Contributions to the Life History, Host Range, and Distribution of *Necremnus tidius* (Hymenoptera: Eulophidae)

L. M. DOSDALL,^{1,2} G.A.P. GIBSON,³ O. OLFERT,⁴ B. A. KEDDIE,⁵ and B. J. ULMER¹

Ann. Entomol. Soc. Am. 100(6): 861-868 (2007)

ABSTRACT Field and laboratory studies investigated the preimaginal developmental time, adult emergence phenology, mating behavior, and weevil hosts of Necremnus tidius (Walker) (Hymenoptera: Eulophidae), a solitary ectoparasitoid of coleopteran larvae. In addition, changes in parasitism levels of the cabbage seedpod weevil, *Ceutorhynchus obstrictus* (Marsham) (Coleoptera: Curculionidae), by N. tidius were determined during 2003–2005 in commercial fields of canola (Brassica rapa L. and Brassica napus L.) in southern Alberta and Saskatchewan, Canada. Mean ± SE developmental time from egg to adult was 18.3 ± 0.23 d for specimens reared at 21° C and a photoperiod of 12:12 (L:D) h. Emergence began in late July in commercial fields near Lethbridge, AB, and 20 d later 81% of the population had emerged. Emergence was completed by the end of August. Mating was preceded by a complex courtship behavior with the male standing on the dorsum of the mesosoma and gaster of the female, flapping its wings without flight, leaning forward and stroking its antennae over the antennae of the female, leaning back, and repeating the sequence several times. The native weevil *Ceutorhynchus neglectus* Blatchley was determined to be an alternate host of *N. tidius* in central and northern Alberta. N. tidius was found in few commercial canola fields in 2003, but in 2004, it occurred over hundreds of thousands of hectares of canola cropland, reaching peak parasitism levels of 45%. In 2005, N. tidius was still common, but parasitism declined relative to that observed in 2004.

KEY WORDS *Ceutorhynchus obstrictus, Ceutorhynchus neglectus,* parasitoid development, courtship behavior, spatio-temporal distribution

Necremnus tidius (Walker) (=*N. duplicatus* Gahan) (Hymenoptera: Eulophidae) is a solitary ectoparasitoid of coleopteran larvae with a Holarctic distribution (Gibson et al. 2005). In North America, N. tidius has been reared only from larvae of the alien weevil Ceutorhynchus obstrictus (Marsham) (Curculionidae) (cabbage seedpod weevil), and the geographic range of N. tidius encompasses much of the continent (Gibson et al. 2005, 2006). In Europe, N. tidius also parasitizes C. obstrictus, but additional hosts recorded include the curculionids *Ceutorhynchus typhae* (Herbst) (Kuhlmann et al. 2001), Ceutorhynchus floralis (Paykull) (Kuhlmann and Mason 2002), and *Ceutorhynchus* sp. (Gomez and Zamora 1994). Noves (2003) also listed species of Apionidae and Chrysomelidae (Coleoptera) plus Agromyzidae and Chloropidae (Diptera) and Ypnomeutidae (Lepidoptera) as putative hosts, but the noncoleopteran host associations likely resulted from incorrect identifications of the parasitoid. In Europe, *N. tidius* ranges from Poland (Miczulski 1968) to Germany (Laborius 1972), Spain (Gomez and Zamora 1994), and England (Nasredlin 1973, McKenna 1992). *N. tidius* also was recorded in the Canary Islands (Askew et al. 2001).

More than 165 yr have elapsed since N. tidius was first described by Walker (1839), yet very little published information exists on its life history, behavior, hosts or plant affinities. Gibson et al. (2005) noted that in North America N. tidius was associated with species of Brassicaceae, including Descurainia sophia (L.) Webb (flixweed), Descurainia pinnata subsp. interme*dia* (Rydb.) Detling (western tansy mustard), and Sisumbrium altissimum L. (tumble mustard), and with Salsola tragus L. (Russian thistle), a member of the Chenopodiaceae. Dosdall et al. (2006) reported N. tidius as a parasitoid of C. obstrictus in canola, Brassica napus L. and Brassica rapa L. (Brassicaceae), in southern Alberta. Larvae of C. obstrictus develop in canola siliques (the elongated dehiscent fruit capsules characteristic of Brassicaceae, having two valves that fall away leaving a central partition) from July to August (Dosdall and Moisey 2004). After a short pupation period in the soil, C. obstrictus adults emerge, feed, and overwinter beneath the soil, usually in shelterbelts (Dosdall and Moisev 2004, Ulmer and Dosdall 2006). Specimens of N. tidius reared from C. obstrictus indicate that emergence occurs from mid-July to mid-

¹ Department of Agricultural, Food and Nutritional Science, 4-10 Agriculture/Forestry Centre, University of Alberta, Edmonton, AB, Canada T6G 2P5.

² Corresponding author, e-mail: lloyd.dosdall@ualberta.ca.

³Eastern Cereal and Oilseed Research Centre, Agriculture and Agri-Food Canada, 960 Carling Ave., Ottawa, ON, Canada K1A 0C6.

⁴ Agriculture and Agri-Food Canada, Saskatoon Research Centre, 107 Science Place, Saskatoon, SK, Canada S7N 0X2.

⁵ Department of Biological Sciences, CW 405 Biological Sciences Centre, University of Alberta, Edmonton, AB, Canada T6G 2E9.

August in southern Alberta and Saskatchewan, late June to late August in British Columbia, mid-May to mid-June in Georgia, mid-June to late July in Idaho and Washington, and late May in Illinois (Gibson et al. 2005). Nothing is known about the overwintering life stage or habitat of *N. tidius*. However, its late-season adult emergence from *C. obstrictus* hosts in western Canada suggests that it may overwinter as an adult.

Dosdall et al. (2006) reported that infestations of canola crops in southern Alberta by C. obstrictus from 2002 to 2004 were associated with substantial increases in the distribution and abundance of several species of Chalcidoidea, including N. tidius. Studies were undertaken to investigate aspects of the life history of N. tidius, including overwintering habitats, mating, and oviposition behaviors and host plant affinities in view of the potential importance of N. tidius for biological control of the cabbage seedpod weevil in western Canada. In addition, we studied changes in its levels of parasitism of C. obstrictus throughout southern Alberta and Saskatchewan from 2003 to 2005, and we investigated a sympatric, native congener of the cabbage seedpod weevil, Ceutorhynchus neglectus Blatchley, as a potential alternate host of N. tidius.

Materials and Methods

Overwintering Habitat and Migrations to Host Plants. Emergence cages were used from 2003 to 2005 to identify possible overwintering habitats of *N. tidius*. In 2003 and 2004, 49 and 57 emergence cages, respectively, were placed at nine sites within a 20-km radius of Lethbridge, AB (49° 27′ N, 112° 39′ W). In 2005, 10 cages were placed within a large shelterbelt of mature poplar (*Populus balsamifera* L.) trees in Lethbridge. Cages were set out on 9 April 2003, 9 April 2004, and 5 May 2005. The first collections were made on 15 April 2003, 15 April 2004, and 11 May 2005, and collections were made weekly thereafter until mid-July of each year. The emergence cages were pyramidal, 1 m^2 at the base, and they followed the design of Dosdall et al. (1996).

In 2003 and 2004, emergence cages were placed in either open, intermediately sheltered or fully sheltered habitats. Cages in open habitats were not shaded from any direction, and the dominant vegetation was either smooth brome (Bromus inermis Leyss.) (Poaceae), crested wheat grass (Agropyron cristatum L.) (Poaceae), or both species. Cages in sheltered habitats were in wooded sites, shaded on at least three sides and from above by trees taller than the cages. The dominant tree species were caragana (*Caragana* arborescens Lam.) (Fabaceae) and poplar (Populus tremuloides Michx. and P. balsamifera) (Salicaceae). American elm (*Ulmus americana* L.) (Ulmaceae), Siberian elm (Ulmus pulmila L.) (Ulmaceae), ash (Fraximus americana L.) (Oleaceae), and willow (Salix spp.) (Salicaceae) also were present at some sites. Cages that were slightly shaded or sheltered on one or two sides were categorized as intermediate. In 2005, all cages were in fully sheltered habitat.

On each collection date, all insects were removed from the cages with battery-powered aspirators (Hausherr's Machine Works, Toms River, NJ). Insect collections were then frozen until specimens could be sorted, counted, and recorded.

Yellow bowl traps (15 cm in diameter, 9 cm in depth) were used in 2004 and 2005 to monitor movement of *N. tidius* to host plants. Each bowl trap was attached with a metal bracket to a metal post anchored into the ground so the height of the bowl could be adjusted to always remain at the top of the plant canopy. Each bowl trap was filled with a 1:1 mixture of water:propylene glycol, and the trap was refilled as needed. 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 *N. tidius* adults were identified, counted, and recorded.

In 2004, one bowl trap was installed at each of 20 sites making up patches of brassicaceous weeds, in an area encompassing a 20-km radius around Lethbridge. Sites were dominated either by flixweed (n = 5), hoary cress (*Lepidium draba* L.) (n = 5), pennycress (*Thlaspi arvense* L.) (n = 5), or wild mustard (*Sinapis arvensis* L.) (n = 5). The area of each site was variable but most commonly encompassed $\approx 60 \text{ m}^2$. Traps were installed on 4 May when the majority of plants were in the rosette to bud stages. Samples were collected weekly until 20 July when all plants were dried and in pod.

On 5 May 2005, two bowl traps were installed at each of 12 sites that were dominated by *D. sophia* in the rosette stage. Samples were collected weekly until 22 July when flixweed plants senesced.

Preimaginal Development and Adult Emergence Phenology. B. napus 'Q2' plants were grown in five 10-cm diameter fiber plant pots (one plant per pot) filled with pasteurized soil mix. Plants were grown in a greenhouse under natural light, watered daily, and provided with weekly additions of water-soluble 20-20-20-10 (N-K-P-S) fertilizer. When plants were still flowering but the lower pods were elongating and beginning to fill (growth stages 4.2-4.3 of Harper and Berkenkamp 1975), they were enclosed in mesh bags (1 m in length, 0.75 m in diameter, and 1-mm mesh) with 50 field-collected adult C. obstrictus added per bag. After 24 h, the bags and weevils were removed. The plants were maintained in the greenhouse for 12 d, when pod dissections indicated the presence of third instars of weevils.

Each canola plant was then placed in a screened cage measuring 40.5 by 40.5 cm at the base and 80.5 cm in height, lined on the sides and the top with 500- μ m Nitex mesh screening and with clear acrylic plastic on one side. Ten pairs of adult *N. tidius* were added to each cage. The *N. tidius* were obtained by placing field-collected *B. rapa* siliques infested with *C. obstrictus* larvae in cardboard rearing containers measuring 18 by 18 cm and 16 cm in height. Each container had a small cylindrical plastic vial attached over a 4-cm-diameter opening in the side of the box for collecting the parasitoids (Dosdall et al. 2006). Within 12–16 h of

emergence, the adult *N. tidius* were transferred to individual insect cages. They were held for 24–96 h at room temperature and under natural light, with vials containing a 20% honey solution. The *N. tidius* were then moved to the larger cages holding the weevilinfested canola plants.

After exposure to canola plants for 24 h, *N. tidius* were removed from the cages by aspiration, and the plants were maintained in a growth chamber at 21° C and a photoperiod of 12:12 (L:D) h. Days to emergence and sex of eclosed *N. tidius* adults were recorded.

In 2004, a portion of a commercial canola field near Lethbridge of $\approx 1,250 \text{ m}^2$ was seeded to *B. rapa* 'Reward' on 28 April. From 19 July to 11 August, weekly collections were made of ≈ 500 siliques. The siliques were placed in cardboard rearing containers as described above for parasitoid emergence. Newly eclosed *N. tidius* adults were removed every 3 d, and their numbers and sex were recorded.

Courtship, Mating, and Oviposition Behaviors. Adult N. tidius were reared from B. rapa siliques. Within 8 h of emergence, adults were placed individually in small insect cages, each with a vial containing a 20% honey solution. Adults remained in these containers, held at room temperature and under natural light, for 48–72 h before observations of their mating and oviposition behaviors. Observations were made using either small plastic vials (4 cm in diameter, 6 cm in height), petri plates (4 cm in diameter), or screened cages (as described above) containing canola plants bearing siliques containing multiple final instars of C. obstrictus. A single B. napus pod that was infested with a third instar of C. obstrictus was placed in each vial or petri plate. The canola had been grown in a greenhouse chamber, and it had been caged for 24 h with several adult weevils ≈ 12 d before the study.

Mating and oviposition behaviors were photographed in petri plates (4 cm in diameter) with an Hitachi solid state color video camera (model VK-C350) fitted with Nikon lenses (Micro-NIKKOR 55 mm and a series of close-up lenses) connected to a television monitor (JVC) and video recorder (JVC). Fiber optic illumination was provided. The petri plate was filled nearly to the top with molten paraffin that was allowed to cool until nearly solid. A canola pod harboring a final instar of *C. obstrictus* was embedded in the paraffin with a space of \approx 5 mm remaining between the pod surface and the lid of the dish. Eight male–female pairs were observed.

Descriptions of courtship behavior were developed by review of the video sequences on a computer monitor, after converting the videotape sequences to digital images. Behavioral descriptions were developed following the terminology of van den Assem et al. (1982).

C. neglectus as a Native Host of *N. tidius.* Populations of *C. neglectus* were investigated in central and northern Alberta in 2005 to determine whether this species is a native host for *N. tidius.* Feeding and preimaginal development of *C. neglectus* occur in plants of *D. sophia* (Dosdall et al. 1999), one of the known plant

associates of *N. tidius* (Gibson et al. 2005). Consequently, patches of *D. sophia* were sampled for the presence of *C. neglectus*.

Fifty survey sites for *C. neglectus* were selected 100–600 km north of the 2004–2005 invasion front of *C. obstrictus*, which extended along an east-west transect from Red Deer (52° 16' N, 113° 48' W) to Stettler (52° 19' N, 112° 43' W) and Oyen, AB (51° 22' N, 110° 28' W) (L.M.D., unpublished data). Collections were made of ≈4,000 *D. sophia* siliques per site. Siliques were separated into 10 samples of ≈400 pods per site, and each sample was placed into a cardboard rearing container as described by Dosdall et al. (2006). Boxes were sealed with tape to prevent escape of *C. neglectus* larvae or parasitoids, and they were maintained under continuous light at room temperature for 6 wk until all parasitoids had emerged.

Parasitoids were identified using published taxonomic keys, type material, or other authoritatively identified specimens. Voucher specimens have been deposited in the Canadian National Collection of Insects and Arachnids (CNC), Ottawa, ON, Canada.

Distribution and Abundance of N. tidius in Canola. The distribution of *N. tidius* and the levels of parasitism of C. obstrictus larvae were assessed in southern Alberta and Saskatchewan from 2003 to 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). In total, 147, 202, and 165 fields were sampled in 2003–2005, respectively. A single sample was collected from each field, making up $\approx 450-850$ canola siliques. Pods were collected from canola racemes first at the field edges and then progressing inward over a distance of ≈35–50 m. The geographical location of each field was determined using highresolution maps or hand-held global positioning system units. Fields were selected to lie within the known range of the cabbage seedpod weevil.

Parasitoids were reared and collected as described above. For each site, the total number of hosts available was determined by counts of all pods and exit holes in the sample. Weevil and parasitoid exit holes could be distinguished because exit holes of *C. obstrictus* larvae are circular but irregular along their margins, whereas those of parasitoids are smaller and uniformly rounded along their margins (Dosdall et al. 2006). Samples were discarded when total numbers of emerged adult parasitoids did not equal total parasitoid exit holes from the pods. Voucher specimens were deposited in the CNC.

Parasitism levels of *N. tidius* adults at each site were used to generate surface maps of abundance by using ArcMap Geographical Information Systems software with Spatial Analyst Extension (ESRI, 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



Fig. 1. Percentage of emergence of *N. tidius* males and females from pods of canola (*B. rapa*) infested with *C. obstrictus* larvae near Lethbridge, AB, in July and August, 2004. Numbers on histograms give total specimens of males and females (n = 443) on each date when emergence was recorded.

search radius of 500 km and an output cell size of 1 km were set. For each year, the spatial distribution of *N. tidius* adults was presented as a contour map of parasitism level of *C. obstrictus* larvae.

Results

Overwintering Habitat and Migrations to Host Plants. No specimens of *N. tidius* were collected from any of the emergence traps, regardless of habitat type, in any of the 3 yr of the study.

In 2004, *N. tidius* were collected in bowl trap samples located in patches of *L. draba* on 5 June $(1 \ 3)$, 16 June $(1 \ 2)$, and 23 June $(1 \ 3, 1 \ 2)$, and *D. sophia* on 5 June $(2 \ 3)$ and 18 June $(1 \ 2)$. No *N. tidius* were recovered from bowl traps located in patches of *T. arvense* or *S. arvensis*. In 2005, *N. tidius* specimens were recovered from bowl trap samples in *D. sophia* patches on three dates: 8 June $(1 \ 3)$, 16 June $(2 \ 3)$, and 23 June $(2 \ 2)$.

Preimaginal Development and Adult Emergence Phenology. In total, 32 *N. tidius* adults were reared from third instars of *C. obstrictus*. The mean \pm SE developmental time from egg to adult was 18.28 \pm 0.226 d. The sex ratio was 17:15(1:0.88).

In 2004, first emergence of *N. tidius* was observed on 30 July (Fig. 1). Emergence of males slightly preceded that of females. By 12 August, 64% of males had emerged compared with only 46% of females (n = 443). A gradual increase in emergence from 30 July to 18 August was followed by several days of comparatively low emergence levels until 30 August, when all *N. tidius* had emerged.

Courtship, Mating, and Oviposition Behaviors. When a newly emerged pair of *N. tidius* was placed in an observation vial containing a canola silique, the male initially walked up and down the silique several times, stroking its antennae across the surface of the pod. Before courtship, the male pursued the female from behind, flapping its wings (without causing flight) and touching its antennae to the antennae of the female. This was followed by the male mounting the female, taking up a position with its two front legs on the dorsum of the female mesosoma and its other legs on the dorsum of the gaster. Although a male sometimes attempted mating without first performing the courtship display, such attempts were invariably terminated by the female. Courtship involved alteration between both "high-" and "low"-phase episodes in the position of the male head relative to that of the female (van den Assem et al. 1982). During both phases, the tarsi remained in the same position but the position of the male head relative to that of the female varied. During the low phase, the male head was aligned approximately with the midpoint of the female mesosoma. The high phase was initiated by the male often flapping its wings and then leaning forward so that its head was aligned with that of the female or slightly forward of the female's head. The high phase always ended with the male stroking its antennae over those of the female. The female antennae were turned forward during both high- and low-phase episodes. The low-to-high phase sequence was repeated without intervals or "rest" periods between. The number of high- to low-phase episodes comprising courtship varied considerably among pairs, but in general, a minimum of five to seven episodes preceded mating.

Sexually receptive females raised the gaster upwards to expose the genital orifice and stretched out the head with antennae pointing upwards. The male would lower itself to the substrate, and during copulation the male antennae also pointed forward. In mating, genitalia were joined for \approx 15–30 s.

Oviposition was preceded by the female drumming its antennae across the surface of the silique. The drumming behavior occurred initially over a wide area of the pod but gradually the search area narrowed as the female located the position of the weevil larva within the pod. Rapid up and down movements of the female gaster just above the pod surface with its ovipositor inserted in the pod often preceded oviposition. Eventually, the female would arch the tip of the gaster so that it contacted the pod wall, followed by insertion of the ovipositor and egg laying. After oviposition, the female often walked forward on the silique a few paces, arched the tip of her gaster, touched it to the silique, and brushed the pod.

C. neglectus as a Native Host of N. tidius. Of 50 sites of flixweed surveyed north of the C. obstrictus distribution front in Alberta, eight were found to harbor populations of C. neglectus: Vegreville (53° 30' N, 112° 06' W), Edmonton (53° 30' N, 113° 32' W), Fort Vermilion (58° 22′ N, 116° 03′ W), High Level (58° 31′ N, 117° 09' W), Sexsmith (55° 21' N, 118° 47' W), Rycroft (55° 45′ N, 118° 42′ W), Fairview (56° 04′ N, 118° 23′ W), and Falher (55° 44' N, 117° 11' W). N. tidius was reared from flixweed at two sites: Vegreville $(2Q, 1\delta)$ and Fort Vermilion $(3\mathcal{Q}, 1\mathcal{S})$. Incidence of parasitism was low: only 0.33% at Vegreville and 0.60% at Fort Vermilion. Other parasitoid species reared from the flixweed pods included *Trichomalus lucidus* (Walker) (Pteromalidae) from Fairview (13), Necremnus sp. from Vegreville (19,53), an unknown Eulophidae from Fort Vermilion (1δ) , an unknown Mymaridae from Vegreville $(1\mathcal{Q})$ and an unknown Scelionidae from Fort Vermilion $(1^{\circ}, 5^{\circ})$ (Platygastroidea). It was not possible to further identify the unknown eulophid, mymarid, and scelionid specimens because they became damaged in the recovery process.

Distribution and Abundance of N. tidius in Canola. In 2003, N. tidius emerged from five canola fields in Alberta and 12 fields in Saskatchewan infested with C. obstrictus (Fig. 2). In Alberta, N. tidius was reared from fields south of Lethbridge near the U.S. border. In Saskatchewan, N. tidius was reared most commonly from fields south of Swift Current, SK. The highest percentages of C. obstrictus larvae parasitized by N. tidius were 4-6% in Alberta and 10-12% in Saskatchewan.

In 2004, *N. tidius* was widespread throughout southern Alberta and southeastern Saskatchewan, with parasitism levels ranging from 0 to 45% (Fig. 2). *N. tidius* was collected from 35 sites spanning a range that extended from the U.S. border north to Swift Current in the east and west to Lethbridge and Claresholm, AB (50° 01' N, 113° 35' W). Percentages of *C. obstrictus* larvae parasitized were greatest near Medicine Hat, AB, and Swift Current with \approx 0.4 parasitoid emerging per weevil-infested pod.

In 2005, *N. tidius* was collected from 32 sites throughout southern Alberta and southwestern Saskatchewan (Fig. 2). The range of *N. tidius* in Saskatchewan was similar for both years, but in Alberta it did not extend as far to the north and west as in 2004. In both provinces, levels of parasitism declined dramatically with only 10-12% parasitism in the most densely populated collection sites south of Medicine Hat and Swift Current.

Discussion

Overwintering habitats of *N. tidius* in southern Alberta remain unknown. We collected all insects emerging from 49, 57, and 10 m² of soil in 2003, 2004, and 2005, respectively, representing a variety of habitats near commercial fields of canola, but we failed to capture any specimens of *N. tidius*. By contrast, other insect species that overwinter as adults in the area, such as *C. obstrictus, Phyllotreta cruciferae*

(Goeze) (Coleoptera: Chrysomelidae), and Lygus spp. (Hemiptera: Miridae) were routinely collected in the traps. In particular, ≈2,400 and 5,400 specimens of *C. obstrictus* were collected in the emergence traps in 2003 and 2004, respectively (Ulmer and Dosdall 2006). These observations suggest that either 1) N. tidius does not overwinter in southern Alberta but instead disperses to this area annually, presumably from the south; 2) N. tidius overwinters in a preimaginal life stage on an alternate native host; or 3) N. tidius overwinters as an adult but in a habitat not represented by our sampling regime. Of these possibilities, it seems most likely that N. tidius overwinters as an adult in southern Alberta, perhaps under tree bark or in soil in riparian habitats, which we did not survey. Movement from regions outside of the geographical area encompassed by our studies could have occurred, but high levels of parasitism of C. obstrictus (e.g., 45% in 2004 and 12% in 2005) and the presence of N. tidius in the far north at Fort Vermilion suggest overwintering. A native congener of N. tidius, Necremnus breviramulus (Gahan), was presumed by Puttler et al. (1973) to overwinter as a diapausing adult, because adults held in vials at 4–6°C and fed with honey lived for 6 mo in the laboratory. Similarly, adult Necremnus metalarus (Walker) entered reproductive diapause in the absence of hosts and lived >3 mo at 20°C (Ryan 1980).

N. tidius was not sufficiently abundant in bowl trap collections to provide substantial insight into species population dynamics, but trap collections did indicate that *N. tidius* adults are active in early June, ≈ 4 wk before final instars of C. obstrictus are abundant in canola crops. The early flowering brassicaceous weed species occurring where N. tidius adults were collected, such as L. draba and D. sophia, probably provide a nutrient source for adults until canola crops begin flowering and pollen and nectar become abundant. Adult activity in early June coincides with the period when *C. neglectus* adults mate and oviposit on D. sophia (Dosdall et al. 1999). Early season activity and feeding by N. tidius could facilitate parasitization later when larvae of C. neglectus are present in flixweed siliques.

The preimaginal developmental time of *N. tidius* (18 d) was similar to those published for other species of this genus. Puttler et al. (1973) reported that *N. breviramulus* developed from egg to adult in 12–16 d under laboratory conditions of $22–24^{\circ}$ C and 40-50% RH. Chamberlin (1925) found that eggs of *Necremnus leucarthros* (Nees) hatched within 1 d and that new generation adults emerged 13–17 d later under unspecified rearing conditions. Ryan (1980) found that N. metalarus required 21 d to develop from egg to adult at 20°C.

The relatively rapid developmental time of *N. tidius* and the ability of new generation adults to readily mate and oviposit in the presence of canola pods infested with *C. obstrictus* larvae suggest that this species is multivoltine in western Canada. Multivoltinism enhances the potential effectiveness of *N. tidius* for the biological control of *C. obstrictus*. Oviposition and larval development of the cabbage seedpod weevil are



Fig. 2. Changes from 2003 to 2005 in the distribution and level of parasitism of *N. tidius* on the cabbage seedpod weevil. The legend indicates the percentages of weevil-infested canola pods parasitized by *N. tidius* in southern Alberta and Saskatchewan.

synchronized with various developmental parameters of their canola host plants (Dosdall and Moisey 2004). Seeding of canola crops occurs over a 3- to 4-wk period in southern Alberta and Saskatchewan, resulting in an extended period when weevil larvae occur in pods. The short developmental time of *N. tidius* makes it possible that a second generation could parasitize *C. obstrictus* larvae and thus have a greater impact on reducing weevil populations than a single generation of the parasitoid.

In the Chalcidoidea, males react to conspecific females by courtship displays that induce sexual receptivity (van den Assem et al. 1980), and the specific characteristics of these displays can have importance for determining evolutionary relationships among taxa (van den Assem et al. 1982). Several aspects of the courtship behavior we have described for *N. tidius* indicate a more plesiomorphic condition compared with contrasting behaviors hypothesized as derived by van den Assem et al. (1982). The features described as plesiomorphic by van den Assem et al. (1982), and making up courtship in *N. tidius*, include alteration of high and low phases rather than a sustained low-phase male posture, the placement of male tarsi on the female mesosoma rather than on the head, a display without leg movements, and male antennation that rubs or lashes the female antennae. As proposed by van den Assem and Povel (1973), such courtship behavior by *N. tidius* likely acts as an ethological barrier between closely related sympatric species.

Host-finding and oviposition behaviors of female N. tidius were similar, but not identical, to those described for the European parasitoid of the cabbage seedpod weevil, Trichomalus perfectus (Walker) (Hymenoptera: Pteromalidae) (Dmoch and Rutkowska-Ostrowska 1978, Dmoch 1998). We found no evidence for "radaring" behavior in N. tidius, and unlike T. perfectus, antennal drumming in N. tidius was followed directly by tapping or stroking the end of the gaster on the pod wall without the intermediate behavior of antennal stroking along the pod. The rapid up and down movements we observed by the female with her ovipositor inserted in the silique are likely similar in function to the "quick stings" observed by Quednau (1967) in *Chrysocharis laricinellae* (Ratzeburg) (Hymenoptera: Eulophidae), which apparently serve to inject paralyzing fluid into its host larva. The final step we observed in the oviposition sequence of *N. tidius*, involving touching and brushing of the tip of the gaster along the silique surface, could indicate deposition of an oviposition deterring pheromone, but further study is needed to validate this hypothesis.

We found no evidence of host feeding by *N. tidius*, although this behavior occurs in many other Chalcidoidea (e.g., Jervis and Kidd 1986). Virgin *N. tidius* females were observed to mate and oviposit without feeding on the hemolymph of *C. obstrictus* larvae. However, the possibility of host feeding by *N. tidius* cannot be discounted because some synovigenic parasitic females can oviposit small numbers of eggs without host feeding, but host feeding is needed for continuous egg production (Jervis and Kidd 1986, Morales-Ramos 2000).

Mymaridae and Scelionidae are egg parasitoids (Gibson 1993, Masner 1993), and their emergence from *D. sophia* siliques does not necessarily indicate that they are a component of the parasitoid fauna of *C. neglectus*. Other insects in the region may have deposited eggs in stems or siliques that could have been hosts for the egg parasitoids. However, there can be little doubt that rearings of *N. tidius*, *Necremnus* sp., and *T. lucidus* represented parasitism of *C. neglectus*, because each of these species attack coleopteran larvae, and *C. neglectus* was the only nonhymenopteran species reared from the pods.

The discovery that the Nearctic weevil *C. neglectus* is a native host for *N. tidius* raises concern that populations of *C. neglectus* may be negatively altered by the invasion of *C. obstrictus*. The development of an abundant resource of *C. obstrictus* larvae in commercial canola fields could flood the system with *N. tidius* and reduce populations of *C. neglectus*, perhaps even leading to localized extinction of *C. neglectus* where the ranges of the two weevils overlap.

The level of parasitism of N. tidius on C. obstrictus varied considerably over the 3 yr of this study, from very low levels throughout southern Alberta and Saskatchewan in 2003 (usually 0%) to higher levels in 2004 (usually 4–6%, but occasionally as high as 45%), with a return to lower levels in 2005 (usually 2%) (Fig. 2). Our study likely underestimated parasitism levels, because our approach of rearing adults from fieldcollected pods left the pods too dried out to enable us to follow rearing with pod dissections to determine numbers of individuals of N. tidius that did not pupate or emerge successfully. The reduction in parasitism levels from 2004 to 2005 could represent a natural decline in N. tidius populations or could represent effects of competition with other Chalcidoidea for C. obstrictus larvae. In 2005, parasitism levels of C. obstrictus by Chlorocytus sp. and Pteromalus sp. (Pteromalidae) increased (L.M.D., unpublished data), and this could indicate that they are better competitors. For example, maximum parasitism levels of Chlorocytus sp. increased from 1.5% in 2003 to 10% in 2005, and parasitism of C. obstrictus by Pteromalus sp. increased from a maximum of 1.5% in 2003 to 9% in 2005 (L.M.D., unpublished data). Further study over several more years is necessary to resolve whether competition with other parasitoid species impacts N. tidius populations.

Acknowledgments

We gratefully acknowledge technical assistance from R. Adams, N. Cowle, A. Kalischuk, B. Peake, and K. Peake. We thank R. Laffin for assisting with the collections and rearing of parasitoids from *C. neglectus*. Special thanks are extended to M. Braun for conducting the Saskatchewan surveys and to M. Herbut for assistance with preparing the N. *tidius* distribution maps. Funding for this project was received from the Alberta Agricultural Research Institute; the canola producer commissions of Alberta, Saskatchewan, and Manitoba; the University of Alberta; Alberta Agriculture, Food and Rural Development; and Agriculture and Agri-Food Canada.

References Cited

- Askew, R. R., J. Blasco-Zumeta, and J. Pujade-Villar. 2001. Chalcidoidea y Mymarommatoidea (Hymenoptera) de un sabinar de *Juniperus thurifera* L. en Los Monegros, Zaragoza. Monogr. Soc. Entomol. Aragonesa 4: 1–76.
- Chamberlin, T. R. 1925. Some observations upon Necremnus leucarthros (Nees) (Hymenoptera: Eulophidae). Proc. Entomol. Soc. Wash. 27: 142–144.
- Dmoch, J. 1998. Kairomones and searching behavior of *Trichomalus perfectus* Walker. Int. Org. Biol. Control Bull. 21: 171–176.
- Dmoch, J., and Z. Rutkowska-Ostrowska. 1978. Host-finding and host-acceptance mechanism in *Trichomalus perfectus* Walker (Hymenoptera, Pteromalidae). Bull. Acad. Pol. Sci. Biol. 26: 317–328.

- Dosdall, L. M., and D.W.A. Moisey. 2004. Developmental biology of the cabbage seedpod weevil, *Ceutorhynchus* obstrictus (Coleoptera: Curculionidae), in spring canola, *Brassica napus*, in western Canada. Ann. Entomol. Soc. Am. 97: 458–465.
- Dosdall, L. M., M. J. Herbut, N. T. Cowle, and T. M. Micklich. 1996. The effect of tillage regime on emergence of root maggots (*Delia* spp.) (Diptera: Anthomyiidae) from canola. Can. Entomol. 128: 1157–1165.
- Dosdall, L. M., M. A. McFarlane, and P. Palaniswamy. 1999. Biology and larval morphology of *Ceutorhynchus neglectus* Blatchley (Coleoptera: Curculionidae), a minor pest of canola (Brassicaceae) in western Canada. Can. Entomol. 131: 231–242.
- Dosdall, L. M., B. J. Ulmer, G.A.P. Gibson, and H. A. Cárcamo. 2006. The spatio-temporal distribution dynamics of the cabbage seedpod weevil, *Ceutorhynchus obstrictus* (Marsham) (Coleoptera: Curculionidae), and its larval parasitoids in canola in western Canada. Biocontrol Sci. Technol. 16: 987–1006.
- Gibson, G.A.P. 1993. Superfamilies Mymarommatoidea and Chalcidoidea, pp. 570–656. In H. Goulet and J. T. Huber [eds.], Hymenoptera of the world: an identification guide to families. Research Branch, Agriculture Canada Publication 1894/E, Agriculture Canada, Ottawa, ON, Canada.
- Gibson, G.A.P., H. Baur, B. Ulmer, L. Dosdall, and F. Muller. 2005. On the misidentification of chalcid (Hymenoptera: Chalcidoidea) parasitoids of the cabbage seedpod weevil (Coleoptera: Curculionidae) in North America. Can. Entomol. 137: 381–403.
- Gibson, G.A.P., M. W. Gates, and G. D. Buntin. 2006. Parasitoids (Hymenoptera: Chalcidoidea) of the cabbage seedpod weevil (Coleoptera: Curculionidae) in Georgia, U.S.A. J. Hymenopt. Res. 15: 187–207.
- Gomez, J. M., and R. Zamora. 1994. Top-down effects in a tritrophic system: parasitoids enhance plant fitness. Ecology 75: 1023–1030.
- Harper, F. R., and B. Berkenkamp. 1975. Revised growthstage key for *Brassica campestris* and *B. napus*. Can. J. Plant Sci. 55: 657–658.
- Jervis, M. A., and N.A.C. Kidd. 1986. Host-feeding strategies in hymenopteran parasitoids. Biol. Rev. 61: 395–434.
- Kuhlmann, U., and P. G. Mason. 2002. Use of field host range surveys for selecting candidate non-target species for physiological host specificity testing of entomophagous biological control agents, pp. 370–377. In R. G. van Driesche [ed.], Proceedings of the 1st International Symposium on Biological Control of Arthropods, 14–18 January 2002, Honolulu, HI. United States Department of Agriculture–Forest Service, Washington, DC.
- Kuhlmann, U., S. Toepfer, M. Grossrieder, F. Zhang, E. Hunt, K. S. Hemachandra, T. Haye, B. Klander, W. Jenner, and C. Gueldenzoph. 2001. Summary report-progress in 2001. Agricultural Pest Research. CABI Bioscience Switzerland Centre, Delémont, Switzerland.
- Laborius, A. 1972. Untersuchungen über die Parasitierung des Kohlschotenrüsslers (*Ceuthorhynchus assimilis* Payk.)

und der Kohlschotengallmücke (*Dasyneura brassicae* Winn.) in Schleswig-Holstein. Z. Ang. Entomol. 72: 14–31.

- Masner, L. 1993. Superfamily Platygastroidea, pp. 558–565. In H. Goulet and J. T. Huber [eds.], Hymenoptera of the world: an identification guide to families. Research Branch, Agriculture Canada Publication 1894/E, Agriculture Canada, Ottawa, ON, Canada.
- McKenna, D. 1992. Study of the effects of insecticide management on the seedpod weevil (*Ceutorhynchus assimilis* Payk.) and its parasites. M. S. thesis, University of London, London, United Kingdom.
- Miczulski, B. 1968. Community studies on Hymenoptera found on *Brassica napus* L. Part VI. Chalcidoidea. Polskie Pismo Entomol. 38: 341–385.
- Morales-Ramos, J. A. 2000. Catolaccus grandis (Burks) (Hymenoptera: Pteromalidae). (http://www.nysaes.cornell. edu/ent/biocontrol/parasitoids/catolaccus grandis.html).
- Nasredlin, N. 1973. A study of the weevil complex on mustard with special reference to the seedpod weevil. Ph.D. thesis, University of London, London, United Kingdom.
- Noyes, J. S. 2003. Universal Chalcidoidea database. (http://www.nhm.ac.uk/research-curation/projects/ chalcidoids/).
- Puttler, B., S. E. Thewke, and R. E. Warner. 1973. Bionomics of three Nearctic species, one new, of *Hypera* (Coleoptera: Curculionidae), and their parasites. Ann. Entomol. Soc. Am. 66: 1299–1306.
- Quednau, F. W. 1967. Notes on mating behavior and oviposition of *Chrysocharis laricinellae* (Hymenoptera: Eulophidae), a parasite of the larch casebearer (*Coleophora laricella*). Can. Entomol. 99: 326–331.
- Ryan, R. B. 1980. Rearing methods and biological notes for seven species of European and Japanese parasites of the larch casebearer (Lepidoptera: Coleophoridae). Can. Entomol. 112: 1239–1248.
- Ulmer, B. J., and L. M. Dosdall. 2006. Spring emergence biology of the cabbage seedpod weevil (Coleoptera: Curculionidae). Ann. Entomol. Soc. Am. 99: 64–69.
- van den Assem, J., and G.D.E. Povel. 1973. Courtship behavior of some *Muscidifurax* species (Hym., Pteromalidae), a possible example of a recently evolved ethological isolating mechanism. Neth. J. Zool. 23: 465–487.
- van den Assem, J., M. J. Gijswijt, and B. K. Nübel. 1980. Observations on courtship and mating strategies in a few species of parasitic wasps (Chalcidoidea). Neth. J. Zool. 30: 208–227.
- van den Assem, J., M. J. Gijswijt, and B. K. Nübel. 1982. Characteristics of courtship and mating behavior used as classificatory criteria in Eulophidae–Tetrastichinae (Hymenoptera), with special reference to the genus *Tetrastichus* s.l. Tijdschr. Entomol. 125: 205–218.
- Walker, F. 1839. Monographia Chalciditum 1., London, United Kingdom. Hyppolitus Baillière, London, United Kingdom.

Received 14 January 2007; accepted 29 May 2007.