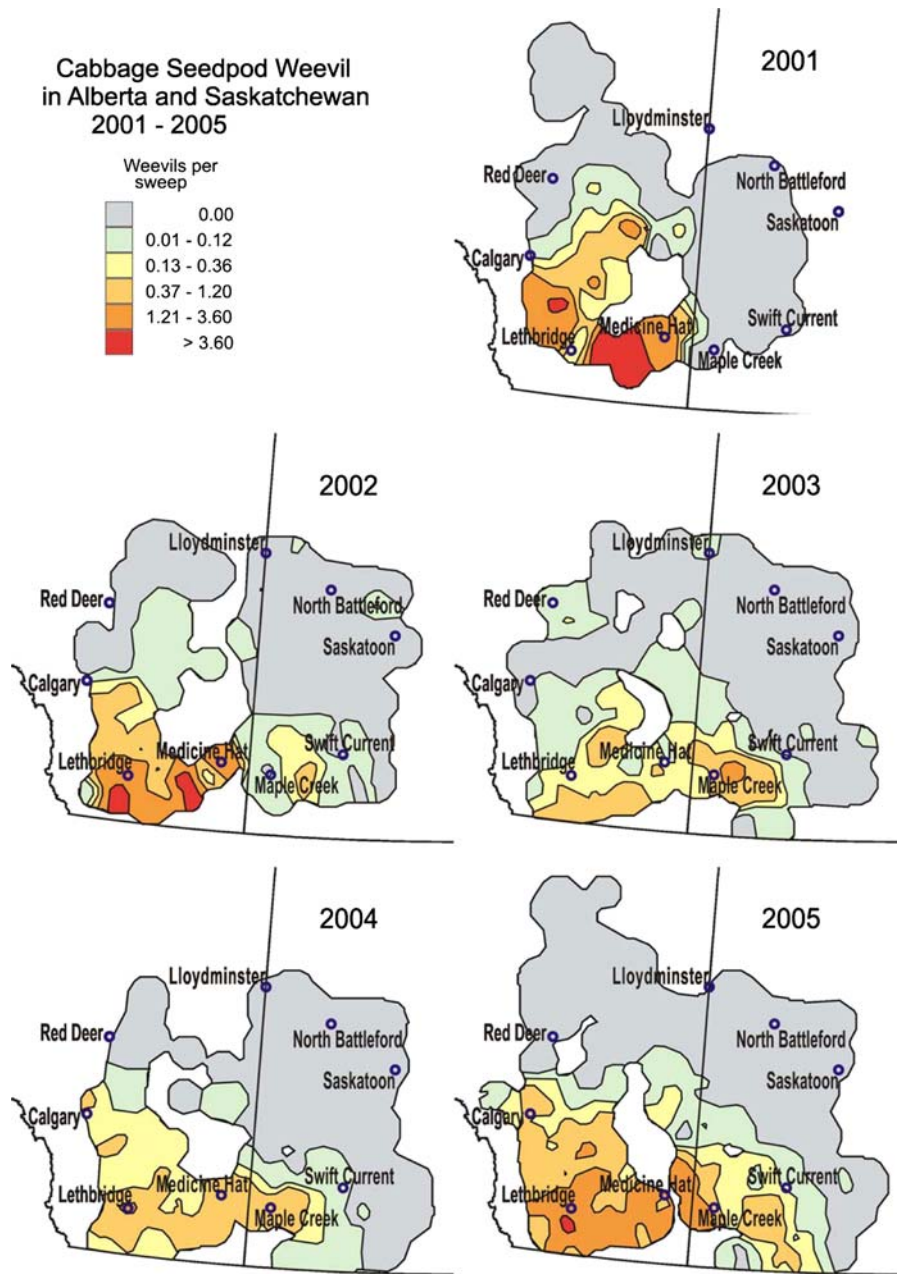
Infestations of *C. obstrictus* increased substantially from 2004 to 2005, especially throughout southern Saskatchewan (Fig. 1). From Calgary south to Lethbridge and Medicine Hat, infestations ranged from approximately 0.4 to 3.6 per sweep. In southwestern Saskatchewan, densities of 3.6 per sweep were recorded near Maple Creek (49°55' N; 109°29' W), and vast areas of canola cropland from Swift Current to the U.S.A. border had populations of approximately 0.4 per sweep.

Distribution and abundance of Chalcidoidea parasitoids

In total, 12 species of Chalcidoidea representing four families were reared from canola pods infested with *C. obstrictus* during the three years of this study. The species reared were *Necremnus tidius* (Walker) and *Euderus albitarsus* (Zetterstedt) (Eulophidae), *Trichomalus lucidus* (Walker), *Chlorocytyus* sp., *Pteromalus* sp., *Mesopolobus moryoides* Gibson, *Lycrus maculatus* (Gahan), *Lycrus incertus* (Ashmead), and *Catolaccus aeneoviridis* (Girault) (Pteromalidae), *Conura torvina* (Cresson) and *Conura albifrons* (Walsh) (Chalcididae), and *Eurytoma tylodermatis* Ashmead (Eurytomidae). Of these, *N. tidius*, *T. lucidus*, *Chlorocytyus* sp., and *Pteromalus* sp. were the species most frequently reared, collectively comprising 53.8, 95.5, and 80.6% of all parasitoids reared in 2003–2005, respectively (Table 1). Of the remaining species, most were collected each year in low numbers, with the exception of *L. incertus* which was collected only in 2005 and *E. tylodermatis* which was collected only in 2004.

In 2003, *T. lucidus* was reared from five canola fields ($n = 147$) infested with *C. obstrictus* larvae north of Lethbridge and west of Medicine Hat in

Fig. 1 Distribution and abundance of *C. obstrictus* in canola in Alberta and Saskatchewan, Canada, from 2001 to 2005. Maps were developed from field survey data (25 sweep net samples per field) using SPANS®



Alberta, but it was not found in Saskatchewan (Fig. 2). The maximum levels of parasitism of *C. obstrictus* larvae by *T. lucidus* were 2–3%. In 2004, *T. lucidus* was found in seven fields ($n = 202$) in southern Alberta spanning a range extending from approximately 75 km north of the U.S.A. border to near Calgary. Parasitism levels ranged from 0–7%. In 2005, *T. lucidus* was reared from 14 sites ($n = 165$) throughout southern Alberta and from six fields in

southwestern Saskatchewan. Its range in Alberta extended from the foothills of the Rocky Mountains, east to Medicine Hat and south to the U.S.A. border. In Saskatchewan, the species was collected most commonly in fields north of Swift Current. Its maximum parasitism level reached 2–3% (Fig. 2).

Chlorocytus sp. emerged from pod collections made in three canola fields infested with *C. obstrictus* larvae in Alberta in 2003, and from collections made

Table 1 Species composition of Chalcidoidea parasitoids of *Ceutorhynchus obstrictus* reared from collections of siliques of *Brassica napus* and *B. rapa* from southern Alberta and Saskatchewan in 2003 to 2005

Parasitoid species	Species composition (%)		
	2003	2004	2005
Pteromalidae			
<i>Trichomalus lucidus</i>	8.1	4.8	12.0
<i>Chlorocyclus</i> sp.	6.7	7.5	26.9
<i>Pteromalus</i> sp.	13.8	8.2	13.8
<i>Mesopolobus moryoides</i>	2.4	0.2	1.1
<i>Lyrus maculatus</i>	0.0	0.9	3.2
<i>Lyrus incertus</i>	0.0	0.0	0.4
<i>Catolaccus aenoviridis</i>	13.8	0.2	1.1
Eulophidae			
<i>Necremnus tidius</i>	25.2	75.0	27.9
<i>Euderus albitarsus</i>	0.8	1.1	1.1
Chalcididae			
<i>Conura torvina</i>	16.2	0.5	10.4
<i>Conura albifrons</i>	13.0	0.9	2.1
Eurytomidae			
<i>Eurytoma tylodermatis</i>	0.0	0.7	0.0

in four fields in Saskatchewan (Fig. 3). The maximum parasitism level was 1.5%. In 2004, *Chlorocyclus* sp. emerged from 12 fields throughout southern Alberta and from six fields in Saskatchewan, spanning a range extending from Lethbridge north nearly to Calgary and east to Medicine Hat and Swift Current. Parasitism levels ranged from 0–6%. In 2005, *Chlorocyclus* sp. was reared from 16 sites throughout southern Alberta and from 18 fields in southwestern Saskatchewan. Its range extended from the foothills of the Rocky Mountains, east to Swift Current, and south to the U.S.A. border. Its maximum parasitism level reached 10% (Fig. 3).

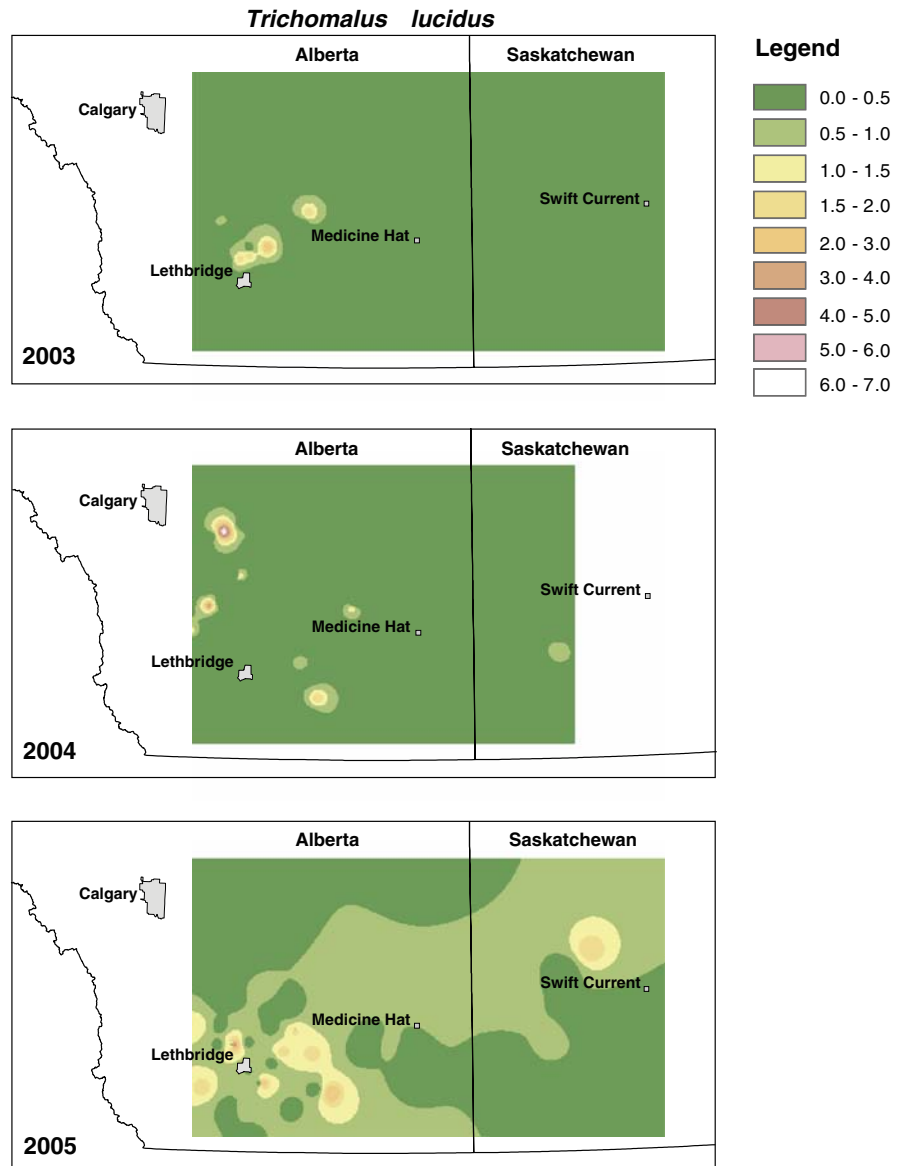
Specimens of *Pteromalus* sp. were reared from eight canola fields infested with *C. obstrictus* larvae in Alberta and from two fields in Saskatchewan in 2003 (Fig. 4). The range of *Pteromalus* sp. extended from the U.S.A. border north to near Medicine Hat and Swift Current, but its densities were low in all fields with maximum parasitism levels of 1.5%. In 2004, *Pteromalus* sp. was reared from canola pods collected in eight fields in Alberta and six in Saskatchewan. In Alberta it occurred in fields near Lethbridge and Medicine Hat, but it was more abundant throughout southern Saskatchewan where

its maximum parasitism level was 7%. In 2005 the abundance and range of *Pteromalus* sp. increased in Saskatchewan, but not in Alberta. Specimens were reared from eight fields in Alberta in 2005 and from 17 fields in southern Saskatchewan. Maximum parasitism levels were 9% in Saskatchewan and 2% in Alberta (Fig. 4).

Discussion

Our surveys to monitor geographical changes in the distribution and abundance of the cabbage seedpod weevil indicate that dispersal rate of the species has slowed considerably since the years immediately following its discovery in southern Alberta. Dossall et al. (2002) reported that from 1997–2000 *C. obstrictus* extended its range northward and eastward at a rate of approximately 55 km per year. In the outbreak of 2000, hundreds of thousands of hectares throughout southern Alberta harbored weevil densities that equaled or exceeded the economic threshold for insecticidal application (Dossall et al. 2001). Since then, populations have never met or exceeded 2000 densities, and our surveys have indicated considerable elasticity in how the species range has varied over time. The most dramatic change in weevil population densities occurred from 2002–2003 when the geographical area with populations that equaled or exceeded the economic threshold density in canola (3.0–4.0 per sweep) declined to zero throughout all of southern Alberta. One likely explanation for this weevil population decline between years is related to lack of moisture. During 2001 and 2002, precipitation levels throughout much of western Canada and all of southern Alberta and Saskatchewan were substantially lower than long-term normal values; in fact, precipitation levels at several sites within this region were the lowest ever recorded (Wheaton et al. 2005). Drought could have severely affected *C. obstrictus* populations in several ways. Larval development and survival within siliques could have been reduced because canola host plants were unable to absorb and translocate sufficient quantities of water from the soil. In addition, drought can leave the soil surface dry, crusted, and hard, making it difficult for final instars that have exited from siliques to burrow below the soil surface for pupation. Lengthening the time required by larvae to burrow beneath the soil surface

Fig. 2 Changes from 2003 to 2005 in the distribution and level of parasitism of *T. lucidus* on *C. obstrictus*. The legend indicates the percentages of weevil-infested canola pods parasitized by *T. lucidus* in southern Alberta and Saskatchewan

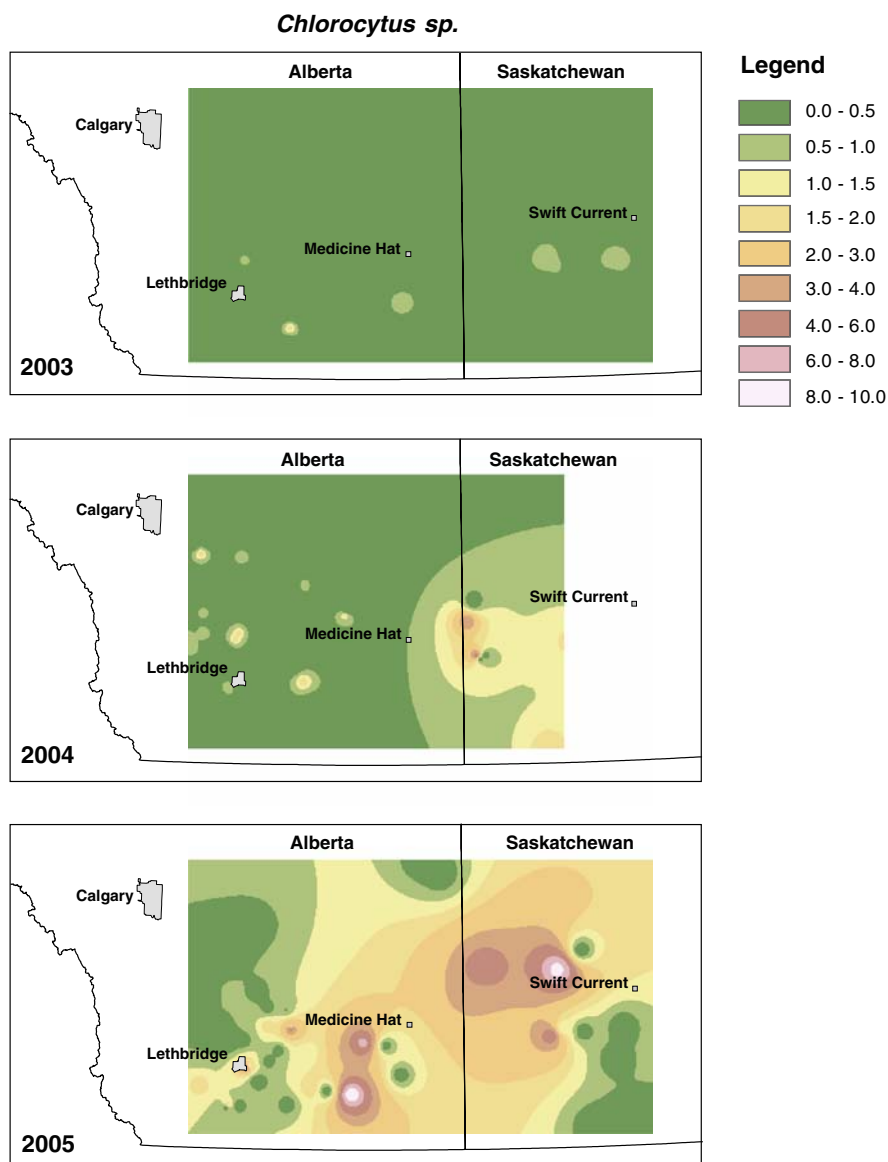


would expose them to greater potential mortality from opportunistic carnivores like species of Carabidae (Coleoptera). Finally, drought conditions would have reduced the availability of host plants for feeding by new generation adults in late summer prior to their migration to overwintering sites. With fewer late-season hosts available, it would be more difficult for weevils to build up the fat stores needed for survival during winter, resulting in lower populations in the following year.

Although the northward expansion of the geographical range of *C. obstrictus* has been minimal

from 2001 to 2005, the weevil has extended its range eastward to currently include much of southern Saskatchewan. Since 2005, *C. obstrictus* continued to spread east in Saskatchewan and was collected in a sample near Moose Jaw (50°20' N; 105°30' W) in 2006 (Olfert et al. 2007). The species range is expected to eventually encompass southern Manitoba because there are no geographical or biotic barriers to hamper its eastward dispersal. Once in Manitoba, however, it is probable that crop losses from weevil infestation will exceed those experienced in southern Alberta and Saskatchewan because ecoclimatic index

Fig. 3 Changes from 2003 to 2005 in the distribution and level of parasitism of *Chlorocytus* sp. on *C. obstrictus*. The legend indicates the percentages of weevil-infested canola pods parasitized by *Chlorocytus* sp. in southern Alberta and Saskatchewan

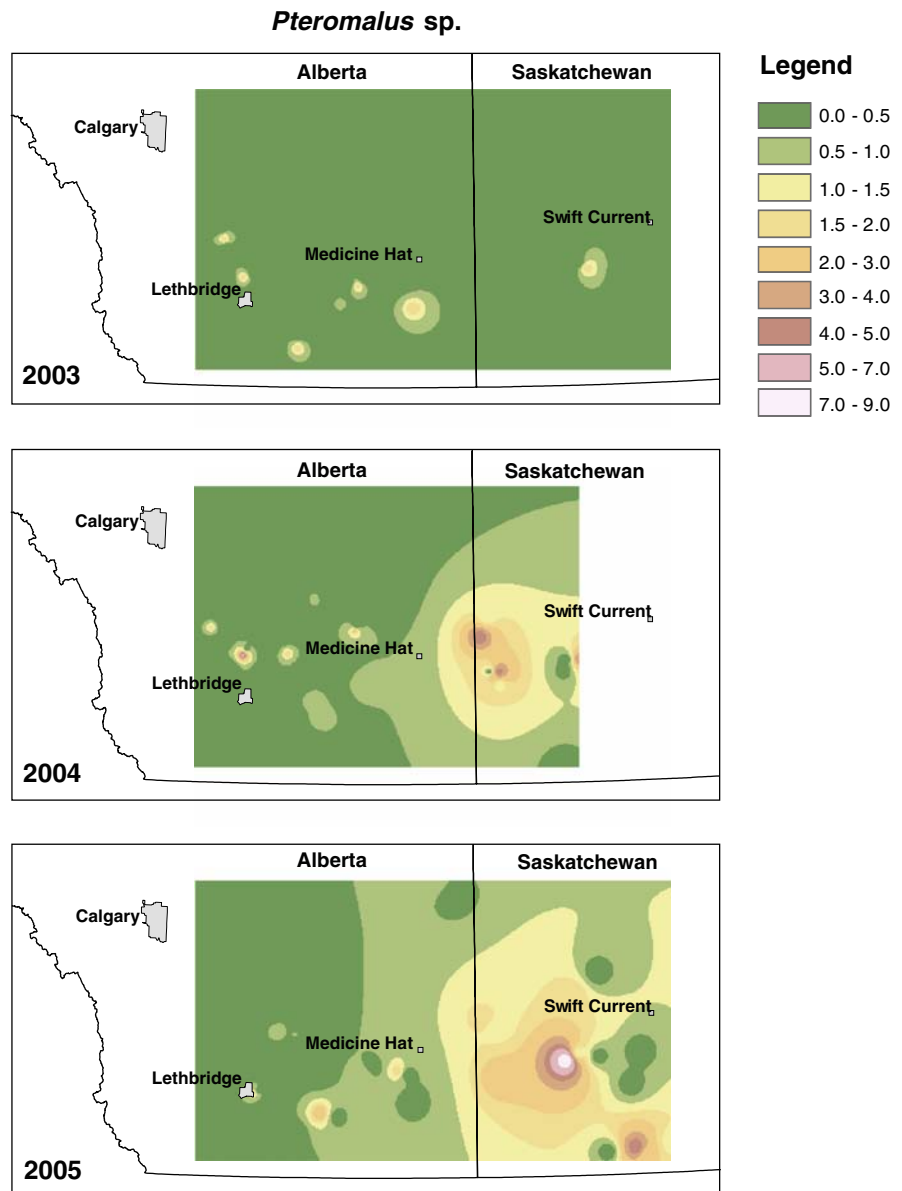


values developed with the CLIMEX[®] model were considerably higher for southern Manitoba than for other regions of western Canada (Dossall et al. 2002). In addition, changes in environmental conditions (particularly temperature and precipitation) throughout western Canada associated with climate change scenarios are predicted to result in a northerly expansion of the geographical range of *C. obstrictus* by 400–600 km (Olfert and Weiss 2006).

The economic costs of the invasion of western Canada by *C. obstrictus* have been substantial. Although a central problem in deriving accurate and comprehensive assessments of damage caused by

invasive species is the paucity of available data to systematically track direct and indirect, market and non-market costs for species (Colautti et al. 2006), data for the impact of the cabbage seedpod weevil on canola producers can at least be estimated broadly based on costs incurred to apply insecticide on cropland. On this basis alone, it is estimated that a total of 180,000 ha of canola and brown mustard crops were sprayed with insecticide to reduce *C. obstrictus* infestations from 1999 to 2005 inclusive, at an estimated cost of \$4.5 million (CAD) (Western Committee on Crop Pests 2001, 2003, 2004; Dossall unpublished data). This cost is an underestimate of total economic loss

Fig. 4 Changes from 2003 to 2005 in the distribution and level of parasitism of *Pteromalus* sp. on *C. obstrictus*. The legend indicates the percentages of weevil-infested canola pods parasitized by *Pteromalus* sp. in southern Alberta and Saskatchewan



because not all farmers sprayed insecticide when their crops had weevil populations at or near the economic threshold, and crops with densities below the threshold still incurred some damage.

Dosdall and Dolinski (2001) reported that many canola pod samples were dissected in 1999 and 2000 and examined for the presence of larval parasitoids, but none were discovered. Fox et al. (2004) found that the braconid endoparasitoid, *Microctonus melanopus* (Ruthe), occasionally infested adult weevils in southern Alberta, but its occurrence was rare. Parasitoids

were first discovered attacking *C. obstrictus* larvae in southern Alberta in 2001 (Dosdall unpublished data). A low incidence of larval parasitism of *C. obstrictus* was reported in 2002 in a field near Lethbridge, and both the numbers of parasitoid species recorded and the incidence of parasitism increased during 2003 and 2004 (Dosdall et al. 2006). Parasitism rates increased from 0.1 to 5.0% during the three-year period from 2002 to 2004 (Dosdall et al. 2006). Our current study involved sampling many additional sites across a broad geographic scale and confirmed that parasitism of

Table 2 Species of Chalcidoidea reared from canola siliques in western Canada, their known distributions and host records

Chalcidoidea species	Distribution	Host(s)	Citations
Pteromalidae			
<i>Trichomalus lucidus</i> (Walker)	Holarctic	Coleoptera: Curculionidae	
		<i>Ceutorhynchus obstrictus</i> (Marsham)	Gibson et al. (2005), Dossall et al. (2006), Present study
		<i>Ceutorhynchus neglectus</i> Blatchley	Dossall et al. (2007)
		<i>Ceutorhynchus alliariae</i> Brisout	Kuhlmann et al. (2000)
		<i>Ceutorhynchus pallidactylus</i> (Marsham)	Kuhlmann et al. (2000)
		<i>Ceutorhynchus roberti</i> Gyllenhal	Klander (2001)
		<i>Ceutorhynchus scrobicollis</i> Nerenheimer & Wagner	Muller et al. (2003)
		<i>Microplontus rugulosus</i> (Herbst)	Muller et al. (2004)
		Coleoptera: Chrysomelidae—1 species	
<i>Chlorocytus</i> sp.	Unknown	Coleoptera: Curculionidae	
		<i>C. obstrictus</i>	Dossall et al. (2006), Present study
<i>Pteromalus</i> sp.	Unknown	Coleoptera: Curculionidae	
		<i>C. obstrictus</i>	Dossall et al. (2006), Present study
<i>Lyrus maculatus</i> (Gahan)	Nearctic	Coleoptera: Curculionidae	
		<i>C. obstrictus</i>	Gibson et al. (2006b), Dossall et al. (2006), Present study
		<i>Desmoris fulvus</i> LeConte	
		<i>Rhinocyllus conicus</i> Froehlich	
		<i>Smicronyx fulvus</i> LeConte	
		<i>Miccotrogus picirostris</i> (Fabricius)	
<i>Lyrus perdubius</i> (Girault)	Nearctic	Coleoptera: Curculionidae	
		<i>C. obstrictus</i>	Dossall et al. (2006)
		<i>Anthonomus grandis</i> Boheman	
		<i>Anthonomus musculus</i> Say	
		<i>Anthonomus nubiloides</i> Fall	
		<i>Anthonomus signatus</i> Say	
		<i>Smicronyx tychoides</i> LeConte	
<i>Lyrus incertus</i> (Ashmead)	Nearctic	Coleoptera: Curculionidae	
		<i>C. obstrictus</i>	Gibson et al. (2006b), Present study
		<i>Anthonomus aeneolus</i> Dietz	
		<i>Anthonomus albopilosus</i> Dietz	
		<i>Anthonomus aphanostephi</i> Pierce	
		<i>Anthonomus disjunctus</i> LeConte	
		<i>Anthonomus eugenii</i> Cano	
		<i>Anthonomus fulvus</i> LeConte	
		<i>A. grandis</i>	
		<i>Anthonomus nigrinus</i> Boheman	
		<i>A. signatus</i>	

Table 2 continued

Chalcidoidea species	Distribution	Host(s)	Citations
		<i>Auleutes tenuipes</i> (LeConte)	
		<i>Baris</i> sp.	
		<i>Baris cuneipennis</i> Casey	
		<i>Chalcodermus aenus</i> Boheman	
		<i>Chalcodermus inaequicollis</i> Horn	
		<i>D. fulvus</i>	
		<i>Eutinobothrus brasiliensis</i> (Hambleton)	
		<i>Rhynchaenus pallicornis</i> (Say)	
		<i>Tachypterellus quadrigibbus</i> Say	
		Coleoptera: Dryophthoridae—2 species	
		Lepidoptera: Gelechiidae—2 species	
		Coleoptera: Apionidae—5 species	
		Coleoptera: Bruchidae—4 species	
		Diptera: 1 species in 1 family	
		Hymenoptera: 4 species in 1 family	
<i>Mesopolobus moryoides</i> Gibson	Nearctic	Coleoptera: Curculionidae <i>C. obstructus</i>	Gibson et al. (2005, 2006a, b), Dossdall et al. (2006), Present study
<i>Mesopolobus bruchophagi</i> Gahan	Nearctic	Coleoptera: Curculionidae <i>C. obstructus</i> Coleoptera: Bruchidae—1 species Diptera: 2 species in 2 families Hymenoptera: 9 species in 3 families	Dossdall et al. (2006)
<i>Catolaccus aeneoviridis</i> (Girault)	Nearctic	Coleoptera: Curculionidae <i>C. obstructus</i> <i>Hypera postica</i> (Gyllenhal) <i>Microlarinus lypriformis</i> (Wollaston) Lepidoptera: 36 species in 13 families Hymenoptera: 26 species in 3 families	Present study
<i>Stenomalina gracilis</i> (Walker)	Palaearctic	Coleoptera: Curculionidae <i>C. obstructus</i> <i>Ceutorhynchus napi</i> (Gyllenhal) <i>C. pallidactyllus</i> <i>C. roberti</i> <i>Hadroplontus litura</i> (Fabricius) <i>Microplontus edentulus</i> (Schultze)	Gibson et al. (2006a), Gillespie et al. (2006), Muller et al. (2004), Haye et al. (2005) Klukowski and Kelm (2000) Kuhlmann and Mason (2002) Kuhlmann and Mason (2002) Kuhlmann and Mason (2002) Kuhlmann and Mason (2002)

Table 2 continued

Chalcidoidea species	Distribution	Host(s)	Citations
		<i>M. rugulosus</i> Lepidoptera: 1 species in 1 family Hymenoptera: 1 species in 1 family Diptera: 15 species in 5 families Eulophidae	Muller et al. (2004)
<i>Necremnus tidius</i> (Walker)	Holarctic	Coleoptera: Curculionidae <i>C. obstructus</i>	Gibson et al. (2005), Gibson et al. (2006b), Gillespie et al. (2006), Dossall et al. (2006), Dossall et al. (2007), Present study
		<i>Ceutorhynchus floralis</i> (Paykull) <i>Ceutorhynchus</i> sp. Coleoptera: Apionidae—1 species Coleoptera: Chrysomelidae—2 species Diptera: 2 species in 2 families Lepidoptera: 2 species in 1 family	Kuhlmann and Mason (2002) Gomez and Zamora (1994)
<i>Euderus albitarsis</i> (Zetterstedt)	Holarctic	Coleoptera: Curculionidae <i>C. obstructus</i>	Dossall et al. (2006), Present study
		Coleoptera: Cerambycidae—1 species Coleoptera: Scolytidae—1 species Diptera: 3 species in 2 families Lepidoptera: 16 species in 7 families Hemiptera: 1 species in 1 family Hymenoptera: 2 species in 2 families	
Chalcididae			
<i>Conura albifrons</i> (Walsh)	Nearctic	Coleoptera: Curculionidae <i>C. obstructus</i>	Dossall et al. (2006), Present study
		<i>Hypera eximia</i> (LeConte) <i>Hympera paludicola</i> Warner <i>H. postica</i> Coleoptera: Buprestidae—1 species Coleoptera: Chrysomelidae—7 species Diptera: 1 species in 1 family Lepidoptera: 36 species in 11 families Hymenoptera: 12 species in 2 families	
<i>Conura torvina</i> (Cresson) ^a	Nearctic	Coleoptera: Curculionidae <i>C. obstructus</i>	Gibson et al. (2006b), Dossall et al. (2006), Present study
		<i>H. postica</i> Coleoptera: Chrysomelidae—1 species Lepidoptera: 2 species in 2 families Hymenoptera: 4 species in 2 families	

Table 2 continued

Chalcidoidea species	Distribution	Host(s)	Citations
Eurytomidae			
<i>Eurytoma tylodermatis</i> Ashmead	Nearctic	Coleoptera: Curculionidae <i>C. obstrictus</i> <i>Anthonomus consors</i> (Dietz) <i>Anthonomus disjunctus</i> LeConte <i>Anthonomus grandis</i> (Boheman) <i>Anthonomus heterothecae</i> Pierce <i>Anthonomus quadrigibbus</i> Say <i>Anthonomus squamosus</i> LeConte <i>Anthonomus vestitus</i> (Boheman) <i>Baris</i> sp. <i>Chalcodermus aeneus</i> (Boheman) <i>Conotrachelus elegans</i> (Say) <i>Cylindrocopturus adpersus</i> (LeConte) <i>Cylindrocopturus longulus</i> (LeConte) <i>Lixus musculus</i> Say <i>Lixus scrobicollis</i> Boheman <i>Macrorhoptus sphaeralciae</i> (Pierce) <i>Orthoris crotchii</i> (LeConte) <i>Smicraulax tuberculatus</i> (Pierce) <i>Trichobaris texana</i> LeConte <i>Trichobaris trinotata</i> (Say) <i>Tyloderma foveolatum</i> (Say) Coleoptera: Anthribidae—1 species Coleoptera: Apionidae—1 species Coleoptera: Bruchidae—5 species Diptera: 1 species in 1 family Lepidoptera: 12 species in 5 families Hymenoptera: 7 species in 4 families	Gibson et al. (2006b), Present study

Host species and citations documenting records are provided only for Ceutorhynchinae species; other host taxa listed are summarized from Noyes (2003)

^a The host list given for *C. torvina* by Noyes (2003) is inaccurate because this species was consistently misidentified as *Conura side* (Walker) prior to Delvare (1992) and most of the 86 species (in 24 families of 3 orders) listed as hosts of *C. side* by Noyes (2003) likely refer to *C. torvina* (Gibson et al. 2006a)

C. obstrictus populations was dominated by larval ectoparasitoid species, most of which appear to be native to North America. The larval parasitoid species, comprising *T. lucidus*, *Chlorocytyus* sp., *Pteromalus* sp., and *N. tidius*, were identified as principal components of the parasitoid fauna of *C. obstrictus* as early as 2002 (Dosdall et al. 2006), and they remain as the key parasitoids attacking this species.

Of the 12 Chalcidoidea species reared from siliques infested with *C. obstrictus*, only *C. aeneo-viridis* has not been reported previously as reared from canola. This species is most commonly reared as a hyperparasitoid of Lepidoptera cocoons through species of Braconidae and Ichneumonidae (Hymenoptera), but it has also been reared as a hyperparasitoid of the alfalfa weevil, *Hypera postica*

(Gyllenhal) (Coleoptera: Curculionidae), as has *C. albifrons* (Putler 1966; Rethwisch and Manglitz 1986) and *C. torvina* (Rethwisch and Manglitz 1986). Rearings of parasitoids from mass collections of canola siliques can be associated with introduction of contaminant insect hosts, and in this study larvae of the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), occurred occasionally in some pod collections. Specimens of *C. aeneoviridis*, *C. albifrons*, and *C. torvina* reared in this study are likely hyperparasitoids of *C. obstrictus* or perhaps hyperparasitoids of *P. xylostella*.

The Chalcidoidea parasitoid fauna of *C. obstrictus* in western Canada consists of some species with restricted host ranges, like *T. lucidus* which but for a single exception is only known from Ceutorhynchinae weevil hosts (Table 2). The only reported non-ceutorhynchine host of *T. lucidus* is the cabbage stem flea beetle, *Psylliodes chrysocephala* (L.) (Chrysomelidae), another pest of canola in Europe (Vidal 1997). Other species, like the presumed hyperparasitoids and *E. albitarsis*, *E. tylodermatidis*, and *L. maculatus* are known from a wider range of hosts from several insect orders and families (Table 2). These species are probably more niche- than taxon-specific. The invasion of western Canadian canola agroecosystems by *C. obstrictus* has evidently provided abundant populations of weevil larvae in siliques that enabled parasitoid species to switch from their native host insects to exploit this new resource.

The Chalcidoidea fauna of *C. obstrictus* includes species with both Nearctic and Holarctic distributions, but in general, the hyperparasitoids are Nearctic and the primary parasitoids are Holarctic (Table 2). It is uncertain whether the Holarctic distributions of *T. lucidus* and *N. tidius* are natural or whether they were inadvertently introduced from Europe with unknown host insects. Neither *T. lucidus* nor *N. tidius* is a principal parasitoid of *C. obstrictus* in Europe (Williams 2003). *Ceutorhynchus obstrictus* is the only known host of *M. moryoides*, a species currently known only from the Nearctic region. *Mesopolobus moryoides* could be a native species with an unknown native host, but it also remains possible that it is an unrecognized adventive European species. The origins of the *Chlorocytus* and *Pteromalus* species will remain unknown until species determinations can be made. Europe and North

America both have a rich fauna of *Pteromalus*, whereas *Chlorocytus* is much more speciose in Europe than in North America (Graham 1969). The taxonomic status of *Chlorocytus* sp. and *Pteromalus* sp. should be clarified to determine whether these species are native, naturally Holarctic, or one or both are introduced European species.

The levels of parasitism of *T. lucidus*, *Chlorocytus* sp., and *Pteromalus* sp. on *C. obstrictus* varied considerably over the three years of this study. In 2003, all three species were rarely collected, probably because the weevil population was reduced from drought during the preceding years. In 2004, however, populations of both *Pteromalus* sp. and *Chlorocytus* sp. increased, especially in western Saskatchewan, reaching parasitism levels of approximately 7% in some sites. Further population increases were observed in 2005. Increased levels of parasitism by *Pteromalus* sp. occurred in eastern Alberta and western Saskatchewan, and an even greater increase in the level of parasitism of *Chlorocytus* sp. occurred throughout both provinces. Increases in parasitism levels of *T. lucidus* also occurred, but not to the same magnitude as for *Chlorocytus* sp. and *Pteromalus* sp. These observations concur with those reported by Dossall et al. (2007) for *N. tidius*, who found that low parasitism levels in 2003 increased in 2004 and 2005 for this species. The large fluctuations both in the levels of parasitism of *C. obstrictus* and the dominance of the species comprising the parasitoid fauna could represent effects of competition among Chalcidoidea for *C. obstrictus* larvae.

Invasion of western Canada by *C. obstrictus* has followed the generalized steps for invasive species outlined by Sakai et al. (2001) where initial transport and establishment in a new area (in this case southwestern British Columbia) was followed by a lag period of population build-up before further dispersal to new habitats (first throughout the Pacific Northwest, then to eastern United States, and later northward to Canada). As with other successful invaders, the cabbage seedpod weevil possesses several traits like small body size, rapid time to maturity, and a high intrinsic growth rate that facilitated establishment of viable, self-sustaining populations (Crawley 1986; Lawton and Brown 1986; Dossall et al. 2001; Dossall and Moisey 2004). But perhaps most importantly, its invasion was successful because it could occupy an

“empty niche” (Mack 1996; Levine and D’Antonio 1999). When *C. obstrictus* dispersed to southern Alberta and Saskatchewan it encountered a vast resource of many billions of siliques of *B. napus* and *B. rapa* that was largely unexploited by other herbivores and that provided a nutritious, high energy food resource for its larvae where they were protected from surface-dwelling predators. This study and those of Gibson et al. (2005, 2006a) and Dossdall et al. (2006) documented a surprisingly diverse fauna of Chalcidoidea species that have responded to the invasion of *C. obstrictus*, so that these parasitoids have now become, in turn, invasive of canola agroecosystems infested with *C. obstrictus* larvae. Along with their hosts, a lag period of low parasitoid population densities (Dossdall and Dolinski 2001) was followed by years of increased numbers (Dossdall et al. 2006), presumably as their populations expanded both numerically and geographically. It is doubtful, however, that the community structure in these systems has yet stabilized. For instance, the fauna of hyperparasitoid species, like *C. aenoviridis* and *Conura* spp., may now perhaps increase to exploit the parasitoids.

Implementing a classical biological control program for the cabbage seedpod weevil could enable partial reconstruction of the natural enemy complex of this insect, and so prevent or reduce its continued dispersal across western Canada. The ability of introduced natural enemies to persist in the environment, to reproduce, and to spread are important advantages of the biological control approach (Greathead 1986). A first attempt at classical biological control of *C. obstrictus* in North America involved releases of three species of pteromalid larval ectoparasitoids in southwestern British Columbia in 1949 (Gibson et al. 2006a; Gillespie et al. 2006). Examination of voucher specimens from the releases determined that the species introduced included *Mesopolobus morys* (Walker), *Trichomalus perfectus* (Walker), and *Stenomalina gracilis* (Walker) (Pteromalidae) (Gibson et al. 2006a). An extensive series of surveys conducted near the original release sites found that of these, only *S. gracilis* appears to have established (Gibson et al. 2006a; Gillespie et al. 2006). However, *M. morys* and *T. perfectus* are considered to be the most effective of the released parasitoids for controlling *C. obstrictus* in Europe (Williams 2003), and therefore hold the greatest potential for facilitating sustainable biological control

of the weevil in North America. Gillespie et al. (2006) proposed that re-releases of one or both of *T. perfectus* and *M. morys* should be considered after taking into account the host ranges of these species. But the question arises of whether additional releases of European parasitoids are warranted when several species of native natural enemies already attack the weevil. Results reported here and those of Dossdall et al. (2006, 2007) indicate that the present parasitoid fauna has sometimes caused substantial levels of parasitism, but current parasitism levels (usually less than 15% for all species combined) are not sufficiently high to adequately control the weevil population. It is not clear whether parasitism levels are still likely to increase over time, since the current situation has shown considerable year-to-year variation (Figs. 2, 3, 4). Parasitism levels should therefore continue to be monitored, along with the dispersal biology of the *C. obstrictus* host, to assess whether a classical biological control program should be implemented.

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