Reproductive Biology of *Ceutorhynchus obstrictus* (Coleoptera: Curculionidae) on Wild and Cultivated Brassicaceae in Southern Alberta[1]

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Abstract Mated and gravid status were assessed for early-season populations of *Ceutorhynchus obstrictus* (Marsham) (Coleoptera: Curculionidae) on wild and cultivated Brassicaceae in southern Alberta, Canada. Mated female *C. obstrictus* were found in the first samples examined (22 May 2001). At least 84% of *C. obstrictus* dispersing to wild host sites up to 23 May 2001 (captured using yellow pan traps) were males. Females of *C. obstrictus* with at least one egg in the lateral oviducts were first encountered on 6, 8 and 18 June 2001 on *Descurainia sophia* (L.) Webb, *Sinapis arvensis* L., and *Cardaria* spp., (Brassicaceae), respectively. Females on *S. arvensis*, a true host with pods that can sustain larvae, had more robust ovary development than females on *Cardaria* spp. and *D. sophia*, food hosts with pods that cannot sustain larvae. The most fecund sample (*n* = 30) from *S. arvensis* was collected on 24 June 2001 when 80% of females had a mean of 7.2 ± 2.7 (±SD) eggs in the lateral oviducts. The most fecund full samples (*n* = 30) from *Cardaria* spp. and *D. sophia* had 6.7% and 40.0%, respectively, of females with at least one egg in the lateral oviducts, and an overall maximum of four eggs in the lateral oviducts per female. There is no apparent reproductive advantage to *C. obstrictus* in developing eggs on early-season food hosts, although food hosts likely play an important role in sustaining *C. obstrictus* until true hosts are encountered. Although gravid status was high in females on *S. arvensis,* this host supported relatively few larvae. The highest infestation level of *C. obstrictus* per sample of *S. arvensis* pods in 2001 was 13.5% (*n* = 891 pods) based on the presence of eggs, larvae, and exit holes. A sample of volunteer *Brassica napus* L. (Brassicaceae) pods (*n* = 100) had a 77% infestation level. The apparent discrepancy between the relatively robust gravid status of *C. obstrictus* on *S. arvensis,* and low pod infestation, was explained as a combination of factors that likely include an inherent unsuitability of wild *S. arvensis* pods for *C. obstrictus.* However, given the wide distribution of *S. arvensis* in southern Alberta, this wild true host would likely maintain low populations of *C. obstrictus* in the absence of volunteer and spring-seeded cultivated hosts.

Key Words Reproduction, *Ceutorhynchus obstrictus*, cabbage seedpod weevil, Brassicaceae

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The cabbage seedpod weevil, *Ceutorhynchus obstrictus* (Marsham) (Coleoptera: Curculionidae) (Colonnelli 1993), is an indigenous pest of cultivated Brassicaceae in Europe that has become well established in North America since it was first discov-

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ered in British Columbia in 1931 (Baker 1936, Brodeur et al. 2001, Cárcamo et al. 2001, McLeod 1953). *Ceutorhynchus obstrictus* was first encountered in Alberta near Lethbridge in 1995, and its prairie range now includes most of southern Alberta and southeastern Saskatchewan, where it has caused substantial economic losses in canola crops, *Brassica napus* L. and *B. rapa* L. (Brassicaceae) (Dosdall et al. 2002).

Ceutorhynchus obstrictus adults overwinter and emerge in spring to feed on Brassicaceae, invading crops in the bud and flowering stages. Eggs are formed only after a period of post-diapause feeding by females. Eggs are deposited in pods where the larvae feed on developing seed causing substantial reductions in yield. Last-instar larvae chew exit holes through the pods and drop to the ground to pupate. After a short pupation period the new generation of univoltine adults emerges (Dmoch 1965a, Dosdall et al. 2001, Free and Williams 1979, Ni et al. 1990). New generation adults can also contribute to crop damage by feeding on late-maturing pods prior to overwintering in leaf litter or soil (Buntin et al. 1995). Females have two pairs of ovarioles and a single spermatheca. Each pair of ovarioles merges to form a lateral oviduct, and the two lateral oviducts merge to form a main oviduct (Bonnemaison 1957, Heymons 1922).

Although *C. obstrictus* adults feed on a range of wild and cultivated Brassicaceae, the larvae only complete development in the pods of a limited number of host-plant species. Dmoch (1965a) used the term "food host" to refer to host-plant species that sustain only adult *C. obstrictus,* and the term "true host" to refer to host-plant species that sustain both adults and larvae. Dmoch's distinction between food hosts and true hosts has relevance to the study of *C. obstrictus* migrating into new ecoregions. For example, migration into a region that contains only food host species could not result in the establishment of an indigenous population of *C. obstrictus.* Understanding the role of wild true hosts in maintaining populations of *C. obstrictus,* especially where cultivated true hosts are not grown, would be useful to support or refute the need to control wild true hosts. Dmoch (1965a) documented four species of wild Brassicaceae that are true hosts. One of these, *Sinapis arvensis* L. (Brassicaceae), is widely distributed in southern Alberta (Frankton and Mulligan 1970).

Nothing is known about the reproductive biology of *C. obstrictus* in the mixed grassland ecoregion of its new prairie range in western Canada. In the current study the mated and gravid status (reproductive status) of female *C. obstrictus* found on food hosts *Cardaria* spp. and *Descurainia sophia* (L.) Webb (Dmoch 1965a), and true hosts *S. arvensis* and *B. napus,* were investigated. *Descurainia sophia* was selected for study because its flower color and pod morphology resemble the true hosts studied, and because it is abundant across the prairies. *Cardaria* spp. were selected for study because they flower early in the season. The objective of the study was to determine the role early-season wild host plants play in the reproductive success of *C. obstrictus* invading *B. napus* crops, and the potential for the true wild host *S. arvensis* to maintain populations of *C. obstrictus.*

Materials and Methods

Sampling sites. Eighteen sites were used over the study period of 2000 and 2001; one *Cardaria* spp. site, four *D. sophia* sites, six *S. arvensis* sites, and seven *B. napus* sites. Sites were numbered chronologically for each plant species, reflecting site recruitment over the 2 yr study period, except for two sites cited alphabetically that were used only for *C. obstrictus* gender ratio determination (*B. napus* Sites A and B).

Sites were within a 15-km radius of Lethbridge, Alberta (49°27′N, 112°39′W) except for *D. sophia* Sites 2 and 4 which were 55 and 45 km east of Lethbridge, respectively, *B. napus* Site-1 which was 25 km northwest of Lethbridge, and *B. napus* Sites 2 and 3 which were 75 km east of Lethbridge. *Brassica napus* Sites 1 to 3 were commercial crops and Sites 4 and 5 were stands of volunteer plants from the previous season's crop. All sites were dryland except for *S. arvensis* Sites 4 and 5 which were in irrigated fields.

Cardaria spp. Site-1 was an open, ungrazed grassland with numerous patches of *Cardaria* spp., *D. sophia* Site-3 was a strip of fallow bordered on the north side by an avenue of mature trees, and *S. arvensis* Site-1 was a shallow depression bordered by a track and fallow. Wild host sites were relatively free of, and isolated from, other stands of Brassicaceae, however *S. arvensis* Site-1 was proximal to areas of *Thlaspi arvense* L. (Brassicaceae). Sites treated with insecticides were excluded from the study.

Abundance and gender ratio. *Ceutorhynchus obstrictus* migrations into sites and larvae dropping from host plants were monitored using 29.8 × 23.5 cm yellow pan traps half filled with a 50:50 mixture of water and propylene glycol. Except for *B. napus* Site-1 and *B. napus* Sites A and B, no more than two pans were used per site, and pans were removed when collections indicated that substantial numbers of *C. obstrictus* were invading the sites. Plants were tied over pans for larval drop surveillance. Abundance of *C. obstrictus* was also assessed by sweeping a 37-cm diam net through a 180° arc in the host plant canopy.

Plots were set aside within sites exclusively for *C. obstrictus* abundance evaluations in 2001, and *C. obstrictus* used to assess reproductive status were captured throughout the remainder of each site. A total of 19 abundance samples (n = 5 sweeps per sample) of *C. obstrictus* in plots within sites was taken starting 22 May, 23 May, 31 May and 19 June 2001 for the *Cardaria* spp. Site-1, *D. sophia* Site-3, *S. arvensis* Site-1 and *B. napus* Site-5, respectively.

Emergence of new generation *C. obstrictus* from pupation was monitored using pyramidal screened cages with a 1.0 m^2 open base. Host plants were cut to ground level and removed before cages were established, and *C. obstrictus* that emerged were removed through a sleeve in the cage. Gender of *C. obstrictus* captured to assess abundance was determined by dissection.

Host plant stage and density. Host plant densities and growth stages were documented for plots used to assess *C. obstrictus* abundance. Plant density was determined by counting plants within a wire hoop placed randomly within a plot. Plant growth stage descriptions were modified from Harper and Berkenkamp (1975).

Reproductive status. In 2000 gravid status was evaluated using *C. obstrictus* preserved in Kahle's solution (Borror et al. 1981) and stored in 70% ethanol. Only chorionated oocytes (eggs) were counted. No distinction was made between eggs found in the ovarioles and eggs found in the lateral oviducts.

In 2001 dissections were made in physiological saline to assess both mated and gravid status. Each specimen was isolated when captured to prevent mating between collection and dissection. Mated status was scored by isolating and severing the spermatheca in physiological saline using minuten pins. Preparations were viewed at 80× magnification using a dissecting microscope. Mated status was documented as negative or positive; however, a small proportion of *C. obstrictus* with only a trace of sperm in the spermatheca was scored as negative (quantified below). Gravid status was documented by recording the most advanced stage of the developing oocytes in the ovary, or the location of eggs in the ovary, using the following criteria modified from Bonnemaison (1957): A, length of oocyte no greater than its width; B, length of oocyte greater than its width; C, oocyte significantly swollen with dense yolk; egg in ovariole; egg descended into lateral oviducts. Samples of 100 *C. obstrictus* were collected for reproductive status assessment, and when 30 female *C. obstrictus* were dissected per sample, the remaining specimens were dissected only for gender determination. Samples of less than 100 *C. obstrictus* documented toward the end of the 2001 study period were the result of extensive sweeps throughout the sample site. A small proportion of female *C. obstrictus* that were parasitized were excluded from the reproductive status assessment data (Bonnemaison 1957), but were included in the gender ratio data.

Larval infestation of host-plant pods. Host-plant pods were collected to document *C. obstrictus* infestation levels. Ripe pods were stored dry for counts of larval exit holes, and maturing pods were stored in 70% ethanol for counts of larval exit holes, larvae and eggs. Contents of dry pods with exit holes, and pods stored in ethanol, were examined using a dissecting microscope.

Results

Abundance and gender ratio. In 2000 *C. obstrictus* abundance at *B. napus* Site-1 (Table 1) decreased from a mean of 4.8 per sweep on 29 June to zero by the

Table 1. *Ceutorhynchus obstrictus* abundance in *Brassica napus* (Site-1) in 2000

	Sample technique	$\bar{x}$/Sample unit	*n*	%♂
Date	# Sweeps	Adults		
6/29	50	4.8	238	38.2
7/11	50	2.5	127	34.6
7/17	50	0.6	32	34.4
7/21	300	0.2	56	0.0
8/01	50	0.0	1	—
8/11	30	5.3	158	55.1
8/18	30	2.1	62	58.1
	# Pans	New generation larvae		
7/26	3	22.3	67	—
8/01	3	29.3	88	—
8/11	3	7.0	21	—
	# Cages	New generation adults		
8/11	3	29.0	87	50.6
8/15	3	15.3	46	50.0
8/18	3	6.0	18	50.0

Pans and cages were established on 21 July and 1 August, respectively.

end of July. By 11 August abundance increased to a mean of 5.3 per sweep due to the emergence of new generation adults. Last-instar larvae were abundant in pan trap collections from 26 July to 1 August. The proportion of male *C. obstrictus* per sample was consistently less than 40% from 29 June until males expired in the third week of July. The proportion of new generation *C. obstrictus* that were males was slightly greater than 50% for sweep net samples and consistently 50% for emergence cage samples.

Pan trap data for *C. obstrictus* invading wild host sites in 2001 (Table 2) revealed little migration at mean daily maximum air temperatures of up to 18°C during May. Migration increased substantially when mean daily maximum air temperatures reached 26°C. Mean numbers of *C. obstrictus* per pan on days of high migration were greatest at *D. sophia* Site-3 > *S. arvensis* Site-1 > *Cardaria* spp. Site-1. The proportion of male *C. obstrictus* ranged from 84.0% to 91.0% for pans sampled at sites above on 14 and 23 May (n = 100 *C. obstrictus,* except May 23 for *Cardaria* spp., n = 63). The proportion of male *C. obstrictus* in pan traps at *B. napus* Site-A in 2000 was 41.2% on 30 May and 30.0% on 6 June. The proportion of male *C. obstrictus* at *B. napus* Site-B in 2001 was 77.2% on 31 May and 66.4% on 7 June (n = 250 *C. obstrictus* per sample date). Additional data on gender ratio are presented in Tables 1, 3 and 4.

In 2001 the mean numbers of *C. obstrictus* per sweep (n = 5 continuous sweeps) on 31 May were 6.4 at *Cardaria* spp. Site-1, 11.8 at *D. sophia* Site-3, and 14.6 at *S. arvensis* Site-1 (highest numbers documented per site). By 19 June mean numbers of *C. obstrictus* per sweep declined at these sites to 1.2 on *Cardaria* spp., 2.0 on *D. sophia* and 5.2 on *S. arvensis.* The highest mean number *C. obstrictus* per sweep documented at *B. napus* Site-5 was 49.2. Sampling ceased at this site on 9 July when the site was cleared. Sampling was terminated at the *D. sophia, Cardaria* spp. and *S. arvensis* sites on 22 June, 27 June and 3 July, respectively, when *C. obstrictus* were scarce and host plants had matured. The highest number of *C. obstrictus* documented in a single sweep was n = 128 at *B. napus* Site-4 on 13 June. Other Curculionidae were encountered in sweeps, e.g., *Ceutorhynchus neglectus* Blatchley (Coleoptera: Curculionidae), a minor pest of *B. napus* that is primarily associated with *D. sophia* (Dosdall et al. 1999); however, numbers were negligible in relation to those of *C. obstrictus.*

Table 2. Mean numbers of *Ceutorhynchus obstrictus* per pan trap at wild host sites in 2001

Date	*Cardaria* spp. site-1	*D. sophia site-3*	*S. arvensis site-1*	MDTH*	MHWS**
5/11	4.0	6.0	0.0	15.0	10.9
5/14	156.0	352.0	198.5	27.5	20.2
5/17	1.0	5.0	1.5	17.5	31.4
5/20	0.0	6.0	0.0	18.0	30.1
5/23	67.5	384.5	176.5	26.0	12.9

Pans were established on 8 May. Data are means of 2 pans.

* Mean daily temperature high in °C for the 2 days preceding the sample collection date.

** Mean hourly wind speed in km/h for the 2 days preceding the sample collection date (weather data extrapolated from records provided by S. McGinn, Agriculture and Agri-Food Canada, Lethbridge).

Host plant stage and density. In 2001 *Cardaria* spp. Site-1 plants were up to 13 cm tall and inflorescence was visible by 8 May. Plants were up to 35 cm tall with 5% of flowers open by 23 May. The first pods formed and the site was in full flower by 31 May. Early pods were ripening and 50% of flowering was completed by 8 June. Flowering was completed on most plants by 19 June when seed heads were a mix of green and brown pods.

Descurainia sophia Site-3 plants were up to 36 cm tall and 25% of plants were in flower by 8 May. Pods started to form and 75% of plants were in flower by 14 May. Plants were up to 74 cm tall by 23 May. Early pods were ripening and flowering was completed on 35% of plants by 8 June. Flowering was completed on most plants and pods were ripening on large plants and shattering on small plants by 19 June.

Sinapis arvensis Site-1 plants were rosettes with up to six leaves by 14 May, and were in the stem elongation stage by 23 May. The first pods were forming and plants were up to 28 cm tall by 31 May. Plants were in full flower with many pods swelling by 19 June. Flowering was completed and seeds in the lower pods were brown by 3 July. *Sinapis arvensis* plant shape and size varied considerably from site to site presumably as a result of moisture availability; plants grew up to 112 cm tall at Site-5.

Brassica napus Site-5 plants were in full flower and pods were forming by 15 June. Lower pods had green seed and flowering was completed by 9 July.

For the 2001 sites above there was a mean of 47.7 ± 22.5 (± SD) *Cardaria* spp. stems, 25.0 ± 17.3 *D. sophia* plants, 1.7 ± 0.6 *S. arvensis* plants, and 63.0 ± 18.3 *B. napus* plants per 0.25 m^2 ($n = 3$).

Reproductive status. Gravid status assessments of *C. obstrictus* in 2000 (Table 3) indicate that the order of plant host suitability for egg development was *B. napus* > *S. arvensis* > *D. sophia* > *Cardaria* spp. The highest proportion of female *C. obstrictus* per sample to develop an egg on a food host was 7.7%, with no more than

Table 3. Gravid status of *Ceutorhynchus obstrictus* on food hosts and true hosts in 2000

Host type	Host plant	Date (site)	%♀* ≥ 1 egg	x̄ Eggs ± SD (range)	%♂
Food host	*Cardaria* spp.	6/02 (1)	0.0	—	92.0
		6/12 (1)	0.0	—	48.5
	D. sophia	6/12 (1)	2.0	1.0 —	57.3
		6/16 (2)	7.7	2.0 ± 1.4 (1-3)	75.0
		6/23 (1)	6.7	2.0 ± 0.0	61.5
True host	*S. arvensis*	6/02 (1)	0.0	—	64.8
		6/12 (1)	14.0	2.6 ± 1.8 (1-6)	61.8
		6/26 (1)	26.0	3.5 ± 1.5 (1-6)	64.9
	B. napus	6/09 (2)	82.0	6.5 ± 2.9 (1-15)	41.9
		6/21 (1)	40.0	2.4 ± 1.2 (1-5)	54.5
		6/29 (1)	76.0	3.8 ± 1.6 (1-8)	33.3
		7/11 (1)	100.0	8.8 ± 3.5 (1-18)	32.4
		7/21 (1)	100.0	7.9 ± 2.6 (4-14)	0.0

* $n = 50$ female *C. obstrictus* except 2 June (*Cardaria* spp.), 16 June and 23 June, $n = 17$, 26 and 45, respectively.

three eggs per female (eggs in ovarioles and lateral oviducts). Up to 18 eggs were found per female on *B. napus,* and all females on this host had at least one egg by 11 July. An increase in the proportion of gravid *C. obstrictus* over time on *B. napus* Site-1 (Table 3) reflects reproductive development in synchrony with the development of the plant host. The *B. napus* Site-2 crop (Table 3) developed earlier than Site-1 because it was seeded earlier and received more moisture. New generation *C. obstrictus* females ($n = 23$) collected from emergence cages on 15 August had tropharia that directly abutted the lateral oviducts, i.e., there was no evidence of the vittelarium. Tropharia appeared translucent in many cases. Two females had vestigial tropharia and one female lacked development of the lateral oviducts. All new-generation females were unmated.

In 2001 *C. obstrictus* with at least one egg in the lateral oviducts were first encountered on 6, 8 and 18 June for *D. sophia* Site-3, *S. arvensis* Site-1, and *Cardaria* spp. Site-1, respectively. The first sampling of *C. obstrictus* on *B. napus* (Site-3) revealed 66.7% of females with at least one egg in the lateral oviducts by 6 June (Table 4). The mean number of eggs in the lateral oviducts was consistently low for *C. obstrictus* collected on the food hosts *Cardaria* spp. and *D. sophia;* however, the proportion of females that developed an egg was substantially higher on *D. sophia* than on *Cardaria* spp. Furthermore, the proportion of *C. obstrictus* females with an egg in the lateral oviducts was consistently higher for *B. napus* than for *S. arvensis* (Table 4). *Ceutorhynchus obstrictus* females with no egg in the lateral oviducts from *S. arvensis* sites on 3 and 10 July (Table 4) had stretched lateral oviducts, a sign that ovulation had likely occurred. Eggs found in dissections were always situated in the ovarioles or lateral oviducts, i.e., no eggs were found in the main oviduct.

The proportion of *C. obstrictus* females mated on food hosts (Table 4) was well below full mated potential (90 to 100%) throughout the study period, despite a significant proportion of females being mated early in the season. Full mated potential was also never realized for *C. obstrictus* females on *S. arvensis;* however, mated status was proportionally much higher than for food hosts. Full-mated potential was realized at *B. napus* Site-5.

In 2001 a total of nine female *C. obstrictus* had ovaries that lacked any sign of oocytes (i.e., the vitellarium was nonexistent); these were found only in early samples. A total of 14 female *C. obstrictus* had only a trace of sperm in the spermatheca. These cases were scored as unmated because we believed they were not functionally reproductive. The agreement in proportions of mated females and females with eggs in the lateral oviducts is not necessarily an indication that the latter category were all mated, e.g., a total of four of the females that had an egg in the lateral oviducts on 13 June, 20 June and 25 June (Table 4) were unmated.

Larval infestation of host-plant pods. On 14 July 2000, 3.4% of *S. arvensis* (Site-1) pods were infested by *C. obstrictus* ($n = 1{,}633$ pods from 25 plants) based on the presence of eggs, larvae, and exit holes. There was a total of two eggs, 28 larvae, and 26 exit holes. Fifty per cent of larvae were third instars and 35.7% were second instars.

The 2001 evaluation of *C. obstrictus* infestation through pod dissection revealed high infestations of *B. napus* pods relative to *S. arvensis* pods (Table 5). The proportions of infested *B. napus* pods ($n = 77$) with 2, 3 and 4 infestations per pod were 32.5%, 14.3% and 2.6%, respectively. *Sinapis arvensis* plants ($n = 15$ per site) were collected for exit hole evaluation at Sites 1 and 3 on 31 July; 2.9% ($n = 1{,}125$) of pods from Site-1 and 2.4% ($n = 3{,}394$) of pods from Site-3 had at least one exit hole. Fifteen

Table 4. Reproductive status of *Ceutorhynchus obstrictus* on food hosts and true hosts in 2001. Maximum oocyte stage was documented according to the most advanced stage of the developing oocytes in the ovary or, when chorionated oocytes (eggs) were present, by the location of the eggs in the ovary: A, length of oocyte no greater than its width; B, length of oocyte greater than its width; C, oocyte significantly swollen with dense yolk; egg in ovariole; egg descended into lateral oviduct

				Maximum oocyte stage (%♀)					
Date (site)	%♂*	#♀	%♀ Mated	A	B	C	Egg in ovariole	Egg in oviduct	$\bar{x}$ Eggs ± SD (range) in oviducts
Cardaria spp.–food host									
5/22 (1)	78.0	22	31.8	100.0	0.0	0.0	0.0	0.0	—
5/28 (1)	78.0	22	31.8	63.6	31.8	4.5	0.0	0.0	—
6/04 (1)	87.0	13	61.5	0.0	100.0	0.0	0.0	0.0	—
6/11 (1)	54.0	30	26.7	13.3	80.0	6.7	0.0	0.0	—
6/18 (1)	61.0	30	53.3	20.0	66.7	3.3	3.3	6.7	2.5 ± 0.7 (2-3)
6/27 (1)	50.0	13	—	0.0	46.2	23.1	0.0	30.8	2.3 ± 1.3 (1-4)
D. sophia–food host									
5/23 (3)	89.0	11	18.2	100.0	0.0	0.0	0.0	0.0	—
5/30 (3)	74.5	28	46.4	53.6	46.4	0.0	0.0	0.0	—
6/06 (3)	67.0	30	30.0	3.3	70.0	13.3	0.0	13.3	2.0 ± 0.8 (1-3)
6/07 (4)	64.0	30	33.3	3.3	46.7	13.3	10.0	26.7	2.0 ± 0.9 (1-4)
6/14 (3)	59.0	30	36.7	10.0	60.0	10.0	6.7	13.3	2.0 ± 1.4 (1-4)
6/19 (3)	52.0	30	36.7	10.0	33.3	10.0	6.7	40.0	2.0 ± 1.2 (1-4)
6/22 (3)	66.7	13	—	0.0	46.2	23.1	7.7	23.1	1.5 ± 0.7 (1-2)
S. arvensis–true host									
5/31 (1)	90.0	10	40.0	40.0	50.0	10.0	0.0	0.0	—
6/08 (1)	66.0	30	26.7	46.7	50.0	0.0	0.0	3.3	2.0 —
6/12 (2)	77.0	23	78.3	4.3	57.0	17.4	17.4	4.3	1.0 —
6/18 (3)	74.3	25	72.0	0.0	36.0	0.0	24.0	40.0	2.7 ± 1.3 (1-5)
6/24 (4)	63.0	30	—	0.0	13.3	3.3	3.3	80.0	7.2 ± 2.7 (2-13)
6/25 (1)	59.0	30	83.3	3.3	20.0	13.3	6.7	56.7	4.5 ± 2.3 (1-8)
6/26 (5)	60.0	30	70.0	3.3	20.0	6.7	16.7	53.3	4.6 ± 2.2 (1-8)
7/03 (1)	57.9	8	75.0	0.0	25.0	0.0	62.5	12.5	1.0 —
7/06 (5)	61.0	30	—	0.0	13.3	3.3	6.7	76.7	4.7 ± 3.3 (1-12)
7/10 (6)	73.7	5	60.0	0.0	20.0	20.0	20.0	40.0	4.0 ± 0.0
B. napus–true host									
6/06 (3)	69.0	30	70.0	0.0	16.7	10.0	6.7	66.7	3.7 ± 2.1 (1-8)
6/13 (4)	87.0	13	69.2	0.0	7.7	7.7	15.4	69.2	4.6 ± 1.9 (2-8)
6/15 (5)	84.0	16	81.3	0.0	6.3	6.3	0.0	88.0	4.4 ± 2.0 (2-9)
6/20 (5)	69.0	30	90.0	0.0	6.7	0.0	3.3	90.0	3.6 ± 2.6 (1-11)
6/25 (5)	70.0	30	93.3	0.0	0.0	0.0	6.7	93.3	5.4 ± 2.4 (1-10)
7/04 (5)	81.0	19	100.0	0.0	0.0	0.0	0.0	100.0	4.4 ± 1.9 (1-9)
7/09 (5)	55.1	30	—	0.0	3.3	6.7	0.0	90.0	3.3 ± 1.4 (1-6)

* *n* = 100 *C. obstrictus* except 27 June, *n* = 26; 30 May, *n* = 110; 22 June, *n* = 39; 18 June (*S. arvensis*), *n* = 101; 3 July and 10 July, *n* = 19; 9 July, *n* = 98. No more than *n* = 30 female (#♀) *C. obstrictus* were assessed for reproductive status.

Table 5. *Ceutorhynchus obstrictus* eggs, first- (1st In), second- (2nd In), and third-instar larvae (3rd In), and exit holes (EH), in pods of wild and cultivated true hosts in 2001

Date (site)	Host plant	*n* Pods	% Pods infested	% Pods >1 infestation	Total % stage of *C. obstrictus*				
					Eggs	1st In	2nd In	3rd In	EH
7/04 (1)	*S. arvensis*	500	4.6	0.0	47.8	17.4	21.7	13.0	0.0
7/04 (5)	*B. napus*	100*	77.0	38.0	61.5	15.4	21.5	1.5	0.0
8/01 (6)	*S. arvensis*	891	13.5	0.1	1.7	1.7	5.8	24.0	66.9

* Subsample of *n* = 574 pods, samples are pods from 5 plants.

plants collected from *S. arvensis* Site-6 on 1 August, including the 5 plants in Table 5, had 5.8% (*n* = 2,944) of pods with at least one exit hole. A total of three *S. arvensis* pods had two exit holes.

A small number of *C. obstrictus* eggs and larvae in *B. napus* pods were found isolated from developing seeds by proliferating tissue. Proliferating tissue was also found in *S. arvensis* pods. Doucette (1947, 1948) used the term proliferating tissue to refer to what Dmoch (1965a) later described as an abnormality of the pod septum initiated by adult *C. obstrictus* feeding during oviposition. The septum expands in folds and thickenings (Dmoch 1965a) that can constrict (Dmoch 1965a) or pinch (Doucette 1948) larvae within the pod.

Pods (*n* = 2,792) from five *Cardaria* spp. stems (Site-1), pods (*n* = 2,130) from five *D. sophia* plants (Site-3), and pods (*n* = 1,527) from ten *T. arvense* plants, were examined for larval infestation using the dissecting microscope. Pods that appeared to be invaded in any way were dissected. The only insect larvae found were plutellid (Lepidoptera) larvae in *T. arvense* pods.

Pans (*n* = 2) set at *S. arvensis* Site-3 on 26 June 2001 to monitor larval drop had a mean of 0.0, 1.0, and 2.5 *C. obstrictus* larvae on 29 June, 3 July and 6 July, respectively.

Discussion

Our results show that *D. sophia,* and to a much lesser extent *Cardaria* spp., provide sufficient nutrition for at least some *C. obstrictus* females to develop a few eggs. There is no apparent advantage to *C. obstrictus* in developing eggs on food hosts as they invade true host crops at the bud and early flowering stage. However, early-season food hosts do provide overwintered adults with sustenance and an opportunity to mate prior to locating true hosts. In southern Alberta true host crops are spring-seeded and are not immediately available to overwintered adults either for food or reproduction. *Sinapis arvensis* and volunteer *B. napus* emerge earlier than spring-seeded crops, and although these true hosts, especially volunteer *B. napus,* potentially play a critical role in maintaining populations of *C. obstrictus,* they may not be sufficiently early or widespread to benefit the majority of *C. obstrictus* when they first emerge from overwintering sites.

Bonnemaison (1957) believed that *C. obstrictus* forage for a few days on Brassicaceae close to their overwintering sites before they can make substantial host seeking migrations. *Thlaspi arvense* and *Capsella bursa-pastoris* (L.) Medic. (Brassicaceae), documented as food hosts by Dmoch (1965a), are common annual or winter annual species on agricultural land across the prairie provinces (Frankton and Mulligan 1970). The role of these food hosts deserves scrutiny in southern Alberta as they are widely distributed when adults leave their overwintering sites. Ni et al. (1990) reported that some ovarian development is possible on a diet of green host-plant material and, therefore, *T. arvense* and *C. bursa-pastoris* could at least provide sustenance to overwintered adults until they encounter true hosts. However, they would not provide the same aggregation foci for mating as dense patches of *Cardaria* spp. and *D. sophia.*

The proportion of *C. obstrictus* females that were mated, although high early in the season, never increased significantly at the food host sites despite the presence of a high proportion of males. Heymons (1922) and Bonnemaison (1957) reported that male *C. obstrictus* were reproductively mature early in the season, and Bonnemaison (1957) and Dmoch (1965b) reported that females in early stages of ovarian development were receptive to mating. It is clear from our results that at least some males are reproductively functional well before any female has developed an egg. Mating could occur at overwintering sites; Bonnemaison (1957) found that mating took place readily at 12°C in the laboratory. Later in the season the overlapping of old and new generations complicates field assessment of mating behavior (Dmoch 1965b), and mating between old generation males and new generation females, prior to overwintering, could occur. This would not have occurred at *B. napus* Site-1.

Studies of *C. obstrictus* in other geographic regions indicate a slightly earlier migration of males than females from overwintering sites (Ankersmit 1956, Bonnemaison 1957, Dmoch 1965a). In our study, early-season samples had consistently high proportions of males in 2001, but more variable results and a ratio favoring females at *B. napus* Site-A were documented in 2000. Assessing *C. obstrictus* migration is complicated by a number of variables, for example, seasonal and habitat variations in ambient temperature and wind speed. Dmoch (1965a) and Free and Williams (1979) recommended pan traps for assessing *C. obstrictus* migration but not for assessing abundance. Using pan traps we found negligible migration activity at mean daily highs of up to 18°C, but greater migration at higher temperatures. It seems that in southern Alberta mean daily highs exceeding 18°C are needed to initiate extensive migration of *C. obstrictus* from overwintering sites.

Bonnemaison (1957) documented the first appearance of eggs in the lateral oviducts of *C. obstrictus* in France to occur as early as 21 April and as late as 10 May (1951 to 1956). Timing of egg development is clearly dependent on annual variations in climatic conditions that affect both insects and host plants. Duration of flowering has been documented as an important factor affecting *C. obstrictus* fecundity and migration (Dmoch 1965b, Lerin 1991). Ni et al. (1990) demonstrated in the laboratory that food quality, post-diapause feeding duration, and ambient temperature directly affected egg development in *C. obstrictus.* The first occurrence of female *C. obstrictus* with at least one egg in the lateral oviducts provided a practical benchmark for early-season reproductive development of *C. obstrictus* on specific host plants in southern Alberta.

Dissection results suggested that *C. obstrictus* feeding only on *S. arvensis* likely had a lower fecundity than *C. obstrictus* feeding on *B. napus.* However, this difference is insufficient to explain the overall paucity of infested pods of *S. arvensis,* relative to *B. napus.* Infestation levels could be influenced by a low proportion of mated *C. obstrictus* on *S. arvensis,* and by species-specific differences in physical and biochemical plant factors, for example, specific glucosinolates (Bartlet 1996, Lamb 1989). Although impossible to prove in the context of the current study, we believe that a strong case can be made to support the hypothesis that low *C. obstrictus* populations could be maintained by *S. arvensis* in the absence of cultivated true hosts.

Rhaphanus raphanistrum L. (Brassicaceae) is a true host of *C. obstrictus* (Dmoch 1965a, Doucette 1947). Bonnemaison (1957) and Doucette (1947) reported that *C. obstrictus* infestation of *Rhaphanus* spp. pods was much higher than for *S. arvensis* pods. However, *R. rhaphanistrum* was not encountered in the current study but may be important in maintaining *C. obstrictus* populations in moister regions of the prairies (Frankton and Mulligan 1970).

Bonnemaison (1957) reported a high mortality of *C. obstrictus* from when larvae exit the pods to when new generation adults emerge and attributed this to dry soil and hard soil surfaces. Bonnemaison reported larval mortality as high as 71% in a laboratory trial. The current study period was one of the driest periods on record for the region and likely explains the low emergence rate of new generation adult *C. obstrictus* relative to larval abundance in 2000. This phenomenon, if further substantiated, could contribute to cultural control recommendations for irrigated *B. napus* crops; for example, it may be appropriate to withhold irrigation prior to and during larval drop.

Insecticide application is currently the only available strategy for producers to control *C. obstrictus* in southern Alberta (Dosdall et al. 2001). Results from the current study demonstrate that wild Brassicaceae and volunteer stands of commercial *Brassica* spp. serve as important early-season refugia for *C. obstrictus,* where feeding, mating, egg development, and, for true hosts, larval development occur. Areas of *S. arvensis* and volunteer *B. napus* are readily identifiable when plants first flower, and the removal of these true hosts, especially volunteer *Brassica* spp., should be encouraged as a control strategy. Early-season control of *S. arvensis* and other wild true hosts in regions with no commercial *Brassica* spp. production could help slow the spread of *C. obstrictus* across the prairies.

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