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# Evaluation of the larval endoparasitoid Campoletis sonorensis Cameron (Hymenoptera: Ichneumonidae) as a biocontrol agent of the cabbage looper, Trichoplusia ni Hübner (Lepidoptera: Noctuidae)

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# EVALUATION OF THE LARVAL ENDOPARASITOID *CAMPOLETIS SONORENSIS* CAMERON (HYMENOPTERA: ICHNEUMONIDAE) AS A BIOCONTROL AGENT OF THE CABBAGE LOOPER, *TRICHOPLUSIA NI* HÜBNER (LEPIDOPTERA: NOCTUIDAE)

By

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## ABSTRACT

*Campoletis sonorensis* is a native parasitoid of the Cabbage Looper, *Trichoplusia ni*, and I found it attacking *T. ni* in multiple field and greenhouse crops in Ontario. I found that *C. sonorensis* is an important factor regulating *T. ni* populations. *Campoletis sonorensis* was the dominant larval parasitoid of *T. ni* with higher rates of parasitism and higher abundances than all other native parasitoids combined. *Campoletis sonorensis* demonstrates potential as a commercial biocontrol agent of *T. ni* because *C. sonorensis* populations were chronologically and physiologically synchronized with those of *T. ni*. Thus, adult parasitoids were always available when suitable *T. ni* host stages were present. Additionally, *C. sonorensis* was a positively density-dependent factor in the regulation of the *T. ni* population. I demonstrated that *C. sonorensis* can successfully parasitise and emerge from 2 to 8 day-old *T. ni* hosts, but that the highest parasitoid fitness is achieved from 3 to 5 day-old *T. ni* hosts. Finally, *C. sonorensis* has a higher intrinsic rate of increase than *T. ni*, which is a desirable trait in potential biocontrol agents. *Campoletis sonorensis* is a native parasitoid that is very well adapted to *T.ni* population dynamics, but also attacks other Noctuidae host species. It appears that in the agricultural and climatic conditions of Ontario, the timing and presence of other Noctuidae host species may be an important factor in the stabilization of *C. sonorensis* populations, allowing it to be the dominant parasitoid species on *T. ni.*

# DEDICATION

To my beloved wife and son, Liliana and Sebastian, Thank you very much for all your support, understanding and patience during the time that this endeavor took me away from both of you.

To my son, Sebastian, keep dreaming and don't worry, all of your dreams will come through, just be patient and work towards them.

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## General Introduction

Biological control is the use of parasitoid, predator, pathogen, antagonist, or competitor populations (natural enemies) to suppress a pest population, making it less abundant and thus less damaging than it would otherwise be (van Driesche and Bellows 1996). It requires investigating the ecology of organisms, how they interact and how natural control regulates populations. It also involves the application of that knowledge to restore or conserve ecosystem functioning in disturbed ecosystems, and to produce resources required by humans in an environmentally sustainable manner in managed ecosystems. This can be accomplished either through (1) importation of exotic enemies against either exotic or native pest (i.e. classical biological control) or (2) conservation and augmentation of enemies that are already in place or are readily available (Ehler 1998).

Augmentation of natural enemies is accomplished by repetitive releases of natural enemies or their hosts (at strategic times) to increase pest mortality by natural enemies. There are two general but overlapping categories of augmentation tactics: 1) environmental manipulation and 2) periodic release of a natural enemy for an immediate (by the released individuals) or time-lag (by progeny of released individuals) control effect on the pest population (Debach and Hagen 1964; Rabb et al. 1976; Huffaker et al. 1977). Augmentation attempts should usually be restricted to those natural enemies which have been demonstrated by research to be inherently effective in prey/host population regulation but are prevented from doing so (DeBach 1974).

Internationally, more than 150 species of natural enemies are commercially available for augmentative biological control (van Lenteren 2006). This form of control is applied in crops that are attacked by only a few pest species, and it is

particularly popular in greenhouse crops, where the complete spectrum of pests can be managed by a suite of natural enemies. When compared with chemical control, there are no phytotoxic effects on young plants and premature abortion of fruit and flowers does not occur (van Lenteren 2000). Release of natural enemies takes less time and safer than applying pesticides. Several key pests can be controlled only with natural enemies, but not with pesticides, and there is no safety or re-entry period after release of natural enemies (van Lenteren 2000). The use of biological control allows continuous harvesting without danger to the health of greenhouse personnel. Although this form of biological control needs periodic introductions, natural enemies can be used indefinitely. Finally, the general public appreciates biological control because of the lessened risk of pesticide residues on produce (van Lenteren 2000)

Currently, world wide, augmentative forms of biological control, including parasitoids, predators and entomopathogens, are applied on up to 17 million hectares. Of these, parasitoids are applied in up to 15.25 million hectares and larval endoparasitoids are applied in up to 0.045 million hectares (van Lenteren 2000). Insect parasitoids are the most commonly employed biological control agents, both, in practice and in theoretical developments (Hochberg and Holt 1999). In biological control, parasitoids are favored over predators because they are more host-specific, usually better adapted and synchronised with the host, have a lower food requirement per individual thereby maintaining a balance with their host species at a lower host densities, and their larvae do not need to search for food (van Lenteren 1986a,b)

**Parasitoids**

The term 'parasitoid' was first defined by Reuter (1913) and then improved by Gauld and Bolton (1988) to describe a group of insects whose larvae develop by feeding on, or within, an arthropod host and this host individual is almost always killed by the developing parasitoid larva. The parasitoid life-history is most

common in certain families of Hymenoptera and Diptera and it is from these groups that most species have been selected for biological control of agricultural pests. The stages in this unique life-history can be summarized as follows: adult female parasitoids forage actively for hosts, depositing eggs through an ovipositor either in, on, or near their hosts. Upon hatching, the larvae locate and begin feeding on host tissues and pass through several developmental stages either within the host, as endoparasitoids, or on the host, as ectoparasitoids. Solitary parasitoids develop singly in the host, while gregarious parasitoids may develop in groups from eggs laid during one or more oviposition events (Waage and Hassell 1982). Specialists and generalists (parasitoids with respectively narrow and broad host ranges, respectively) and koinobionts and idionbionts (parasitoids that permit the host to grow and metamorphose beyond the stage attacked or not, respectively) are two more ways of characterizing their life history traits.

Parasitoid species exhibit remarkable biological and taxonomic diversity. Parasitoid taxa have diversified into a staggering number of species – about 1 in 10 metazoan species is an insect parasitoid. This diversification has been most prolific in the parasitic Hymenoptera, which may possess more than 200,000 species, constituting slightly more than 75% of all insect parasitoids (Waage and Hassell 1982; Eggleton and Belshaw 1992). Parasitoid life histories constitute greater stability to ecosystem than any other life histories such as predators, phytophagous forms etc (La Salle 1993).

**Parasitic Hymenoptera**

Among the natural enemies used in biological control of insect pests, the parasitic Hymenoptera have been the most successful (Debach 1964, 1974; Waage and Hassell 1982; Noyes 1985). There are innumerable examples to show that parasitic Hymenoptera are extremely successful in biological control programmes. The main reason for this success is that they are capable of living

and interacting at lower trophic levels and can operate in a density dependent manner; an effective species may maintain its hosts in low numbers and therefore be in low numbers itself (La Salle and Gauld 1991; La Salle 1993; Narendram 2001). The fact that parasitic Hymenoptera predominate among the various kinds of natural enemies successfully used in biological control is, in part, the effect of certain unique morphological, physiological, and psychological adaptations which enhance the host-finding capacity of the female parasitoid and enable it, individually and collectively, to maintain the host population at relatively low densities (Flanders 1962).

Parasitic Hymenoptera consist of mostly keystone species which have a major influence on the character or structure of an ecosystem (Reid and Miller 1989; LaSalle and Gauld 1991, 1993). Removal or loss of keystone species would have a noticeable effect on the ecosystem (Paine 1969; DeBach 1974; Paine and Levin 1981; La Salle 1993). The presence of the high level of diversity within parasitic Hymenoptera has potential value to biological control projects. The native parasitic Hymenoptera parasitising any particular pest or potential pest are important not only to that pest, but may also prove to be important to other related introduced pests (La Salle 1993).

**Selecting parasitoids as biological control agents**

Augmentative biological control consists of the following four general elements: 1) the selection of the biological control agent through basic life history studies; 2) the mass production of an augmentative biological control agent(s) and its economics; 3) the agent's release and impact on a target's population density in the field, that is, the mechanics of release along with the ecology and population dynamics of the agent and its host or prey; and 4) the economics associated with pest suppression and crop production in a commodity in relation to the development of a sustainable pest management program at a specific

geographical location (van Driesche and Bellows 1996; van Lenteren 2000, 2006).

Criteria for selecting parasitoids have been compiled by van Lenteren (1986a,b) from numerous sources (Varley 1951; Flanders 1957; Sweetman 1958; Andrewartha 1961; DeBach 1964, 1971, 1974; Askew 1971; Huffaker et al. 1971, 1976; Krebs 1972; Hassell and Rogers 1972; Hassell and May 1973; Varley et al. 1973; van Emden 1974; Huffaker 1976; Coppel and Mertins 1977; Ridgway and Vinson 1977; Waage and Hassell 1982):

1. Seasonal synchronization with host
2. Internal synchronization with host
3. Climatic adaptation
4. No negative effects
5. Good culture methods
6. Host specificity or potential for development of host preference
7. Great reproductive potential
8. Good density responsiveness

Models have identified searching efficiency, fecundity, larval survival, sex ratio, interference, spatial heterogeneity and developmental time of the natural enemy as key contributors to the suppression of a host population equilibrium and/or to the stability of the pest-enemy interaction. Three of these factors – searching efficiency, interference and spatial heterogeneity – relate particularly to density responsiveness (Waage and Hassell 1982; van Lenteren 1986a,b).

The most relevant studies for pre-introductory evaluation criteria of natural enemies to be used in seasonal augmentation releases in greenhouses are points 2 to 5 and 7, as described above. In Figure 1, a flow diagram is presented outlining an evaluation programme. By using such a flow diagram, it is possible to

separate useless from potentially useful biological control candidates at an early phase of research (van Lenteren and Manzaroli 1999).

### *Trichoplusia ni* Hübner (Lepidoptera: Noctuidae)

The Cabbage Looper, *Trichoplusia ni* (Hübner) (Lepidoptera: Noctuidae), is a widely distributed polyphagous insect that is usually considered to have a tropical or subtropical origin, native to the southern half of North America (Kostrowicki 1961). Widespread in southern Europe, North, East and South Africa, extending eastwards through Pakistan, India and Bangladesh to much of Southeast Asia, to China, Taiwan, Korea and Japan; present in South America in Argentina, Bolivia, Brazil, Chile, Colombia and Uruguay (Apablaza and Norero 1993; CIE 1974). It does not overwinter in many areas where it commonly occurs, but instead migrates annually to these locations. *Trichoplusia ni* adults are strong fliers and can migrate considerable distances. As an example, they annually migrate along the eastern coast of the USA. Although the insects cannot overwinter north of the coastal plain of Georgia, they follow the advancing spring and move northward (Mitchell and Chalfant 1984). In Canada, they have been found overwintering inside vegetable greenhouses (Cervantes 2005). *Trichoplusia ni* is a sporadic migrant only in the UK and northern Europe.

Larvae of *T. ni* have been recorded causing damage to over 160 species in 36 families, although cultivated brassicas (*Brassica oleracea* L., Brassicaceae) are the most favored host plants when available (Martin et al. 1976; Sutherland and Greene 1984). Brassicas and cotton (*Gossypium hirsutum* L., Malvaceae) are most frequently cited as being damaged, although the list of commercial crops affected also includes the Asparagaceae (asparagus, *Asparagus officinalis* L.), the Leguminosae (beans, *Phaseolus vulgaris* L.; pea, *Pisum sativum* L.; soybean, *Glycine max L.*), the Chenopodiaceae (sugarbeet, *Beta vulgaris* L.), the Cucurbitaceae (cantaloupes, *Cucumis melo* var. *cantalupensis* Naud.; cucumber (*Cucumis sativus* L.; squash, *Cucurbita pepo* L.; watermelon, *Citrullus lanatus*

Thunb.), the Apiaceae (carrot, *Daucus carota* subsp. *sativus* Hoffm.; celery, *Apium graveolens* Mill.; parsley, *Petroselinum crispum* Mill.)), the Gramineae (maize (silks), *Zea mays* L.), the Asteraceae (lettuce, *Lactuca sativa* L.), the Solanaceae (pepper, *Capsicum annum* L.; potato, *Solanum tuberosum* L.; tobacco, *Nicotiana tabacum* L.; tomato, *Licopersicum esculentum* L.), and the Amaranthaceae (spinach, *Spinacia oleracea* L.) (Waterhouse 1998). *Trichoplusia ni* is a major pest of commercial brassicas in North America and many other areas where it occurs, and also causes significant economic damage to lettuce, tomatoes, celery and cotton. Larvae chew large irregular holes, leaving only main veins, in the outer leaves of cabbage, cauliflower and related plants, often leaving them riddled with holes. Later, the outer layers of cabbage heads are eaten and masses of faecal pellets contaminate the feeding sites. So much leaf tissue is eaten that heads of cabbage and cauliflower are stunted and other leafy vegetables are rendered unfit to eat (Greene 1984; Waterhouse 1998).

*Trichoplusia ni* adults are strong fliers and are primarily nocturnal. During the day, the adults can be found resting in foliage or in crop debris. Moths feed on various wild and cultivated hosts where they obtain water and dissolved nutrients (Mitchell and Chalfant 1984). Mating primarily occurs shortly before sunset (Shorey et al. 1962). Adults emerge in spring. There is a pre-ovipositional period of about 4 days, after which mating begins, and most mating occurs after 3-4 days and can continue up to 16 days (Mitchell and Chalfant 1984). Oviposition of viable eggs reaches a peak at 3-6 days and the number of eggs laid can vary between 300-1600 per female. The eggs are laid singly on plants (Banham and Arrand 1970). There are five larval stages and the total development time of the larval period can vary widely depending on temperature; the normal duration of the larval stage is 2-4 weeks and the pupal stage lasts about 2 weeks (Metcalf et al. 1962). Pupation occurs in a folded webbed leaf or between two webbed leaves. There are 3-4 generations per year and *T. ni* can overwinter as a pupa in a cocoon attached to the foliage of its host plants.

Canadian populations are established through annual migration of adult moths from the south (Lafontaine and Poole 1991). *Trichoplusia ni* became a chronic pest of greenhouse vegetable crops in the early 1990s (Gillespie et al. 2002). Outside greenhouses, *T ni* is an important pest of brassicas and in many other crops in Ontario, but it is less important in other vegetable-producing areas of Canada (Howard et al. 1994). In greenhouse crops, caterpillars cause serious defoliation in cucumber, lettuce, pepper, and tomato. Crop losses result from a combination of plant defoliation, direct damage to fruit, destruction of purchased biological control agents by pesticides applied against *T. ni* and subsequent damage by other pests as a result of their release from biological control (Gillespie et al. 2002). In commercial settings, growers rely on Btk (*Bacillus thuringiensis var. kurstaki)* products against outbreaks of *T. ni* which appears to be compatible with the other natural enemies and insect pollinators. The ability of *T. ni* to overwinter inside greenhouses enables this pest to colonize plants at the beginning of the season, when plants are first brought into the greenhouse. This has resulted in increased sprays of Btk to control *T. ni* and development of resistance to Btk in populations of *T. ni* in British Columbia (Janmaat and Myers 2003, 2006; Cervantes 2004). Subsequently, chemical pesticides are used which are not compatible with biocontrol agents for other pests or bumble bee pollinators, which is of major concern to the greenhouse industry. In Canada, the pollination of vegetable in greenhouses relies on the periodic introduction of bumble bee's colonies instead of manual or mechanical pollination.

### ***Campoletis sonorensis*** **Cameron (Hymenoptera: Ichneumonidae)**

In late summer of 2002, I discovered cocoons of a *T. ni* larval endoparasitoid in two tomato greenhouses in the Leamington – Kingsville area of Ontario. It was identified as *Campoletis sonorensis* (Cameron) (Hymenoptera: Ichneumonidae) by Dr. Andrew Bennett at the Canadian National Collection – Agriculture and Agrifood Canada. Since then, I have collected this parasitoid from, 1 cucumber, 2 pepper and 12 tomato greenhouses in Ontario.

The genus *Campoletis* is taxonomically complicated, being placed in subfamily Campopleginae, tribe Campoplegini (Burks et al. 1979) or in the tribe Porizontini (Townes 1971). In the Americas, two species, *C. sonorensis* (Cameron) and *C. flavicincta* (Ashmead) are the most common and share some of the same hosts. *Campoletis sonorensis* is frequently misidentified as *C. perdistincta* (Viereck), which is a non-preferred synonym for *C. flavicincta* (Carlson 1972). The confusion is further complicated because it was previously identified as *Limneria sonorensis*, *Campoletis websteri, Sagaritis websteri and Sagaritis provancheri* (Carlson 1972; Korytkowski and Casanova 1966; CABI 2005).

*Campoletis sonorensis* is a generalist solitary larval endoparasitoid that has been reported on about 30 species of Lepidoptera, primarily of the family Noctuidae which are considered to be insect pests in different economic crops (Lingren and Noble 1972; de Moraes et al. 1991; Machuca et al. 1989; CABI 2005). *Campoletis sonorensis* is widely distributed in the Americas where it has been reported to parasitise relatively large numbers of its hosts from Chile to Canada (Machuca et al. 1986; Carlson 1972; Hoballah 2001; Molina et al. 2003). Larvae of the tobacco budworm, *Helicoverpa virescens* (Fabricious) (Lepidoptera: Noctuidae), the corn earworm / tomato fruitworm, *Helicoverpa zea* (Boddie) and the fall armyworm *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae) are the most preferred hosts in crops like cotton, tobacco, corn and tomato (Lingren and Noble 1972; Carlson 1972). Although *C. sonorensis* has been considered as a potential biocontrol agent for these three pest species (Lingren et al. 1970; Lingren 1977; Siabatto 1991; Hoelscher and Vinson 1971; Isenhour 1985, Hoballah et al. 2004) and most of the research, to date, has been conducted using these three species as hosts, it is better known as a model system for the study of the effects of polydnaviruses on the host during the parasitism process (Stoltz et al. 1984). Certain endoparasitic wasps carry polydnaviruses (PDVs), a family of insect viruses characterized by a multipartite or segmented double-stranded DNA genome that exist in two states, as integrated proviral DNA in the

wasp chromosomal DNA and as extra-chromosomal DNA segments within the virions (Fleming and Summers 1991; Fleming 1992; Webb 1998). Two genera are recognized in this virus family: the bracoviruses, which are associated with braconid wasps, and the ichnoviruses, which are associated with the ichneumonid wasps (Stoltz et al. 1995). Polydnaviruses are of crucial importance for the survival of the braconid wasps and ichneumonid wasps. *Campoletis sonorensis* has a symbiotic mutualism with an ichnovirus (CsIV) which is integrated in the genome of the wasp. During oviposition of the endoparasitoid egg into the lepidopteran host, the wasp also injects venoms, ovarian proteins and CsIV. The ovarian and venom proteins transiently inhibit lepidopteran immune response over the initial 24 hours and later disrupt encapsulation. Viral protein titrers become high enough over this period to induce pathologic effects on the host, notably the viral proteins suppress cellular and humoral immunity, arrest host development, and suppress synthesis of some host proteins (Edson et al. 1981; Vinson and Stoltz 1986; Davies and Vinson 1988; Davies et al. 1987; Prevost et al. 1990; Webb and Luckhart 1994, 1996; Tanaka et al. 2002; Gill and Webb 2006).

Host finding studies had revealed that *C. sonorensis* females are attracted to many, but not all, plants on which their hosts feed by synomones produced after damage (Elzen et al. 1983, 1984; Baehrecke et al. 1989; McAuslane et al. 1990a, b; Vinson et al. 1994) Once on the damaged plant, antennal examination and ovipositor thrusting in response to kairomones present on the cuticle of larval hosts are the mechanisms by which hosts are located (Norton and Vinson 1974; Schmidt 1974; Wilson et al. 1974; Vinson 1975; Elzen et al. 1983).

Behavioural studies of *C. sonorensis* host-selection have found that females prefer third-instar host larvae of *S. frugiperda* and 2-5 day-old larvae of six different hosts, including *T. ni* (Isenhour 1985, Noble and Graham 1966; Lingren et al. 1970). Host age and color has no influence on acceptance behaviour by *C. sonorensis* but shape has an appreciable effect, a straight cylindrical shape is

more acceptable than a round or flat one (Schmidt 1974; Wilson et al. 1974); both experience and learning play a role in host selection by *C. sonorensis* (McAuslane et al. 1991; Vinson and Williams 1991),

Male *Campoletis sonorensis* courtship behaviour is elicited by sex pheromones released by females (Vinson 1972a) and both plant olfactory and visual cues are also involved in the location of mates (McAuslane et al. 1990b). The offspring sex allocation by *C. sonorensis* is influenced mostly by photoperiod, mating status and female age. Offspring produced from unmated females are all males and females may or not be produced after copulation but the exposure of older females to males for mating and a 12:12 (L:D) photoperiod yielded offspring with a greater percentage of females (Hoelscher and Vinson 1971). *Campoletis sonorensis* exhibited a type-II functional response when it was exposed to varying densities of *S. frugiperda* larvae at 2 temperature regimes and significantly more larvae were parasitised at 25$^0$C than at 30$^0$C (Isenhour 1985). Locomotory studies revealed maximum phototactic responses of *C. sonorensis* to yellow substrates and wavelengths of light in the green region (≈560 nm) with strong responses in the near-UV region (Schmidt et al. 1978; Hollingsworth et al. 1970). *Campoletis sonorensis* does not discriminate between non-parasitised larvae and larvae parasitised once by *C. sonorensis* but does discriminate against superparasitised larvae immediately following superparasitism (Vinson 1972b; Isenhour 1988). Elimination of competitors is through physical attack and later through physiological suppression. Female parasitoids mark their hosts to avoid superparasitism (Vinson 1972b; Isenhour 1988, Escribano et al. 2000).

Until today, the most valuable studies supporting the potential of *C. sonorensis* as a commercial biological control agent are: 1) the evaluation of *C. sonorensis* hosts and host age preferences (Lingren et al. 1970; Lingren and Noble 1972; Isenhour 1985); 2) the measurement of its functional response at different host densities and temperatures, as well as its developmental time, fecundity and lifespan (Isenhour 1985, 1986); 3) the evaluation of the effects of host stage

attacked on *C. sonorensis* using *H. virescens* as the host (Gunasena et al. 1989); 4) the description of the developmental morphology and behaviour of *C. sonorensis* larvae in *H. virescens* (Wilson and Ridgway 1974, 1975; Danks et al. 1979); 5) the evaluation of the relationships between *C. sonorensis* and several other larval parasitoids (Vinson and Ables 1980; Isenhour 1988); 6) the evaluation of augmentative releases of *C. sonorensis* against *H. virescens* (Lingren 1977; Lingren and Lukefahr 1977; Lingren et al. 1978); and, 7) the preliminary development of an in vitro mass rearing system (Hu 1998; Hu and Vinson 1997a,b).

The overall objective of the current research was to evaluate the potential of *C. sonorensis* as a biocontrol agent of *T. ni* in vegetable greenhouses. The current research examined three aspects of the interaction of *C. sonorensis* with *T. ni*:

1. Seasonal abundance of *T. ni* and natural levels of parasitism by *C. sonorensis* in field and greenhouse tomato in Southwestern Ontario (Chapter 2);
2. Host preference and fitness of *C. sonorensis* as a parasitoid of *T. ni* (Chapter 3); and,
3. Reproduction of *C. sonorensis* as an endoparasitoid of *T. ni* under laboratory conditions (Chapter 4).

The information obtained through the current research should also be useful in the development of a field conservation biological control program, which is of value to both field crop and greenhouse production, because it would assist in regulation of insect pests before they migrate into greenhouses.

## References

Andrewartha HG (1961) Introduction to the study of animal populations. Methuem, London.

Apablaza JU, Norero AL (1993) Captures of *Agrotis ipsilon*, *Heliothis zea* and *Trichoplusia ni* (Lepidoptera: Noctuidae) with synthetic pheromone traps in the Metropolitan region. Ciencia e Investigación Agraria 20:73-81

Askew RR (1971) Parasitic Insects. Heinemann, London.

Banham FL, Arrand JC (1970) Recognition and life history of the major insect and allied pests of vegetables in British Columbia. Ministry of Agriculture, Victoria, BC.

Baehrecke EH, Williams HJ, Vinson S B (1989) Electroantennogram responses of Campoletis sonorensis (Hymenoptera: Ichneumonidae) to chemicals in cotton (*Gossypium hirsutum* L.). Journal of Chemical Ecology 15: 37-45.

Burks BD, Hurd PD Jr, Krombein KV, Smith DP (1979) Catalog of Hymenoptera in America North of Mexico. Vol. 1. Smithsonian Institution Press, Washington D.C

CAB International (2005) Crop Protection Compendium. CABI Publishing. Wallingford, Oxfordshire. UK.

Cervantes V (2004) The overwinter survival of cabbage looper (*Trichoplusia ni*) in vegetable greenhouses: a potential factor for continued resistance to *Bt.* Annual Meeting of the Entomological Society of British Columbia. Simon Fraser University, Burnaby, BC. October 29.

Cervantes V (2005) Population ecology of *Trichoplusia ni* in vegetable greenhouses and the potential of *Autographa californica* nucleopolyhedrovirus for their control. MSc. Thesis. University of British Columbia, Vancouver, BC.

CIE (1974) Distribution Maps of Pests. Series A, No. 328. Wallingford, UK: CAB International.

Carlson RW (1972) Suppression of the name *Campoletis persdistincta* (Hymenoptera: Ichneumonidae) and the identity of species to which the name has been applied. Entomological News 83: 75-82

Coppel HC, Mertins JW (1977) Biological insect suppression. Springer, Berlin.

Danks HV, Rabb RL, Southern PS (1979) Biology of insect parasites of *Heliothis* in North Carolina. Journal of the Georgia Entomological Society 14: 36-64.

Davies DH, Strand MR, Vinson SB (1987) Changes in differential haemocyte count and in vitro behaviour of plasmatocytes from host *Heliothis virescens* caused by *Campoletis sonorensis* polydnavirus. Journal of Insect Physiology 33: 143-153.

Davies DH, Vinson SB (1988) Interference with function of plasmatocytes of *Heliothis virescens* in vivo by calyx fluid of the parasitoid *Campoletis sonorensis.* Cell Tissue Research 251: 467-475.

DeBach P (1964) Success, trends, and future possibilities. In: DeBach P (ed) Biological Control of Insect Pests and Weeds. Chapman and Hall, London. pp. 673-713

DeBach P, Hagen KS (1964) Manipulation of entomophagous species. In: DeBach P (ed) Biological Control of Insect Pests and Weeds. Chapman and Hall, London. pp. 429-458

DeBach P (1971) The use of imported natural enemies in insect pest management ecology. Proceedings of the Tall Timbers Conference on Ecological Animal Control and Habitat Management 3: 211-234.

DeBach P (1974) Biological control by natural enemies. Cambridge University Press. Cambridge.

de Moraes RR, Loeck AE, Belarmino LC (1991) Natural enemies of *Rachiplusia nu* (Guenée, 1852) and *Pseudoplusia includens* (Walker, 1857) (Lepidoptera: Noctuidae) on soybean in Rio Grande do Sul [In Portuguese.] Pesquisa Agropecuária Brasileira 26: 57–64.

Edson KM. Vinson SB, Stoltz DB, Summers MD (1981) Virus in a parasitoid wasp: suppression of the cellular immune response in the parasitoid's host. Science 211: 582-583

Eggleton P, Belshaw R (1992) Insect parasitoid; an evolutionary overview. Philosophical Transaction of the Royal Society. Series B, 337: 1-20.

Ehler LE (1998) Conservation biological control: past, present, and future. In Barbosa P (ed) Conservation biological control. Academic press, San Diego, California. pp. 1-8.

Elzen GW, Williams HJ, Vinson SB (1983) Response by the parasitoid *Campoletis sonorensis* (Hymenoptera: Ichneumonidae) to chemicals (synomones) in plants: implications for host habitat location. Environmental Entomology 12:1872-1876.

Elzen GW, Williams HJ, Vinson SB (1984) Isolation and identification of cotton synomones mediating searching behaviour by parasitoid *Campoletis sonorensis*. Journal of Chemical Ecology 10:1251-1264.

Escribano A, Williams T, Goulson D, Cave RD, Caballero P (2000) Parasitoid-pathogen-pest interactions of *Chelonus insularis* (Hymenoptera: Braconidae), *Campoletis sonorensis* (Hymenoptera: Ichneumonidae) and a nucleopolyhedrovirus in *Spodoptera frugiperda* larvae (Lepidoptera: Noctuidae). Biological Control 19: 265-273

Flanders S (1957) Principles and practices of biological control utilizing entomophagous insects. Division of Biological Control, University of California, Riverside, CA.

Flanders SE (1962) The parasitic Hymenoptera: Specialists in population regulation. The Canadian Entomologist 94: 1133-1147.

Fleming JGW (1992) Polydnaviruses: mutualists and pathogens. Annual Review of Entomology 37: 401–425.

Fleming JGW, Summers MD (1991) Polydnavirus DNA is integrated in the DNA of its parasitoid wasp host. Proceedings of the National Academy of Science. *U.S.A.* 88: 9770–9774.

Gauld ID, Bolton B (1988) The Hymenoptera. Oxford University Press. Oxford.

Gill TA, Webb BA (2006) Structural and functional characterization of a *Campoletis sonorensis* Ichnovirus (CsIV) Cys-motif protein (WHv1.6). In: Adams M, Bosco G, Denlinger D, Dhadialla T, Field L, Hildebrand J, James A, Kanost M, Moran N, Raikhel A, Sattelle D, Strausfeld N, Willis J, Wolfner M (eds). The Fifth

International Symposium on Molecular Insect Science. pp. 93-111. Journal of Insect Science *6:46*, available online: insectscience.org/6.46.

Gillespie DR, Raworth DA, Shipp JL (2002) *Trichoplusia ni* Hübner, Cabbage Looper (Lepidoptera: Noctuidae). In: Mason PG, Huber JT (eds) Biological Control Programmes in Canada, 1981-2000. CABI Publishing. New York. NY, pp. 269-271.

Greene GL (1984) Seasonal population of eggs and larvae in North America, In: Lingren PD, Green GL (eds) Suppression and management of cabbage looper populations. U.S. Department of Agriculture, Technical Bulletin No 1684: 30–35.

Gunasena GH, Vinson SB, Williams HJ (1989) Interrelationships between growth of *Heliothis virescens* (Lepidoptera: Noctuidae) and that of its parasitoid *Campoletis sonorensis* (Hymenoptera: Ichneumonidae). Annals of the Entomological Society of America 82: 187-191

Hassell MP, May RM (1973) Stability in sect host –parasite models. Journal of Animal Ecology 42: 693-726

Hassell MP, Rogers DJ (1972) Insect parasite responses in the development of population models. Journal of Animal Ecology 41: 661-676

Hassell MP, May RM (1973) Stability in Insect Host-Parasite Models. The Journal of Animal Ecology 42: 693-726

Hoballah ME (2001) Benefits, costs, and exploitations of caterpillar-induced odour emission in Maize plants. PhD Thesis. University of Neuchatel. Switzerland

Hoballah ME, Degen T, Bergvinson D, Savidan A, Tamo C, Turlings TCJ (2004) Occurrence and direct control potential of parasitoids and predators of the fall

armyworm (Lepidoptera: Noctuidae) on maize in the subtropical lowlands of Mexico. Agricultural and Forest Entomology 6: 83-88

Hochberg ME, Holt RD (1999) The uniformity and density of pest exploitation as guides to success in biological control. In: Hawkins BA, Cornell HV (eds.) Theoretical approaches to biological control. Cambridge University Press. Cambridge, pp 71-88.

Howard RJ, Garland JA, Seaman WL (1994) Diseases and pests of vegetables crops in Canada. Canadian Phytopathology Society and Entomological Society of Canada, Ottawa. Ontario.

Hoelscher CE, Vinson SB (1971) The sex ratio of a Hymenopterous parasitoid, *Campoletis perdistinctus*, as affected by photoperiod, mating, and temperature. Annals of the Entomological Society of America 64: 1373-1376.

Hollingsworth JP, Harstack AW Jr, Lingren PD (1970) The spectral response of *Campoletis perdistinctus*. Journal of Economic Entomology 63: 1758-1761.

Hu JS (1998) The in vitro development from egg to prepupa of *Campoletis sonorensis* (Hymenoptera: Ichneumonidae) in an artificial medium: Importance of physical factors. Journal of Insect Physiology 44: 455-462.

Hu JS, Vinson SB (1997a) In vitro development of *Campoletis sonorensis* (Hymenoptera: Ichneumonidae), a larval endoparasitoid of *Heliothis virescens* (Lepidoptera: Noctuidae) in an artificial medium with insect sources from egg to third larval instar. Entomophaga 42: 405-415.

Hu JS, Vinson SB (1997b) In vitro rearing of *Campoletis Sonorensis*, a larval endoparasitoid of *Heliothis virescens* from egg to third instar in an artificial medium devoid of insect sources. Entomologia Experimentalis et Applicata 85:

263-273.

Huffaker CB (1976) An overview of biological control, with particular commentary on biological weed control. In: Freeman TD (ed) Proceedings of the 4th International Symposium of Biological Control of Weed. Center for Environmental Progress. University of Florida at Gainesville, pp. 3-12.

Huffaker CB, Messenger PS, DeBach P (1971) The natural enemy component in natural control and the theory in biological control. In: Huffaker CB (ed) Biological Control. Plenum, New York. pp. 16-67.

Huffaker CB, Simmonds FJ, Laing JE (1976) The theoretical and empirical basis of biological control. In: Huffaker CB, Messenger PS (eds) Theory and practice of biological control. Academic Press, New York. pp. 41-80.

Huffaker CB, Rabb RL, Logan JA (1977) Some aspects of population dynamics relative to augmentation of natural enemy action. In: Ridgway RL, Vinson SB (eds) Biological control by augmentation of natural enemies, Insect and Mite Control with Parasites and Predators. Plenum press, New York and London, pp. 3-38.

Isenhour DJ (1985) *Campoletis sonorensis* (Hym.: Ichneumonidae) as a parasitoid of *Spodoptera frugiperda* (Lep.: Noctuidae): host stage preference and functional response. Entomophaga 30: 31-36.

Isenhour DJ (1986) Developmental time, adult reproductive capability, and longevity of *Campoletis sonorensis* (Hymenoptera: Ichneumonidae) as a parasitoid of fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae). Annals of the Entomological Society of America 79: 893-897.

Isenhour DJ (1988) Interactions between two hymenopterous parasitoids of the fall armyworm (Lepidoptera: Noctuidae). Environmental Entomology 17: 616-620.

Janmaat AF, Myers JH (2003) Rapid evolution and the cost of resistance to *Bacillus thuringiensis* in greenhouse populations of cabbage looper, *Trichoplusia ni*. Proceedings of the Royal Society of London *B.* 270: 2263-2270

Janmaat AF, Myers JH (2006) The influences of host plant and genetic resistance to *Bacillus thuringiensis* on trade-offs between offspring number and growth rate in cabbage loopers, *Trichoplusia ni.* Ecological Entomology 31: 172-178.

Korytkowski CH, Casanova P (1966) Estudios de *Campoletis perdistinctus* (Viereck)(Hym.: Ich.) parasito de *Heliothis virescens* Fab. (Lep.: Phalaen.). Revista Peruana de Entomologia 9: 24-29.

Kostrowicki AS (1961) Studies on the Palaerctic species of the subfamily Plusiinae (Lepidoptera, Phalaenidae). Acta Zoologica Cracoviensia 6: 367-472.

Krebs CJ (1972) Ecology, the experimental analysis of distribution and abundance. Harper and Row, New York.

La Salle J (1993) Parasitic Hymenoptera, biological control and biodiversity, In: La Salle J, Gauld ID (eds) Hymenoptera and Biodiversity. CAB International, Wallingford, UK, pp. 197-215.

La Salle J, Gauld ID (1991) Parasitic Hymenoptera and the biodiversity crisis. *Redia* 74: 315-334

La Salle J, Gauld ID (1993) Hymenoptera and Biodiversity. CAB International, Wallingford, UK.

Lafontaine JD, Poole RW (1991) Noctuoidea, Noctuidae (part) – Plusiinae. Fascicle 25.1. In: Hodges RW, Davis DR, Dominick T, Ferguson DG, Franclemont JC, Munroe EG, Powell JA (eds) The moths of America North of Mexico. The Wedge Entomological Research Foundation, Washington, DC.

Lingren PD (1977) *Campoletis sonorensis*: maintenance of a population on tobacco budworms in a field cage. Environmental Entomology 6: 72-76.

Lingren PD, Guerra RJ, Nickesen JW, White C (1970) Host and host-age preference of *Campoletis perdistinctus*. Journal of Economic Entomology 63: 518-522

Lingren PD, Noble LW (1972) Preference of *Campoletis perdistinctus* for certain noctuid larvae. Journal of Economic Entomology 65:104-107.

Lingren PD, Lukefahr MJ (1977) Effects of nectariless cotton on caged populations of *Campoletis sonorensis*. Environmental Entomology 6: 586-588

Lingren PD, Lukefahr MJ, Diaz M JR, Hartstack A JR (1978) Tobacco Budworm control in caged cotton with a resistant variety, augmentative releases of *Campoletis sonorensis*, and natural control by other beneficial species. Journal of Economic Entomology 71:739-745.

Machuca JR, Arretz P, Araya, JE (1989) Presencia de *Campoletis sonorensis* (Cameron, 1886) (Hymenoptera: Ichneumonidae) en Chile. Acta Entomologica Chilena 15: 269-270.

Martin PB, Lingren PD, Greene GL (1976) Relative abundance and host preferences of cabbage looper, soybean looper, tobacco budworm, and corn earworm on crops grown in northern Florida. Environmental Entomology 5: 878-882.

McAuslane HJ, Vinson SB, Williams HJ (1990a) Effect of host diet on flight behaviour of the parasitoid *Campoletis sonorensis* (Hymenoptera: Ichneumonidae). Journal of Entomological Science 25: 562-570.

McAuslane HJ, Vinson SB, Williams HJ (1990b) Influence of host plant on mate location by the parasitoid *Campoletis sonorensis* (Hymenoptera: Ichneumonidae). Environmental Entomology 19: 26-31.

McAuslane HJ, Vinson SB, Williams HJ (1991) Influence of adult experience on host microhabitat location by the generalist parasitoid, *Campoletis sonorensis* (Hymenoptera: Ichneumonidae). Journal of Insect Behavior 4: 101-113.

Metcalf CL, Flint WP, Metcalf RL (1962) Destructive and useful insects. 4th ed. McGraw-Hill. New York, USA.

Mitchell ER, Chalfant RB (1984) Biology, behavior and dispersal of adults. In: Lingren PD, Greene GL (eds) Suppression and management of cabbage looper populations. US Department of Agriculture, Technical Bulletin No. 1684, pp. 14-18.

Molina-Ochoa J, Carpenter JE, Heinrichs EA, Foster JE (2003) Parasitoids and parasites of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in the Americas and Caribbean Basin: an inventory. Florida Entomologist 86: 254–289

Narendram, TC (2001) Parasitic Hymenoptera and biological control. In: Upadhyay RK, Mukerji KG, Chamola BP (eds) Biocontrol potential and its exploitation in sustainable agriculture Volume 2: Insect pests. Kluwer Academic / Plenum Publishers. New York, NY. pp. 1-12.

Noble LW, Graham HM (1966) Behavior of *Campoletis perdistinctus* (Viereck) as a parasite of the Tobacco budworm. Journal of Economic Entomology 59: 1118-1120

Norton WN, Vinson SB (1974) Antennal sensilla of three parasitic hymenoptera. International Journal of Insect Morphology and Embryology 3: 305-316.

Noyes JS (1985) Chalcidoids and biological control. Chalcid Forum 5: 5-10.

Paine RT (1969) A note on trophic complexity and community stability. American Naturalist 103: 91-93.

Paine RT, Levin SA (1981) Intertidal landscapes: disturbance and the dynamics of pattern. Ecological Monographs 51: 145-178.

Prevost G, Davies DH, Vinson SB (1990) Evasion of encapsulation by parasitoid correlated with the extent of host hemocyte pathology. Entomologia Experimentalis et Applicata 55: 1-10

Rabb RL, Stinner RE, van den Bosch R (1976) Conservation and augmentation of natural enemies. In: Huffaker CB, Messenger PS (eds) Theory and practice of biological control. Academic Press, New York, NY. pp. 233-254.

Reid WV, Miller, KR (1989) Keeping Options Alive: The Scientific Basis for Conserving by Biodiversity, World Research Institute, Washington, DC.

Reuter OM (1913) Lebensgewohnheiten und Instinkte der Insekten. Berlin: Friedlander.

Ridgway RL, Vinson SB (1977) Biological control by augmentation of natural enemies: insect and mite control with parasites and predators. Plenum Press, New York.

Siabatto PA (1991) Introducción del parasito *Campoletis* sp., agente benéfico para el control de *Heliothis* spp en la zona del Tolima. Research proposal. National Federation of Cotton Growers. Colombia.

Schmidt GT (1974) Host-acceptance behaviour of *Campoletis sonorensis* toward *Heliothis zea*. Annals of the Entomological Society of America 67: 835-844.

Schmidt GT, Masseidvaag F, Pickett EE, Booth GD (1978) Oviposition by *Campoletis sonorensis* as a function of light source and substrate color. Journal of the Georgia Entomological Society 13: 192-201.

Shorey HH, Andres LA, Hale RL (1962) The biology of *Trichoplusia ni* 1: Life history and behavior. Annals of the Entomological Society of America 55: 591-597.

Stoltz DB, Krell PJ, Summers MD, Vinson SB (1984). Polydnaviridaea proposed family of insect viruses with segmented, doublestranded, circular DNA genomes. Intervirology 21: 1–4.

Stoltz DB, Beckage NE, Blissard GW, Fleming JGW, Krell PJ, Theilmann DA, Summers MD, Webb BA (1995) Polydnaviridae In: Murphy FA, Fauquet CM, Bishop DHL, Ghabrial SA, Jarvis AW, Martelli GP, Mayo MA, Summers MD (eds.), Virus Taxonomy. Sixth Report of the International Committee on Taxonomy of Viruses. Springer-Verlag, Vienna and New York, pp. 143–147.

Sutherland DW, Greene SGL (1984) Culitvated and wild host plants. In: Lingren PD, Greene GL (eds) Suppression and management of cabbage looper populations. US Department of Agriculture, Technical Bulletin No. 1684. pp. 1-13.

Sweetman HL (1958) The principles of biological control. Brown, Dubuque.

Tanaka K, Matsumoto H, Hayakawa Y (2002) Analysis in the course of polydnavirus replication in ovarian calyx cells of the parasitoid wasp, *Cotesia kariyai* (Hymenoptera: Braconidae). Applied Entomology and Zoology 37: 323-328

Townes H (1971) The Genera of Ichneumonidae. Part 4. Memoirs of American Entomological Institute 17: 1-372.

van Driesche RG, Bellows TS Jr. (1996). Biological Control. Kluwer Academic Publishers.

van Lenteren JC (1986a) Parasitoid in the greenhouse: successes with seasonal inoculative release systems. In: Waage J, Greathead D (eds) Insect Parasitoids. Academic Press, London. pp. 341-374

van Lenteren JC (1986b) Evaluation, mass production quality control and release of entomophagous insects. In: Frang JM (ed) Biological Plant and Health Protection. Fisher Veriag, Stuttgart. pp. 31-56.

van Lenteren JC (2000) Success in biological control of arthropods by augmentation of natural enemies. In: Gurr G, Wratten S (eds) Biological control: measures of success. Kluwer Academic Publishers, Netherlands. pp. 77-103.

van Lenteren JC (2006) IOBC Internet Book of Biological Control. Version 4. International Organization of Biological Control.

van Lenteren JC, Manzaroli G (1999) Evaluation and use of predators and parasitoids for biological control of pests in greenhouses. In: Albajes R, Gullino MR, van Lenteren JC, Elad Y (eds) Integrated pest and disease management in greenhouse crops. Kluwer Publishers, Dordrecht, Netherlands. pp. 183-20

Varley GC (1951) Ecological aspects of population regulation. Transactions of the 9th International Congress of Entomology in Amsterdam 2: 210-214.

Varley GC, Gradwell GR, Hassell MP (1973) Insect population ecology, an analytical approach. Blackwell, Oxford.

Vinson SB (1972a) Courtship behavior and evidence for a sex pheromone in the parasitoid *Campoletis sonorensis* (Hymenoptera: Ichneumonidae). Environmental Entomology 1: 409-414.

Vinson SB (1972b) Competition and host discrimination between two species of tobacco budworm parasitoids. Annals of the Entomological Society of America 65: 229-236.

Vinson SB (1975) Biochemical coevolution between parasitoids and their hosts. In: Price PW (ed) Evolutionary strategies of parasitic insects and mites. Plenum, New York, pp. 14-48.

Vinson SB, Ables JR (1980) Interspecific competition among endoparasitoids of tobacco budworm larvae. Entomophaga 25: 357-362.

Vinson SB, Stoltz DB (1986) Cross-protection experiments and two parasitoid viruses. Annals of the Entomological Society of America 79: 216-218.

Vinson SB, Williams HJ (1991). Host selection behavior of *Campoletis sonorensis*: a model system. Biological Control 1: 107-117.

Vinson SB, Williams HJ, Lu J (1994) Identification of different compounds from different plants responsible for the orientation of *Campoletis sonorensis* host sites. Norwegian Journal of Agricultural Science (Supplement 16) pp. 207-210.

Waage JK, Hassell MP (1982) Parasitoids as biological control agents – a fundamental approach. Parasitology 84: 241-268.

Waterhouse DF (1998) Biological Control of Insect Pests: Southeast Asian Prospects. ACIAR Monograph No. 51. Brown Prior Anderson, Melbourne.

Webb BA (1998) Polydnavirus biology genome structure and evolution In: Ball A, Miller LK (eds) The Insect Viruses. Plenum Press, New York, NY. pp. 105–139.

Webb BA, Luckhart S (1994) Evidence for an early immunosuppressive role for related *Campoletis sonorensis* venom and ovarian proteins in *Heliothis virescens*. Archives of Insect Biochemistry and Physiology 26: 147–163.

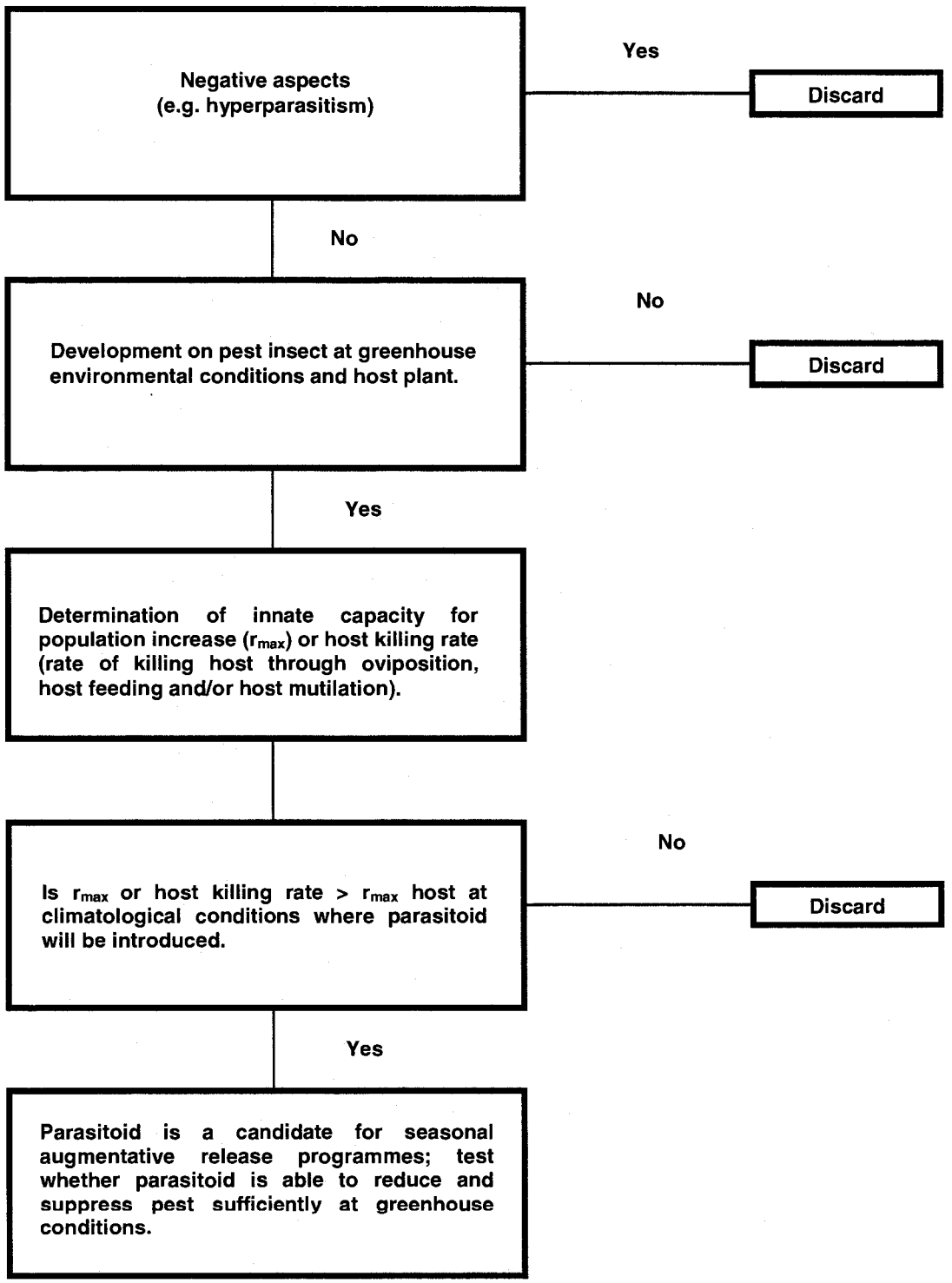
Webb BA, Luckhart S (1996) Factors mediating short- and long-term immune suppression in a parasitized insect. Journal of Insect Physiology 42: 33-40

Wilson DD, Ridgway RL (1974) Cocoon spinning behaviour of the parasitoid *Campoletis sonorensis*. Environmental Entomology 3: 714-717.

Wilson DD, Ridgway RL, Vinson SB (1974) Host acceptance and oviposition behavior of the parasitoid *Campoletis sonorensis* (Hymenoptera: Ichneumonidae). Annals of the Entomological Society of America 67: 271-274.

Wilson DD, Ridgway RL (1975) Morphology, development, and behavior of the immature stages of the parasitoid, *Campoletis sonorensis* (Hymenoptera: Ichneumonidae). Annals of the Entomological Society of America 68: 191-196.

Figure 1.1: Flow diagram depicting an evaluation programme for natural enemies to be used in seasonal augmentative releases (van Lenteren and Manzaroli, 1999).


Negative aspects
(e.g. hyperparasitism)
Yes
Discard
No
Development on pest insect at greenhouse environmental conditions and host plant.
No
Discard
Yes
Determination of innate capacity for population increase ($r_{max}$) or host killing rate (rate of killing host through oviposition, host feeding and/or host mutilation).
Is $r_{max}$ or host killing rate > $r_{max}$ host at climatological conditions where parasitoid will be introduced.
No
Discard
Yes
Parasitoid is a candidate for seasonal augmentative release programmes; test whether parasitoid is able to reduce and suppress pest sufficiently at greenhouse conditions.

## Chapter 2

**Seasonal Abundance of *Trichoplusia ni* (Lepidoptera: Noctuidae) and its parasitism by *Campoletis sonorensis* (Hymenoptera: Ichneumonidae) in field and greenhouse tomato in Southwestern Ontario.**

### Introduction

Insects have the potential to increase their numbers dramatically and to adjust their numbers in response to the dynamic environment in which they occur. Nevertheless, changes in population numbers often occur slowly because of the continual adjustment caused by abiotic and biotic factors (Ridgway and Vinson 1977). Pest situations arise as a result of environmental disturbances of an unusual nature or degree and man generates many of them. The introduction of potential pests, either intentionally or accidentally, into favorable environments where natural enemies are not present often leads to serious pest problems (Ridgway and Vinson 1977). It is a common occurrence that the growth of susceptible crops or animals in monoculture allows large pest populations to build-up. The widespread disruption of the ecosystem that occurs when crops are planted or harvested destroys alternative hosts/prey for natural enemies, and reduces shelter, non-prey food sources and oviposition material (Ridgway and Vinson 1977). This limits the response of natural enemies to pest resurgence. Use of pesticides adversely affects these beneficial organisms and induces the development of resistance in the pest populations, which further encourages pest population outbreaks (Ridgway and Vinson 1977).

The study of numerical changes occurring in populations, or population dynamics, is really the study of quantitative population ecology and is concerned not only with observing and describing how the population size of a species varies in time and space, but also with separating out and understanding the processes which cause this variation (Coppel and Mertins 1977). Mortality factors

acting on an insect population can cause dynamic changes such as the mean population density and degree of fluctuation around the mean population equilibrium density. Natural enemies contribute to population regulation through mortality factors that can act by returning populations to an equilibrium after some perturbation (i.e. stabilizing population numbers) or by restricting population numbers within certain limits, but allowing fluctuations in numbers (e.g. cycles) within those limits (DeBach 1974, Huffaker and Messenger 1964, 1976; Murdoch and Walde 1989; Kidd and Jervis 2005).

In order for a mortality factor such as parasitism to regulate a population, the strength of its action must be dependent on the density of the population affected. That is, it needs to be density-dependent with its proportional effect being greater at higher population densities. If the proportion of host parasitised varies with changing host density, either temporally or spatially, this can profoundly affect the dynamics of the interaction (Howard and Fiske 1911; Smith 1935; Morris 1959; Huffaker et al. 1971; Varley and Gradwell 1971; Kuno 1973; Hassell and Waage 1984; Hassell 1987; Solow and Steele 1990; DeBach and Rosen 1991; Boivin 1993; Turchin 1995; Murdoch and Briggs 1996; van Lenteren 2000; Sigiura and Osawa 2002; Matsumoto et al. 2004; Kidd and Jervis 2005). A strong density-dependent response is one of the key criteria in the selection of potential natural enemies for biocontrol (van Lenteren 1986; Waage and Hassell 1982)

The Cabbage Looper, *Trichoplusia ni,* (Hübner) (Lepidoptera: Noctuidae) is a cosmopolitan insect pest that causes damage in more than 160 species of plants (Martin et al. 1976; Sutherland and Greene 1984), although Brassicas (*Brassica oleracea* L., Brassicaceae) and cotton (*Gossypium hirsutum* L. Malvaceae) are most frequently cited as being damaged (Waterhouse, 1998). Each spring the overwintering population of *T. ni* in the southern United States migrates north to establish seasonal populations in Canada (Lafontaine and Poole 1991). *Trichoplusia ni* became a chronic pest of Canadian greenhouse vegetable crops in the early 1990s (Gillespie et al. 2002). Outside greenhouses, *T. ni* is an

important pest of brassicas and in many other crops in Ontario, but it is less important in other vegetable-producing areas of Canada (Howard et al. 1994). In commercial settings, growers rely on Btk *(Bacillus thuringiensis var. kurstaki)* products against outbreaks of *T. ni* which appears to be compatible with the other natural enemies and insect pollinators. However, the recent development of *T. ni* resistance to Btk is a major concern in the industry (Janmaat and Myers 2003, 2006; Cervantes 2005).

*Campoletis sonorensis* (Cameron) (Hymenoptera: Ichneumonidae) is a generalist larval endoparasitoid of at least 30 different Lepidoptera hosts mostly belonging to the Noctuidae family (Lingren and Noble, 1972; de Moraes et al. 1991; Machuca et al. 1989; CABI 2005). The geographic distribution of this parasitoid includes all the Americas (Chile to Canada) and it is an important natural agent in the regulation of pest populations within agro-ecosystems of various countries including the tobacco budworm, *Helicoverpa virescens* (Fabricious) (Lepidoptera: Noctuidae), the corn earworm / tomato fruitworm, *Helicoverpa zea* (Boddie) and the fall armyworm *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae), in cotton (*Gossypium hirsutum* L.) (Malvaceae) and corn (*Zea mays* L.) (Gramineae) (Wene, 1943; Korytkowski and Casanova, 1966; Graham et al. 1972; Pair et al. 1982; Isenhour 1985; Machuca et al. 1989; de Moraes et al. 1991; Siabatto, 1991).

Starting in 2002, I have collected *C. sonorensis* as a common larval endoparasitoid of *T. ni* in the vegetable greenhouses in Essex County, Ontario each year. Although this parasitoid has never been reported as an important natural enemy of *T. ni* in field or greenhouse crops, the agroclimatic conditions in Southwestern Ontario have allowed *C. sonorensis* to become a common natural enemy of *T. ni.* The objective of this study was to measure the natural seasonal population dynamics of the larval stages of *T. ni* and its parasitoids. Specifically, I measured: 1) The seasonal changes in abundance of each larval stage of *T. ni;* 2) The community composition and diversity of the parasitoid assemblage on

larval stages of *T. ni;* 3) The proportion of *T. ni* larvae parasitised within each larval stage; 4) The parasitism rate of *T. ni* larvae by *C. sonorensis;* and 5) The potential for density dependent population regulation of *T. ni* by *C. sonorensis.*

**Materials and Methods**

The population dynamics of larval stages of *T. ni* and its native larval parasitoids were measured on tomato (*Lycopersicum esculentum* Mill.) (Solanaceae) crops in 2005 and 2006. Three 2000-plant conventional fields and three 1.6 hectare greenhouses in Leamington and Essex County (Ontario, Canada) were chosen. As these were commercial crops, the fields and greenhouses in 2005 were managed using insecticides. In 2006, the fields were managed without insecticides; however, insecticides were still used within the greenhouses. Number and active ingredients of the insecticide sprays, planting dates, crop variety and other crop details are provided in Table 2.1a and b.

Sampling Method:

*Trichoplusia ni* larvae were sampled weekly. In greenhouses, *T. ni* larvae sampling began the first week of May (Week 1) for both years. In fields, *T. ni* larvae sampling began on different dates, depending on weather conditions. In fields in 2005, it began on May 20 (Week 3) and in 2006, the first week of sampling began on June 13 (Week 8). In greenhouses, rows were selected from the front, middle and back of the greenhouse for a total of 1.5 hours of sampling time per greenhouse (mean ± SE of 1103 ± 66 plants in 2005; mean ± SE of 1358 ± 141 plants in 2006). In each selected row, all the plants were examined for the presence of *T. ni* larvae. For each field, a total of 100 plants were sampled. Starting from a different corner of the field on each sampling date, plants were selected and examined for *T. ni* larvae every 10 steps in a zigzag pattern. All *T. ni* larvae were collected and their location, stage and the date of collection was recorded. Larvae were reared individually on a pinto bean diet

(Shorey and Hale 1965) in a growth chamber at 24°C, 12L:12D photoperiod and 60% RH. The immatures were checked every other day for either emergence of a parasitoid or an adult *T. ni* moth. For each emerging parasitoid, the host stage at which the parasitoid cocoon developed was recorded. This information provided the means to calculate the percentage of *T. ni* larvae parasitised (% parasitism) and natural host stage preference by the parasitoids. A representative specimen of each species of parasitoid that emerged from *T. ni* was sent for identification to Dr. John Huber, Director of the parasitoid systematic department at the Canadian National Collection, Agriculture and Agri-food Canada, Ottawa.

For calculation *of T. ni* parasitism by *C. sonorensis,* only the 2nd larval instar was considered. From both years there were just 10 instances of parasitism within the 3rd instar stage of *T. ni* and all other occurrences of parasitism were in the 2nd instar.

Percentage of parasitism was calculated as follows:

$$RP = P_L \times 100 / T_L$$

Where RP = rate of parasitism, $P_L$ = number of 2nd instar parasitised larvae, $T_L$ = total number of 2nd instar larvae.

Alternative plant and insect hosts of *C. sonorensis*:

In one of the tomato fields during 2006, *T. ni* larvae were sampled on weeds and in one 0.2-hectare sweet corn (*Zea mays* L., Gramineae) field beside the tomato field that was under attack by a high population of fall armyworm, *S. frugiperda,* which was also sampled. In addition, one pepper (*Capsicum annum* L., Solanaceae) and one cucumber (*Cucumis sativus* L., Cucurbitaceae) greenhouse contained populations of *T. ni* and these larvae were sampled.

Statistical Analysis:

The seasonal abundance of *T. ni* larvae was calculated from the mean number of larvae per plant from the three tomato fields and from the greenhouses by year, respectively.

The descriptive statistics for the parasitoid species assemblage from the tomato fields in both years (not calculated from tomato greenhouses because just one species was found) consist of species richness, relative abundance, Simpson's diversity index and Simpson's measure of evenness as follows (Magurran 2004):

The relative abundance of parasitoids was determined using the formula (Krebs 1985):

$$\textit{Relative abundance} = \frac{\text{Nr. of individuals per particular species}}{\text{Total no. of individuals of all species}} \times 100$$

*Simpson's diversity Index*

$$\mathbf{D} = 1 - \Sigma \left[ n_i (n_i - 1) / N (N - 1) \right]$$

Where $n_i$ = the number of individuals in the *ith* species and, N = the total number of individuals.

*Measure of parasitoid evenness*

This measure of evenness was calculated by dividing the reciprocal form of the Simpson's index by the number of species in the sample (Smith and Wilson 1996; Krebs 1999):

$$E_{1/D} = \frac{(1/D)}{S}$$

Where, D = Simpson's diversity index, and S = number of species in the sample.

Chi-Square tests were used to compare the number of parasitised larvae of each instar of *T. ni.* ANOVA was used to compare the parasitism rate of *C. sonorensis* on *T. ni* 2$^{nd}$ instar larvae by field and by years. Kruskal-Wallis tests were used to compare the number of *T. ni* 2$^{nd}$ instar larvae per plant between fields and between years as these data did not meet the normality and variance criteria for ANOVA.

Pearson correlations were used to initially determine if *C. sonorensis* appeared to have an impact on *T. ni* 2$^{nd}$ instar population dynamics in fields in 2006. Due to the numerous Btk sprays in greenhouses in both year and chemical pesticides in 2005 fields, this test was not conducted using the data obtained from them.

Although no method is likely to be efficient at detecting all forms of density dependence and no consensus has been reached as to which technique is most appropriate (Kuno 1973; Hassell 1987; Solow and Steele 1990; Boivin 1993; Turchin 1995; van Lenteren 2000; Sigiura and Osawa 2002;), linear regression is frequently used (e.g., Reeve and Murdoch 1985; Strong 1989; Boivin 1993, Sigiura and Osawa 2002; Matsumoto et al. 2004). To specifically examine the possibility of density dependent population regulation of *T. ni* by *C. sonorensis*, the relationship between density of 2$^{nd}$ instar *T. ni* and percent parasitism by *C. sonorensis* was examined using linear regression analysis from the 2006 field data, as no insecticides were applied to these fields. Temporal density-dependence was analyzed by comparing the density and percent parasitism in the 2$^{nd}$ larval instar among the sampling periods when parasitised larvae were found. These data were analyzed by pooling data from the 100 plants for a given sampling day. Before the regression analyses, the proportion of parasitised hosts was square root-arcsine transformed (Sokal and Rohlf 1981), and host densities were log-transformed. In this regression analysis, a significant positive or

negative slope indicates positive or inverse density dependence, respectively. All analyses were conducted in SPSS v.15 (2006)

## Results

Seasonal abundance of larval instars of *T. ni*

The number of *T. ni* larvae varied seasonally (Figure 2.1a-b), and *T. ni* generations overlapped (Figure 2.2a-d). In both tomato fields and greenhouses, all stages of *T. ni* larvae were present across the growing season, however, population density varied. In 2005, the first larvae were collected on July 6 (Week 10) in fields, however this occurred 3 weeks later in 2006 (July 20). In 2005, it is hard to describe the real growth pattern of the population of *T. ni* because the three plots were sprayed with chemical insecticides during the time the mean number of larvae per plant was the lowest (Weeks 11-12) (Figure 2.1a). In 2006, the larvae population increased almost steadily until Week 18 when there is a peak of 0.43 larvae per plant. By the end of the season, the mean number of larvae began declining (Figure 2.1a). In vegetable greenhouses in British Columbia, pest incidence of 1 large *T. ni* larvae per plant would trigger a spray of a *Bacillus thuringiensis* product, as would, in all likelihood, 1 large caterpillar per 2 plants (Gillespie et al. 1997)

It is impossible to define a real growth population pattern of *T. ni* in the tomato greenhouses because as soon as the first larvae were found, the insecticide *Btk* was sprayed continuously until the end of the season. However, there was a peak in larval numbers after mid-July (Week 12) in both years (Figure 2.1b) of 0.052 and 0.084 larvae per plant, respectively. In both fields and greenhouses, the 2$^{nd}$ larval instar was the most abundant stage collected, followed by the 3$^{rd}$ instar in fields and the 1$^{st}$ instar in greenhouses (Figure 2.2).

Because insecticide sprays were used in fields in 2005 and greenhouses in both years, the most natural population growth of *T. ni* is only represented by the fields in 2006, where no sprays were used (Figures 2.1a and 2.2b). The mean number of 2nd instar larvae increased throughout the season and by the end of August (Week 18) the population of 2nd instar larvae started to decrease. In fields in 2005 and in greenhouses for both years, although the increase in the mean number of the 2nd instar larvae of *T. ni* is notable through the season, it is interrupted, likely by the numerous insecticide sprays.

Parasitism of *T. ni* by larval parasitoids

During the two year study, the total parasitoid species richness in fields was 10 (Table 2.2). Within each year, the total parasitoid species richness was 7, with 4 species not collected in both years. All of the parasitoids were hymenopterans, with the exception of 1 dipteran that could not be identified to species. Nine were primary parasitoids, of which 7 were larval endoparasitoids, 1 egg-larval endoparasitoid and 1 larval ectoparasitoid. There was also 1 hyperparasitoid reared from *C. sonorensis*, *Trichomalopsis viridescens* (Walsh)(Hymenoptera: Pteromalidae). Although the family Braconidae had the greatest species richness, the family Ichneumonidae had the greatest relative abundance due to the dominance of the solitary larval endoparasitoid, *C. sonorensis* (Table 2.3). Simpson's diversity index of 0.7 in 2005 and 0.58 in 2006 for fields demonstrates that the field tomato ecosystems tend to be homogeneous in parasitoid diversity. Simpson's evenness indexes of 0.20 in 2005 and 0.25 in 2006 for fields represent that the relative abundance of the species found within the field tomato parasitoid community each year diverge due to the high dominance of *C. sonorensis* (Table 2.3).

Of the 400 *T. ni* larvae collected within fields in 2005, 51 were parasitised by *C. sonorensis* (12.75%) and 10 were parasitised by six other larval parasitoid species (2.5%) (Table 2.4). The second most common parasitoid species were

*Euplectrus* spp. (Westwood) (Hymenoptera: Eulophidae) and *Copidosoma floridanum* (Ashmead) (Hymenoptera: Encytidae) representing 0.75% of the total parasitism. Of the 365 *T. ni* larvae collected within fields in 2006, 62 were parasitised by *C. sonorensis* (16.98%) and 21 were parasitised by six other larval parasitoid species (5.46%). The second most common parasitoid species was *Cotesia marginiventris* (Cresson) (Hymenoptera: Braconidae) with just 1.64% of the total parasitism (Table 2.4).

Inside tomato greenhouses, *C. sonorensis* was the only larval parasitoid reared from *T. ni*. Of the 838 *T. ni* larvae collected in 2005, 22 were parasitised by *C. sonorensis* (2.63%) and in 2006, 22 of the 1645 *T. ni* larvae collected were parasitised by *C. sonorensis* (2.37%) (Table 2.5).

In both, fields (2005: $X^2_{4,1}$ = 443.052, P< 0.0001; 2006: $X^2_{4,1}$ = 62.982, P< 0.0001) and greenhouses (2005: $X^2_{4,1}$ = 14.678, P<0.005; 2006: $X^2_{4,1}$ = 21.864, P<0.0001) regardless of year, the 2$^{nd}$ instar of *T. ni* was the most commonly parasitised stage of development by *C. sonorensis* and other parasitoid species (Table 2.5). The number of parasitised 2$^{nd}$ instars differed from all other parasitised instars combined for both fields (2005: $X^2_{1,1}$ = 43.422, P< 0.0001; 2006: $X^2_{1,1}$ = 59.038, P< 0.0001) and greenhouses (2005: $X^2_{1,1}$ = 14.311, P<0.0001; 2006: $X^2_{1,1}$ = 20.739, P<0.0001) within both years (Table 2.5).

Percent parasitism of *T. ni* 2$^{nd}$ instar larvae by *C. sonorensis* in fields ranged from 11.5 to 75.0% in 2005 and 14.3 to 87.5% in 2006 (Figures 2.3a-b). The first *C. sonorensis* were found on July 6 and July 20, in 2005 and 2006 respectively. The highest parasitism rates occurred on August 10 (week 15) in 2005 and on August 9 (week 8) in 2006. In both years, there was no difference in *C. sonorensis* parasitism rates between fields (2005: $F_{2,17}$=3.18, P=0.05; 2006: $F_{2,23}$=0.618, P=0.097). However, there was a difference between years ($F_{1,41}$=6.272, P=0.016). There was no difference in the number of *T. ni* 2$^{nd}$ instar larvae

per plant between fields (2005: Kruskal-Wallis $X^2_2 = 0.416$, P=0.812; 2006: $X^2_2 = 2.878$, P= 0.237) nor between years ($X^2_1 = 1.358$, P= 0.244).

The parasitism rates by *C. sonorensis* on *T. ni* larvae in greenhouses ranged from 5.0 to 60% in 2005 and from 2.5 to 75.0% in 2006. The highest parasitism rate was found on August 19 (Week 16) in 2005 and on July 5 (Week 10) in 2006. The first *C. sonorensis* were found on June 16 and on June 5, respectively. The highest mean parasitism rate by *C. sonorensis* within fields was 58.17% on July 28 (Week 13) in 2005 and 76.33% on August 9 (Week 15) in 2006 (Figure 2.3). Within greenhouses, the highest mean parasitism rate was 20.1% on August 19 (Week 16) in 2005 and 25% on July 5 (Week 10) in 2006 (Figure 2.3).

In 2006, the number of 2nd instar larvae of *T. ni* and the number of parasitised larvae by *C. sonorensis* in fields was positively correlated overall (Pearson correlation r=0.946, p<0.0001, n=22), and individually within two of the three fields (Table 2.6). Additionally, the overall relationship between the number of 2nd instar larvae of *T. ni* and percent parasitism by *C. sonorensis* in fields in 2006 was positively density-dependent (b= 0.322, $r^2 = 0.182$, P= 0.048) (Table 2.7). On a weekly basis, it was only during week 11 (August 24, 2006) that the relationship was positively density dependent (b=0.940, $r^2$=0.998, p=0.025) (Table 2.8).

Alternative plant and insect hosts of *C. sonorensis*:

In 2006, from a weed of one of the tomato fields, identified as *Galinsoga ciliata* (Raf.) Blake (Asteraceae)(Common name: Hairy Galinsoga) six cocoons of *C. sonorensis* and 12 second instar of *T. ni* larvae were collected. The six cocoons and 4 of the larvae collected which also yielded parasitoid cocoons subsequently developed as adults of *C. sonorensis*.

From the sweet corn field beside the same tomato field, 8 cocoons and 38 2nd and 3rd instar of *S. frugiperda* larvae were collected. Six cocoons developed into

adults of *C. sonorensis* and 2 did not hatch. Thirteen cocoons which yielded adults of *C. sonorensis* were obtained from the larval sample as well.

In the cucumber greenhouse, from 12 2nd instar larvae of *T. ni* that were collected, 2 *C. sonorensis* and 1 *Cotesia marginiventris* were obtained. Finally, in the pepper greenhouse 4 cocoons were collected, which developed into adults of *Cotesia marginiventris.* Sixteen larvae of *T. ni* were collected (7 1st instar 1, 4 2nd instar and 5 3rd instar). From the 2nd instar *T. ni* larvae, 1 *C. sonorensis* and 1 *C. marginiventris* were obtained.

**Discussion**

Herbivores and natural enemies both consist of fluctuating populations. Thus, the development and effective use of biological control depends in large measure on an understanding of population dynamics (Huffaker and Messengers 1964; Hassell 1976; May 1976; Ridgway and Vinson 1977). The dynamics of *T. ni* in tomato fields compared to greenhouses in Southwestern Ontario are different but likely to be inter-related. The first *T. ni* generation may begin to develop inside tomato greenhouses as early as the last week of May and 3 to 4 weeks later in tomato fields, resulting in at least 1 more generation within greenhouses compared with fields. Janmaat (2004) reported that *T. ni* can cycle monthly in greenhouses throughout the growing season. In Eastern Ontario and in the Southwestern counties of Chatham-Kent and Essex, the first *T. ni* adults are found in Brassica crops by late-May (Harcourt 1963; OMAF, 2004), which agrees with what I have found in tomato greenhouses. In British Columbia, *T. ni* is collected outside greenhouses as early as April (Cervantes 2005) due to the mild temperature in BC at this time.

In North America, *T. ni is* often present in tomato fields but is not usually an economically important pest in this crop. In some years, control measures are required but natural control by beneficial insects usually keeps them under

control (Harcourt, 1963; Hoffman et al. 1990; Howard et al. 1994, Metcalfe et al. 2002). This is likely why population dynamics of *T. ni* have not been studied in field tomatoes. In tomato greenhouses, this is the first study of *T. ni* population dynamics in tomato greenhouses in Southwestern Ontario. Cervantes (2005) studied the dynamics of migrating *T. ni* moths into greenhouses in British Columbia and confirmed the results of Sutherland (1966) and Poe and Workman (1984) that the pupal stage is unable to overwinter outside the greenhouses but that it is able to overwinter inside greenhouses as it has been found in Southwestern Ontario greenhouses as well (OMAFRA 2005). In concordance with the results of this study, Cervantes (2005) also reported that the first *T. ni* generation in greenhouses may start in late May.

The number of parasitoid species per host species is strongly associated with herbivore feeding biology. Host feeding biology is the single most important correlate of how many parasitoids species an herbivore is known to support (Hawkins and Lawton 1987; Hawkins 1988, 1990; Hawkins et al. 1992). During two years, the parasitism by larval parasitoids of *T. ni* was studied as one of the major mortality factors in the regulation of *T. ni* populations in tomato fields. The assemblage or the parasitoid species richness consisted of ten species. In a review of the global analysis of the patterns in the number of parasitoid species that individual herbivore species support and their associations by Hawkins (1994), he stated three patterns. The first is that completely or partially exophytic hosts support the richest parasitoid assemblages in areas experiencing high thermal variability. For lepidopteran external hosts where the mean low temperature in the coldest months is under 0°C, the species richness is about 7 species per host species. In the current study, winter temperatures are below 0°C and with the lepidopteran host of *T. ni,* the overall parasitoid species richness was 10 across both years, with only 7 in any one year. Although the time frame of the studies under Hawkins's (1994) analysis was not considered as a variable, it should be included in a future analysis because, as shown in this study, not all parasitoid species are present each year. Differences in parasitoid species

presence/absence may be in response to climatic conditions changes, cultivation effects, host abundance, competition, etc. I only collected larval parasitoids in the current study, thus, the actual species richness could be higher if egg and pupal parasitoids were present.

The second pattern stated by Hawkins (1994) is that parasitoid complexes on completely or partially exophytic insects are dominated by ichneumonoids (Ichneumonidae – Braconidae). Ichneumonoids are the most common parasitoids in feeding niches containing larger hosts as macrolepidoptera. In the current study of *T. ni,* which is a macrolepidoptera, the parasitoid complex is dominated by ichneumonoids (6 out of 10 species) and of those 6, 1 species is an ichneumonid and 5 are braconids.

The third pattern stated by Hawkins (1994) is that hosts in all feeding niches support both idiobiont (those that do not permit continued host development following parasitisation) and koinobiont parasitoids (those that permit continued host development following parasitisation); in the case of exophytics (external and roller / webber hosts), all koinobionts attack larval stages. In the current study, with the exception of the egg-larval koinobiont parasitoid *Copidosoma floridanum* (Ashmead), all the other koinobionts species were larval parasitoids (8 species).

Previous studies on the natural enemies of *T. ni* in North America have listed the parasitoid species richness as between 1 to 31 species, with a mean of 8.5 (McKinney 1944; Pimentel 1961; Harcourt 1963; Oatman 1966; Sutherland 1966; Brubaker 1968; Clancy 1969; Oatman and Platner 1969; Elsey and Rabb 1970; Beirne 1971; Ehler and van den Bosch 1974; Wall and Berberet 1975; Harding 1976; Martin et al. 1981; Oatman et al. 1983; Roltsch and Mayse 1983; Marston et al. 1984; Chamberlin and Kok 1986; Henneberry et al. 1991; Biever et al. 1992; Godin and Boivin 1998; Shelton 2002; Caron 2005; Wold-Burkness et al. 2005). From these studies, I conclude that the parasitoid richness of *T. ni*

depends on the crop or crops where the study is performed, the time frame of the study and the location. The highest parasitoid species richness was obtained when the studies sampled more that one host crop, and crops other than Brassica. Parasitoid species richness was the lowest overall in Brassica crops. When the studies were done over a longer time frame (more than 2 years), in the southern USA, and including Brassica crops, the number of parasitoid species recovered from *T. ni* increases. In Canada, all previous studies have sampled Brassica crops in British Columbia, Ontario and Southern Quebec. Within these studies, the mean parasitoid species richness was 4.5, with the highest value of 7 in British Columbia. This contradicts Hawkins (1994) who states that completely or partially exophytic hosts support the richest parasitoid assemblages in areas experiencing high thermal variability and/or low winter temperature, with richness falling as climates become more stable or with increasingly milder low temperature. In contrast, the highest parasitoid richness was 31 species in Texas. However, study time frame and host crop has to be considered as important factors to defining a general pattern. It is my opinion that *Brassica oleracea* crops are not the best host crops to use to evaluate the species richness of parasitoids attacking *T. ni.* Finally, *Brassica* cultivated varieties are not native of America, which may explain why not as many native parasitoids are able to find *T. ni* hosts if they have not yet adapted to finding *T. ni* host cues in a *Brassica* crop.

Previous literature has reported *Compsilura concinnata* (Meigen)(Diptera: Tachinidae) from Ontario and Quebec (Harcourt 1963; Godin and Boivin 1998). As this is the only dipteran *T. ni* parasitoid reported in this region, it is likely that this is the identity of the dipteran parasitoid. In the current study *C. floridanum* was found; Harcourt (1963) reported *C. truncatellum* in Eastern Ontario but Godin and Bovin (1998) reported *C. floridanum* in Southwestern Quebec. *Copidosoma floridanum* has almost invariably been misidentified as *C. truncatellum* (Noyes 1988). I collected *C. floridanum* in this study, and based on the 24 studies about the natural enemies of *T. ni* in North America mentioned above, I agree with the

conclusion of Jones et al. (1983) and Waterhouse (1998) that across *T. ni*'s range the most common parasitoids that contribute in the regulation of the populations of *T. ni* are *Trichogramma spp, Voria ruralis, C. truncatellum* and *Hyposoter exiguae*, although in the current study egg parasitoids were not evaluated. Most of the 10 species of parasitoid collected in this study are reported as common parasitoids of *T. ni* except for *C. sonorensis* which has rarely been collected from *T. ni* and *Cotesia plathypenae* which may be a new record for *T. ni* as no previous host association with *T. ni* was found.

During this two-year study, *C. sonorensis* was the dominant species and its abundance was much higher compared with all the other parasitoid species together. Southwestern Ontario may provide some special conditions that allow *C. sonorensis* to be the dominant larval parasitoid of *T. ni.* *Campoletis sonorensis* is either rarely, or not reported at all as a natural enemy of *T. ni* (McKinney 1944; Pimentel 1961; Harcourt, 1963; Oatman 1966; Sutherland 1966; Brubaker 1968; Clancy 1969; Oatman and Platner 1969; Elsey and Rabb, 1970; Beirne 1971; Ehler and van den Bosch 1974; Wall and Berberet 1975; Harding 1976; Martin et al. 1981; Oatman et al. 1983; Roltsch and Mayse 1983; Marston et al. 1984; Chamberlin and Kok 1986; Waterhouse 1988; Henneberry et al. 1991; Biever et al. 1992; Godin and Boivin 1998; Yu 1999; Shelton 2002; Caron 2005; CABI Protection compendium 2005; Wold-Burkness et al. 2005). There are only three possible references of the presence of this species within Canada; one is reported for Alberta as the synonym *Campoletis websteri* (Viereck) without information about the insect host (Strickland, 1946); one from Oliver, British Columbia as the synonym *Sagaritis websteri* (Viereck) without information about host (Criddle 1924); and *Campoletis perdistincta*, a junior synonym of *Campoletis flavicincta* which is often a mis-identification of *Campoletis sonorensis* (Carlson 1972), is reported in New Brunswick as a parasitoid of *Syngrapha epigea* (Grote)(Lepidotera: Noctuidea) (Graham 1965). In the rest of North America, *C. sonorensis* has been reported as a parasitoid of *T. ni* once in Southern California in lettuce (*Lactuca sativa* L., Asteraceae)

(Henneberry et al. 1991) and once in Texas but the crop host was not reported (Harding 1976). Oatman et al. (1983) in Southern California and Wold-Burkness et al. (2005) in Rosemount, Minnesota reported *Campoletis* spp as a parasitoid of *T. ni* on tomato and cabbage, respectively. Rosemount, Minnesota is the closest location to Southern Ontario where *Campoletis* spp has been reported as a parasitoid of *T. ni,* although it could be *C. flavicincta*, another rare parasitoid of *T. ni* that together with *C. sonorensis* are the only species of this genus reported as *T. ni* parasitoids.

I propose four reasons why *C. sonorensis* has not been reported as an important natural enemy of *T. ni* before: first, most of the *T. ni* parasitoid assemblages studies have been done in *Brassica* species crops. In choice and no-choice experiments, *Brassica* crops are not attractive to *C. sonorensis* (Elzen et al. 1983). *Brassica* crops may not produce the synomones that cotton or tobacco, *Nicotiana tabacum* L. (Solanaceae) produce after insect damage and that mediate searching behavior in *C. sonorensis* (Elzen el al. 1984). In 14 studies on *Brassica* varieties (cabbage, broccoli, collard and cauliflower) (Pimentel, 1961; Harcourt 1963; Oatman 1966; Sutherland 1966; Brubaker 1968; Oatman and Platner 1969; Elsey and Rabb 1970; Martin et al. 1981; Chamberlin and Kok 1986; Biever et al. 1992; Godin and Boivin 1998; Shelton 2002; Caron 2005), there is only one reference of *Campoletis* spp as an infrequent parasitoid of *T. ni* in cabbage in Rosemount, Minnesota (Wold-Burkness et al. 2005). No *Brassica* plants are on the list of 20 *C. sonorensis* host plants reported by Yu (1999). Two field studies measured parasitism of *H. zea* and *H. virescens* in a mix of wild and cultivated crops in Mississippi and in eastern Tennessee: percent parasitism by *Microplitis croceipes* reached 94.73%, parasitism by *Cotesia marginiventris* was 1.31% and the parasitism by *C. sonorensis* was 1.05% in cutleaf geranium (*Geranium dissectum* L.)(Geraniaceae); only *M. croceipes* was present in crimson clover (*Trifolium incarnatum* L.) and soybean (*Glycine max* L.) (Leguminoseae); in cotton both *M. croceipes* and *C. marginiventris* reached 100% and *C. sonorensis* 16.67%; and in tobacco *M. croceipes* reach up to 1.62%

and *C. sonorensis* up to 94.75% (Bidlack et al. 1991, Stadelbacher et al. 1984). de Moraes and Lewis (1999) found that the most important host-location cues for *M. croceipes* were materials associated with damaged plants. *Microplitis croceipes* demonstrated a significant preference for volatiles released from plants damaged by *H. virescens* larvae, over those released from undamaged tobacco and cotton plants. In choice experiments with damaged tobacco versus cotton, *M. croceipes* showed a significant preference for cotton plants. Studies by Lewis and Brazzel (1968), Graham et al. (1972), Pair et al. (1982, 1986), Puterka et al. (1985) and Eger et al. (1982) in different localities also support the host plant preferences of *C. sonorensis* for different wild and cultivated host plants with *Helicoverpa* spp and *S. frugiperda* as insect hosts.

The second reason why it has not been reported may be that under many circumstances, competitors do not allow *C. sonorensis* to be successful and outcompete *C. sonorensis* for hosts. Eggs or 1$^{st}$ instar larvae may be depleted by other natural enemies such as *Trichogramma* spp. which is able to parasitise up to 65% of the *T. ni* eggs (Graham 1970). In the study by Wold-Burkness et al. (2005) on cabbage, *Campoletis* spp parasitised 0.6% of the *T. ni* larvae and the dominant parasitoid, *Voria ruralis,* parasitised 69%. *Voria ruralis* is a parasitoid of the late 3$^{rd}$ and early 4$^{th}$ instar larvae of *T. ni* when it may already be parasitised by *C. sonorensis*. The faster development and the larger size of *V. ruralis* may allow it to be a better competitor. At 24°C, *V. ruralis* develops from egg to pupae in 7-8 days and when the eggs are deposited they are nearly ready to hatch (Brubaker, 1968), while *C. sonorensis* develops from egg to pupae in about 10 days (reported in Chapter 3 results) and eclosion requires 36-48 hours (Wilson and Ridgway, 1975). Browning and Oatman (1984) reported that *C. truncatellum* and *V. ruralis* exhibited a competitive advantage when multiple parasitisation occurred between these species and other *T. ni* larval parasitoids, and that between the two species, the timing of parasitisation by *V. ruralis* affected the competitive outcome. In a study in lettuce, of 1750 *T. ni* larvae collected, 65 were

parasitised by *M. brassicae*, 42 by *C. truncatellum*, 42 by *V. ruralis* and only 4 by *C. sonorensis* (Henneberry et al. 1991).

The third reason why it has not been reported may be the preference of *C. sonorensis* for other hosts that are more abundant than *T. ni* in non-*Brassica* crops. *Campoletis sonorensis* frequents fields of cotton, tobacco, alfalfa and tomatoes (Carlson 1972). In 10 of the 24 studies on *T. ni* parasitoid diversity, *T. ni* was a secondary problem in that crop and the *T. ni* population was very low or not present (McKinney 1944; Clancy 1969; Beirne 1971; Ehler and van den Bosch 1974; Wall and Berberet 1975; Harding 1976; Oatman et al. 1983; Roltsch and Mayse 1983; Marston et al. 1984; Henneberry et al. 1991). The preference of *C. sonorensis* for other hosts has been demonstrated by Lingren and Noble (1972), who concluded that *H. zea*, *S. frugiperda* and *H. virescens* were the most preferred hosts whereas *T. ni* was the least preferred host. The current study is the first where the main objective was to evaluate the parasitism by *C. sonorensis* on *T. ni*, as all the other studies on *C. sonorensis* have been conducted with *Helicoverpa* spp and *S. frugiperda* as the target hosts.

The fourth reason why it has not been reported is that the distribution and habitat range of *C. sonorensis* may still be expanding through America. As reported by Carlson (1972), the geographic distribution of *C. sonorensis* was Sandpoint, Idaho (USA) as the northernmost point of distribution and Lima (Peru) as the southernmost locality. According to Machuca et al. (1989), this parasitoid colonized Chile relatively recently. *Campoletis* spp was only observed in field studies in 2000 in Rosemount, Minnesota, however field studies have been conducted there since 1968 (Wold-Burkness et al. 2005). This change in the distribution of *C. sonorensis* may be explained by the migration habits of most of the Noctuidae it parasitises. As *C. sonorensis* may be trying to follow the migration of its most important hosts, *S. frugiperda* and *Helicoperva* spp or probably other Noctuidae, the parasitoid has migrated into the Northern USA and Southwestern Ontario. Its ability to diapause has evolved to allow it to overwinter

in Southwestern Ontario and take advantage of the Noctuidae moth migrations in spring and/or emerging moths overwintering in Canada. To overcome stressful periods and to keep in synchrony with the seasonal occurrence of their biotic requisites, parasitoids have evolved different adaptations such as regulation of development and reproduction, such as through diapause (Tauber et al. 1986). Parasitoids undergo diapause like other insects (Tauber et al. 1983, 1986). As the parasitoid spread into new habitats, the abundance of non-preferred host species such as *T. ni* likely influenced C. sonorensis to evolve in a geographic strain or ecotype well adapted to the population dynamics of this host species. It is well documented that different strains of the same parasitoid species have preferences for different host species in different geographic areas (Pak, 1986; Pak and De Jong, 1987; Kraaijeveld and van Alphen, 1995; Kraaijeveld et al. 1995; Arakaki et al. 1997; Bertschy et al. 1997; Heimpel et al. 2004; Vos and Vet 2004; Geden et al. 2006).

As soon as warmer conditions begin in early spring, *C. sonorensis* may start emerging from diapause and at this time preferred hosts such as *S. frugiperda, Helicoverpa* species and other migrating hosts are not present in this region. However, by May, one of the first migrant Noctuidae to arrive is *T. ni,* both from migrations from the south and emergence from overwintering in greenhouses. Pupae of *T. ni* are able to survive inside unheated greenhouses during the winter for 5 weeks (Cervantes, 2005) and likely *C. sonorensis* as well. Some other Noctuidae species such as *Hydraecia micacea* which are first captured in early May, are able to overwinter in Southern Ontario (West et al. 1983; Howard et al. 1994, Kullik et al. 2005; Chaput 2000) and could be the first host of *C. sonorensis*. *Campoletis* spp has been reported as a parasitoid of *H. micacea* from corn fields around Guelph Ontario (West et al. 1983). When *S. frugiperda, Helicoverpa* species, *Peridroma saucia* (Lingren et al. 1972; Marino et al. 2006) and other reported *C. sonorensis* migrating host species colonize by mid-summer (Hudon et al. 1985; Howard et al. 1994), the population of *C. sonorensis* on *T. ni*

is stable and high enough that *C. sonorensis* can start moving into other crops and other wild host plants looking for hosts.

The population dynamics of *T. ni* are a major component of the success of *C. sonorensis* in this region. The perfect synchronization of *C. sonorensis* and the first generation of *T. ni* larvae as found in this study, is the main factor to explain the high level of *T. ni* parasitism by *C. sonorensis*. By early spring, the first *T. ni* generation starts developing inside tomato greenhouses and at the same time, *C. sonorensis* is found parasitising 2$^{nd}$ instar larvae in greenhouses. After about 2 weeks, when the first *T. ni* larvae are found in field tomato crops, *C. sonorensis* is also found parasitising 2$^{nd}$ instar larvae in the field crops. From this point onwards, the *C. sonorensis* population starts increasing in the fields on *T. ni* in a positively density dependent manner until harvest, reaching up to 87.5% parasitism. At this point, populations of other hosts on other plants become available in larger numbers such as *S. frugiperda* in corn, possibly allowing *C. sonorensis* to switch hosts and crop plants.

In conclusion, *C. sonorensis* is a major factor in the regulation of the *T. ni* populations in tomato fields in Southern Ontario. This conclusion is based on the following evidence: 1) in non-pesticides sprayed tomato fields and sprayed-tomato fields, *C. sonorensis* was the dominant larval parasitoid and its abundance was much higher than the abundance of the other parasitoids found; 2) there was chronological synchrony between the populations of *T. ni* and *C. sonorensis*; 3) in non-pesticide sprayed tomato fields, the populations of *T. ni* was the same as in tomato fields that were sprayed but the *C. sonorensis* parasitism was higher in the insecticide-free fields; 4) in the same non-sprayed fields, *C. sonorensis* was a positively density-dependent factor in the regulation of the *T. ni* population; and 5) the presence of other Noctuidae host species in the area could be an important factor in the stabilization of *C. sonorensis* populations throughout the year.

## References

Arakaki N, Wakamura S, Yasuda T, Yamagishi K (1997) Two regional strains of a phoretic egg parasitoid, *Telenomus euproctidis* (Hymenoptera: Scelionidae), that use different sex pheromones of two allopatric tussock moth species as kairomones. Journal of Chemical Ecology 23:153-161.

Beirne BP (1971) Pest insects of annual crop plants in Canada. I. Lepidoptera. Memoirs of the Entomological Society of Canada. 78: 1-47.

Bertschy C, Turlings TC, Bellotti A, Dorn S (1997) Chemically-mediated attraction of three parasitoid species to mealybug-infested cassava leaves. Florida Entomologist 80: 383–395.

Bidlack DS, Grant JF, Pless CD (1991) Seasonal incidence of larvae of the tobacco budworm and corn earworm, and their parasitoids, on tobacco in eastern Tennessee. Journal of Agricultural Entomology 8: 155–162.

Biever KD, Chauvin RL, Reed GL, Wilson RC (1992) Seasonal occurrence and abundance of lepidopterous pests and associated parasitoids on Collards in the Northwestern United States. Journal of Entomological Science 27: 5-18

Boivin, G. 1993. Density dependence of *Anaphes sordidatus* (Hymenoptera: Mymaridae) parasitism on eggs of *Listronotus oregonensis* (Coleoptera: Curculionidae). Oecologia 93: 73-79.

Browning HW, Oatman ER (1984) Intra- and interspecific relationships among some parasites of *Trichoplusia ni* (Lepidoptera: Noctuidae). Environmental Entomology 13:551-556.

Brubaker RW (1968) Seasonal occurrence of *Voria ruralis*, a parasite of the cabbage looper in Arizona and its behavior and development in laboratory culture. Journal of Economic Entomology 61: 306-309.

CAB International (2005) Crop Protection Compendium. CABI Publishing. Wallingford, Oxfordshire, UK.

Caron V (2005) Ecological interactions between Cabbage Looper, a parasitoid, host plants and *Bacillus thuringiensis*. MSc. Thesis. University of British Columbia.

Carlson RW (1972) Suppression of the name *Campoletis persdistincta* (Hymenoptera: Ichneumonidae) and the identity of species to which the name has been applied. Entomological News 83: 75-82.

Cervantes V (2005) Population ecology of *Trichoplusia ni* in vegetable greenhouses and the potential of *Autographa californica* nucleopolyhedrovirus for their control. MSc. Thesis. University of British Columbia.

Chamberlin JR, Kok LT (1986) Cabbage lepidopterous pests and their parasites in southwestern Virginia. Journal of Economic Entomology 79: 629–632.

Chaput J (2000) Managing Cutworms in vegetable crops. Ontario Ministry of Agriculture, Fact Sheet 00-055.

Clancy DW (1969) Parasitisation of cabbage and alfalfa loopers in southern California. Journal of Economic Entomology 62: 1078-1083.

Coppel HC, Mertins JW (1977) Biological insect pest suppression. Springer-Verlag. Berlin.

Criddle N (1924) The entomological record, 1924. Ontario Entomological Society Annual report, pp. 89-106.

DeBach P (1974) Biological control by natural enemies. Cambridge University Press. Cambridge.

DeBach P, Rosen D (1991) Biological control by natural enemies. Cambridge University Press. Cambridge.

de Moraes CM, Lewis WJ (1999) Analyses of two parasitoids with convergent foraging strategies. Journal of Insect Behavior 12: 571-583.

de Moraes RR, Loeck AE, Belarmino LC (1991) Natural enemies of *Rachiplusia nu* (Guenée, 1852) and *Pseudoplusia includens* (Walker, 1857) (Lepidoptera: Noctuidae) on soybean in Rio Grande do Sul. [In Portuguese.] Pesquisa Agropecuária Brasileira 26: 57–64.

Eger JE, Sterling WL, Hartstack AW Jr. ( 1982) Population dynamics of *Heliothis* spp. on *Castilleja indivisa*, an unreported host plant, and *Lupinus texensis* in Texas. Environmental Entomology 11: 327-333.

Ehler LE, van den Bosch R (1974) An analysis of the natural biological control of *Trichoplusia ni* (Lepidoptera: Noctuidae) on cotton in California. Canadian Entomologist 106: 1067–1073.

Elsey KD, Rabb RL (1970) Analysis of seasonal mortality of the cabbage looper in North Carolina. Annals of the Entomological Society of America 63: 1597-1604.

Elzen GW, Williams HJ, Vinson SB (1983) Response by the Parasitoid *Campoletis sonorensis* (Hymenoptera: Ichneumonidae) to Synomones in Plants:

Implications for Host Habitat Location, Environmental Entomology 1983, 12, 1872-1877.

Elzen GW, Williams HJ, Vinson SB (1984) Isolation, identification, and bioassay of cotton synomones mediating searching behavior by parasitoid *Campoletis sonorensis* (Hymenoptera: Ichneumonidae). Journal of Chemical Ecology 10: 1251-1264.

Geden CJ, Moon RD, Buttler JF (2006) Host Ranges of Six Solitary Filth Fly Parasitoids (Hymenoptera: Pteromalidae, Chalcididae) from Florida, Eurasia, Morocco, and Brazil. Environmental Entomology 35: 405-412.

Gillespie D, Opit G, McGregor R, Johnston M, Quiring D, Foisy M (1997) Use of *Cotesia marginiventris* (Cresson) (Hymenoptera: Braconidae) for biological control of cabbage loopers, *Trichoplusia ni* (Lepidoptera: Noctuidae) in greenhouse vegetable crops in British Columbia. Final report to the BC Greenhouse Vegetable Research Council. Projects 96-12 and 97-06. Pacific Agriculture Research Centre (Agassiz). Technical Report Nr. 141.

Gillespie DR, Raworth DA, Shipp JL (2002) *Trichoplusia ni* Hübner, Cabbage Looper (Lepidoptera: Noctuidae). In: Mason PG, Huber JT (eds) Biological Control Programmes in Canada, 1981-2000. CABI Publishing. New York. NY, pp. 269-271.

Godin C, Boivin G (1998) Lepidopterous pests of *Brassica* crops and their parasitoids in southwestern Quebec. Environmental Entomology 27: 1157–1165.

Graham AR (1965) A preliminary list of the natural enemies of Canadian agricultural pests. Canada Department of Agriculture, Research Institute, Information Bulletin 4.

Graham HM (1970) Parasitism of eggs of bollworms, tobacco budworms and loopers by *Trichogramma semifumatum* (Hymenoptera: Chalcididae) in the lower Rio Grande Valley, Texas. Journal of Economic Entomology 63: 686-688.

Graham HM, Hernandez NS, Llanes JR (1972) The role of host plants in the dynamics of populations of *Heliothis* spp. Environmental Entomology 1: 424-31.

Harcourt DG (1963) Biology of Cabbage caterpillars in Eastern Ontario. Proceedings of the Entomological Society of Ontario 93: 61-75.

Harding JA (1976) Seasonal occurrence, hosts, parasitism and parasites of cabbage and soybean loopers in the Lower Rio Grande Valley. Environmental Entomology 5: 672–674.

Hassell MP (1976) The Dynamics of Competition and Predation. Institute of Biology's Studies in Biology no.72. Edward Arnold Publishers, London.

Hassell MP (1987) Detecting regulation in patchily distributed animal populations. Journal of Animal Ecology 56: 705-713.

Hassell MP, Waage JK (1984) Host-parasitoid population interactions. Annual Review of Entomology 29: 89–114.

Hawkins BA (1988) Species diversity in the third and fourth trophic levels: patterns and mechanisms. Journal of Animal Ecology 57:137-162.

Hawkins, B. A. 1990. Global patterns of parasitoid assemblage size. Journal of Animal Ecology 59:57-72.

Hawkins BA (1994) Pattern and process in host-parasitoid interactions. Cambridge University Press, Cambridge.

Hawkins BA, Lawton JH (1987) Species richness for parasitoids of British phytophagous insects. Nature 326:788-790.

Hawkins BA, Shaw MR, Askew RR (1992) Relations among assemblage size, host specialization, and climatic variability in North American parasitoid communities. The American Naturalist 139: 58-79.

Heimpel GE, Ragsdale DW, Venette R, Hopper KR, O'Neil RJ, Rutledge CE, Wu Z (2004) Prospects for Importation Biological Control of the Soybean Aphid: Anticipating Potential Costs and Benefits. Annals of the Entomological Society of America 97: 249-258

Henneberry TJ, Vail PV, Pearson AC, Sevacherian V (1991) Biological control agents of noctuid larvae (Lepidoptera: Noctuidae) in the Imperial Valley of California. Southwestern Entomologist 16: 81-89.

Howard LO, Fiske WF (1911) The importation into the United States of the parasites of the gipsy-moth and the browntail moth. USDA Bureau of Entomology Bulletin. 91.

Howard RJ, Garland JA, Seaman WL (1994) Diseases and pests of vegetables crops in Canada. Canadian Phytopathology Society and Entomological Society of Canada, Ottawa. Ontario.

Hudon M, Foott WH, Martel P (1985) Insects damaging corn in Eastern Canada. Agriculture Canada. Publication 1788/E.

Huffaker CB, Messenger PS (1964) The concept and significance of natural control. In: DeBach P (ed) Biological Control of Insect Pests and Weeds. Chapman and Hall Ltd., London, pp. 74-117.

Huffaker CB, Messenger PS (1976) Theory and practice of biological control. Academic Press, New York, NY, USA.

Huffaker CB, Messenger PS, DeBach P (1971) The natural enemy component in natural control and the theory in biological control. In: Huffaker CB (ed) "Proceedings of an AAAS Symposium on Biological Control". Plenum, New York. NY. pp. 16-67.

Isenhour DJ (1985) *Campoletis sonorensis* (Hym.: Ichneumonidae) as a parasitoid of *Spodoptera frugiperda* (Lep.: Noctuidae): host stage preference and functional response. Entomophaga 30: 31-36.

Janmaat AF (2004) The evolution of resistance to *Bacillus thuringiensis* in greenhouses *Trichoplusia ni* populations. Ph.D. Thesis – Depart. Of Zoology, University of British Columbia, Vancouver.

Janmaat AF, Myers JH (2003) Rapid evolution and the cost of resistance to *Bacillus thuringiensis* in greenhouse populations of cabbage looper, *Trichoplusia ni.* Proceedings of the Royal Society of London *B.* 270: 2263-2270

Janmaat AF, Myers JH (2006) The influences of host plant and genetic resistance to *Bacillus thuringiensis* on trade-offs between offspring number and growth rate in cabbage loopers, *Trichoplusia ni.* Ecological Entomology 31: 172-178.

Jones D, Snyder, M, Granett J (1983) Can insecticides be integrated with biological control agents of *Trichoplusia ni* in celery? Entomologia Experimentalis et Applicata 33: 290–296.

Kraaijeveld AR, Nowee B, Najem RW (1995) Adaptive variation in host-selection behaviour of *Asobara tabida*, a Parasitoid of *Drosophila* Larvae. Functional Ecology 9: 113-118.

Kraaijeveld AR, van Alphen JJM (1995) Variation in diapause and sex ratio in the parasitoid *Asobara tabida*. Entomologia Experimentalis et Applicata 74: 259-265.

Kidd AAC, Jervis MA (2005) Population dynamics. In: Jervis MA (ed) Insects as natural enemies: A practical perspective. Springer. Dordrecht, Netherlands. pp. 435-523.

Korytkowski Ch, Casanova P (1966) Estudios de *Campoletis perdistinctus* (Viereck) (Hym.: Ich.) parasito de *Heliothis virescens* Fab. (Lep.: Phalaen.). Revista Peruana de Entomología 9: 24-29.

Krebs, C.J. 1985. Ecology: The Experimental Analysis of Distribution and Abundance. Third Edition. Harper and Row, New York.

Krebs, C.J. 1999. Ecological Methodology. 2nd ed. Benjamin Cummings, Menlo Park, California.

Kuno E (1973) Statistical characteristics of the density-independent population fluctuation and the evaluation of density-dependence and regulation in animal populations. Research Population Ecology 15: 99-120.

Kullik SA, Sears MK, McLeod DGR, Gualtieri LL, Schaafsma AW (2005) Phenology and field biology of Black Cutworm (Lepidoptera: Noctuidae) in Ontario no-till corn. Journal of Economic Entomology 98: 1594-1602.

Lafontaine JD, Poole RW (1991) Noctuoidea, Noctuidae (part) – Plusiinae. Fascicle 25.1. In: Hodges RW, Davis DR, Dominick T, Ferguson DG, Franclemont JC, Munroe EG, Powell JA (eds) The moths of America North of Mexico. The Wedge Entomological Research Foundation, Washington, DC.

Lewis WJ, Brazzel JR (1968) A three-year study of parasites of the bollworm and the tobacco budworm in Mississippi. Journal of Economic Entomology 61: 673-676.

Lingren PD, Noble LW (1972) Preference of *Campoletis perdistinctus* for certain Noctuidae larvae. Journal of Economic Entomology 65: 104-107.

Machuca Jr, Arretz P, Araya J (1989) Presencia de *Campoletis sonorensis* (Cameron, 1886) (Hymenoptera: Ichneumonidae) en Chile. Acta Entomologica Chilena 15: 269-270.

Marino PC, Landis DA, Bradford AH (2006) Conserving parasitoid assemblages of North American pest Lepidoptera: Does biological control by native parasitoids depend on landscape complexity? Biological Control 37: 173–185.

Marston NL, Hostetter DL, Pinnell RE, Dickerson WA, Smith DB (1984) Natural mortality of lepidopteran eggs and larvae in Missouri soybeans. Annals of the Entomological Society of America 77: 21-28.

Martin PB, Lingren PD, Greene GL (1976) Relative abundance and host preferences of cabbage looper, soybean looper, tobacco budworm, and corn earworm on crops grown in northern Florida. Environmental Entomology 5: 878-882.

Martin PB, Lingren PD, Greene GL, Grissell EE (1981) The parasitoid complex of three noctuids (Lep.) in a northern Florida cropping system: seasonal occurrence, parasitisation, alternate hosts, and influence of host habitat. Entomophaga 26: 401–419.

Matsumoto T, Itioka T, Nishida T, Inoue T (2004) A test of temporal and spatial density dependence in the parasitism rates of introduced parasitoids on host, the

arrowhead scale (*Unaspis yanonensis*) in stable host–parasitoids system. Journal of Applied Entomology 128: 267-272.

May RM (1976) Theoretical ecology: principles and applications. W. B. Saunders Co., Philadelphia.

McKinney KB (1944) The Cabbage Looper as a pest of lettuce in the southwest. USDA Bull. 846.

Metcalfe M, McWilliams B, Hueth B, van Steenwyk R, Sunding D, Zilberman D (2002) The Economic Importance of Organophosphates in California Agriculture. Depart. Agric. Res. Econ. – Depart. ESPM. Coop. Ext. Entom. University of California, Berkeley.

Morris RF (1959) Single-factor analysis in population dynamics. Ecology 40: 580-588.

Magurran AE (2004) Measuring biological diversity. Oxford: Blackwell Science.

Murdoch WW, Walde SJ (1989) Analysis of insect population dynamics. In: Whittaker J, Grubb PI (eds) Towards a more exact ecology. Blackwell Publishers, Oxford. U.K. pp. 113-140.

Murdoch WW, Briggs CJ (1996) Theory for biological control: recent developments. Ecology 77: 2001-2013.

Noyes JS (1988) *Copidosoma truncatellum* (Dalman) and *C. floridanum* (Ashmead) (Hymenoptera, Encyrtidae), two frequently misidentified polyembryonic parasitoids of caterpillars (Lepidoptera). Systematic Entomology 13:197-204.

Oatman ER (1966) An ecological study of cabbage looper and imported cabbageworm populations on cruciferous crops in Southern California. Journal of Economic Entomology 59: 1134-1139.

Oatman ER, Platner GR (1969) An ecological study of insect populations on cabbage in southern California. Hilgardia 40: 1–40.

Oatman, ER, Platner GR, Wyman JA, van Steenwyk RA, Johnson MW, Browning HW (1983) Parasitization of lepidopterous pests on fresh market tomatoes in southern California. Journal of Economic Entomology 76: 452-55.

OMAFRA (2005) Growing greenhouses vegetables. Publication 371. Ontario Ministry of Agriculture, Food and Rural Affairs.

Pair SD, Laster ML, Martin DF (1982) Parasitoids of *Heliothis* spp. (Lepidoptera: Noctuidae) larvae in Mississippi associated with sesame interplantings in cotton, 1971-1974: Implications of host habitat interaction. Environmental Entomology 11: 509-512.

Pair SD, Raulston JR, Sparks AN, Martin PB (1986) Fall armyworm (Lepidoptera: Noctuidae) parasitoids: Differential spring distribution and incidence on corn and sorghum in the Southern United States and Northeastern Mexico. Environmental Entomology 15: 342-348.

Pak, G.A. (1986) Behavioral variation among strains of *Trichogramma* spp: A review of the literature on host selection. Journal of Applied Entomolology 101:55-64.

Pak GA, De Jong EJ (1987) Behavioral variations among strains of *Trichogramma* spp. host recognition. Netherlands Journal of Zoology 37: 137-166.

Pimentel D (1961) Natural control of caterpillar populations on Cole Crops. Journal of Economic Entomology 54: 889-892.

Poe SL, Workman RB (1984) Potential for dispersal by winter shipments of vegetables, ornamental plants and cut flowers. Technical Bulletin USDA 1684: 26-29.

Puterka GJ, Slosser JE, Price JR (1985) Parasites of *Heliothis* spp. (Lepidoptera: Noctuidae): parasitism and seasonal occurrence for host crops in the Texas Rolling Plains. Environmental Entomology Journal of Economic Entomology 14: 441-446.

Ridgway RL, Vinson SB (1977) Biological control by augmentation of natural enemies. Insect and mite control with parasites and predators. Plenum Press, New York, New York.

Roltsch WJ, Mayse MA (1983) Parasitic insects associated with Lepidoptera on fresh-market tomato in southeast Arkansas. Environmental Entomology 12: 1708-1713.

Shelton AM, Wilsey WT, Hoebeke ER, Schmaedick MA (2002) Parasitoids of cabbage Lepidoptera in Central New York. Journal of Entomological Science 37: 270-271.

Shorey HH, Hale RL (1965) Mass-rearing of the larvae of nine noctuid species on a single artificial medium. Journal of Economic Entomology 58: 522-524.

Siabatto PA (1991) Introducción del parasito *Campoletis* sp., agente benéfico para el control de *Heliothis* spp en la zona del Tolima. Research proposal. National Federation of Cotton Growers. Colombia.

Smith HS (1935) The role of biotic factors in the determination of population densities. Journal of Economic Entomology 28: 873-898.

Smith B, Wilson JB (1996) A consumer's guide to evenness indices. Oikos 76:70-82.

Sokal RR, Rohlf FJ (1981) Biometry, 2nd ed. W. H. Freeman, San Francisco.

Solow AR, Steele JH (1990) On sample size, statistical power, and the detection of density dependence. Journal of Animal Ecology 59: 1073-1076.

SPSS for Windows, Rel. 15.0.0. (2006) Chicago: SPSS Inc.

Stadelbacher EA, Powell JE, King EG (1984). Parasitism *of Heliothis zea* and *Heliothis virescens* (Lepidoptera: Noctuidae) larvae in wild and cultivated host plants in the Delta of the Mississippi. Environmental Entomology 13: 439-451.

Strickland EH (1946) An annotated list of Ichneumomoidea of Alberta. Canadian Entomologist 78: 36-46.

Sugiura S, Osawa N (2002) Temporal response of parasitoids to the density of the Leafroller *Eudemis gyrotis* (Lepidoptera: Tortricidae) on Bayberry *Myrica rubra* (Myricaceae). Environmental Entomology 31: 988-994.

Sutherland DWS (1966) Biological investigations of *Trichoplusia ni* (Huebner) and other Lepidoptera damaging cruciferous crops on Long Island, New York, NY. Agricultural Experiment Station Memorandum 399.

Sutherland DW, Greene SGL (1984) Cultivated and wild host plants. In: Lingren PD, Greene GL (eds) Suppression and management of cabbage looper populations. USDA, Technical Bulletin 1684: 1-13.

Tauber MJ, Tauber CA, Nechols JR, Obrycki JJ (1983) Seasonal activity of parasitoids: control by external, internal and genetic factors. In: Brown, V.K., Hodek, I. (Eds.), Diapause and Life Cycle Strategies. Junk Publishers, The Hague, pp. 87-108.

Tauber MJ, Tauber CA, Masaki I (1986) Seasonal Adaptations of Insects. Oxford University Press, Oxford.

Turchin P (1995) Chaos in microtine populations. Proceedings of the Royal Society of London B 262: 357-361.

van Lenteren JC (1986) Parasitoid in the greenhouse: successes with seasonal inoculative release systems. In: Waage J, Greathead D (eds) Insect Parasitoids. Academic Press, London. pp. 341-374.

van Lenteren JC (2000) Success in biological control of arthropods by augmentation of natural enemies. In: Gurr G, Wratten S (eds) Biological control: measures of success. Kluwer Academic Publishers, Netherlands. pp. 77-103.

Varley GC, Gradwell GR (1971) The use of models and life tables in assessing the role of natural enemies. In: Huffaker CB (ed.) Proceedings of an AAAS Symposium on Biological Control. Plenum, New York. NY. pp. 93-111.

Vos M, Vet LEM (2004) Geographic in host acceptance by an insect parasitoid: genotype versus experience. Evolutionary Ecology Research 6: 1021-1035.

Waage JK, Hassell MP (1982) Parasitoids as biological control agents – a fundamental approach. Parasitology 84: 241-268.

Wall R, Berberet RC (1975) Parasitoids associated with lepidopterous pests on peanuts. Oklahoma fauna. Environmental Entomology 4: 887–892.

Waterhouse DF (1998) Biological Control of Insect Pests: Southeast Asian Prospects Australian Centre for International Agricultural Research. Canberra.

Wene G (1943) *Sagaritis provancheri* (D.T.) an important parasite of the Tobacco Budworm. Journal of Economic Entomology 36: 333-334.

West RJ, Laing JE, Marshall SA (1983) Parasites of the potato stem borer *Hydraecia micacea* (Lepidoptera: Noctuidae). Proceeding of the Entomological Society of Ontario 114:69-82.

Wilson DD, Ridgway RL (1975) Morphology, development, and behavior of the immature stages of the parasitoid, *Campoletis sonorensis* (Hymenoptera: Ichneumonidae). Annals of the Entomological Society of America 68: 191-196.

Wold-Burkness SJ, Hutchison WD, Lee JC, Hines RL, Bolin C, Heimpel GE (2005) A long-term survey of parasitoid species composition and parasitism of *Trichoplusia ni* (Lepidoptera: Noctuidae), *Plutella xylostella* (Leipidoptera: Plutellidae), and *Pieris* (=*Artogeia*) *rapae* (Lepidoptera: Pieridae) in Minnesota cabbage. Journal of Entomological Science 40: 211-221.

Yu DS (1999) Interactive catalog of world Ichneumonoidae, Taxapad. Bentall Centre, Vancouver, B.C., Canada (www.taxapad.com)

Table 2.1a: Crop management of the tomato fields and greenhouses used in the 2005 survey.

| Year | 2005 | | | | | |
|---|---|---|---|---|---|---|
| **Crop System** | **Field** | | | **Greenhouse** | | |
| **Character** | **1** | **2** | **3** | **1** | **2** | **3** |
| **Planting date** | May 15 | May 15 | May 15 | Jan. 5 | Dec. 28/2004 | Jan. 5 |
| **Variety** | Multiple hybrids | Q909 (58rows) TH4 (10 Rows) | Sonoma and Marianna | Clarance | Big Dina Macarena | Dundee |
| **Intercropping date** | - | - | - | Jun. 30 Jul. 15 | - | Jul. 6 |
| **Variety** | - | - | - | Tresco | - | Dundee |
| **Sampling start date** | May 20 | May 20 | May 20 | May 3 | May 3 | May 3 |
| **Sampling finish date** | Aug. 10 | Aug. 10 | Aug. 10 | Sep 1 | Sep 1 | Sep 1 |
| **Number of chemical insecticide sprays** | 4 | 2 | 4 | 1 | 3 | 4 |
| **Chemical insecticides** | Spinosad, Cyhalithrin-Lamda , Dymethoate | Cyhalithrin-Lamda, Imidacloprid | Permethrin Imidacloprid | Tebufenozide | Tebufenozide | Tebufenozide |
| **Number of *Bt* products sprays*** | 2 | - | - | 6 | 8 | 8 |

**Bt = Bacillus thuringiensis.*

Table 2.1b: Crop management of the tomato fields and greenhouses used in the 2006 survey.

| Year | 2006 | | | | | |
|---|---|---|---|---|---|---|
| **Crop System** | **Field** | | | **Greenhouses** | | |
| **Character** | **1** | **2** | **3** | **1** | **2** | **3** |
| **Planting date** | Jun. 13 | Jun. 13 | Jun. 13 | Dec. 12/2005 | Dec. 1/2005 | Jan. 6/2006 |
| **Variety** | Heinz 9478 | Heinz 9478 | Heinz 9478 | Clarance | Big Dina Macarena | Dundee |
| **Sampling start date** | June 20 | June 20 | June 20 | May 3 | May 3 | May 3 |
| **Sampling finish date** | Sep. 17 | Sep. 17 | Sep. 17 | Sep 1 | Sep 1 | Sep 1 |
| **Number of chemical insecticide sprays** | - | - | - | 7 | 7 | 12 |
| **Chemical insecticides** | - | - | - | Tebufenozide, Methoxyfenozide | Tebufenozide | Tebufenozide |
| **Number of *Bt* products sprays*** | - | - | - | 17 | 19 | 12 |

**Bt* = *Bacillus thuringiensis*.

Table 2.2: Parasitoids reared from *Trichoplusia ni* Larvae in Fields in 2005 and 2006 in the Kingsville-Leamington area.

| Order | Family | Species | Habit |
|---|---|---|---|
| **Hymenoptera** | Ichneumonidae | *Campoletis sonorensis* (Cameron) | Solitary larval endoparasitoid - koinobiont |
| | Braconidae | *Cotesia marginiventris* (Cresson) | Solitary larval endoparasitoid - koinobiont |
| | | *Cotesia plathypenae* (Muesebeck) | Gregarious larval endoparasitoid - koinobiont |
| | | *Microplitis alaskensis* (Ashmead) | Solitary larval endoparasitoid - koinobiont |
| | | *Meteorus spp.* (Haliday) | Solitary larval endoparasitoid - koinobiont |
| | | Species not identified | Solitary larval endoparasitoid - koinobiont |
| | Encytidae | *Copidosoma floridanum* (Ashmead) | Polyembrionic egg-larval parasitoid - koinobiont |
| | Eulophidae | *Euplectrus spp.* (Westwood) | Gregarious larval ectoparasitoid – koinobiont. Probably two species. |
| | Pteromalidae | *Trichomalopsis ?viridescens* (Walsh) | Hyperparasitoid of *Campoletis sonorensis* |
| **Diptera** | | The specimens deteriorated too fast and were impossible to be identified. | Larval endoparasitoid - koinobiont |

Table 2.3: Relative abundance and Diversity's indexes of larval parasitoids of *Tricholusia ni* in tomato fields.

| Year | Field | Species' relative abundance | | | | | | | Diversity's indexes | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | ***Campoletis sonorensis*** | ***Euplectrus spp*** | ***Copidosoma floridanum*** | ***Cotesia marginiventris*** | ***Microplitis alaskensis*** | ***Cotesia plathypenae*** | ***Braconidae*** | **Simpson's diversity Index** | **Simpson's evenness index** |
| **2005** | 1 | 93.3 | 6.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.87 | 0.58 |
| | 2 | 78.6 | 0.0 | 14.3 | 7.1 | 0.0 | 0.0 | 0.0 | 0.62 | 0.54 |
| | 3 | 81.3 | 6.3 | 3.1 | 0.0 | 3.1 | 3.1 | 3.1 | 0.66 | 0.25 |
| | **Total** | 83.6 | 4.9 | 4.9 | 1.6 | 1.6 | 1.6 | 1.6 | 0.70 | 0.20 |
| | **Mean (± SE)** | 84.4±4.5 | 4.3±2.2 | 5.8±4.3 | 2.4±2.4 | 1.0±1.0 | 1.0±1.0 | 1.0±1.0 | 0.72±0.08 | 0.46±0.10 |
| **2006** | **Field** | ***Campoletis sonorensis*** | ***Euplectrus spp*** | ***Copidosoma floridanum*** | ***Cotesia marginiventris*** | ***Microplitis alaskensis*** | ***Meteorus spp*** | **Diptera** | **Simpson's diversity Index** | **Simpson's evenness index** |
| | 1 | 80.0 | 5.0 | 0.0 | 10.0 | 5.0 | 0.0 | 0.0 | 0.64 | 0.39 |
| | 2 | 77.3 | 9.1 | 4.5 | 4.5 | 4.5 | 0.0 | 0.0 | 0.59 | 0.34 |
| | 3 | 72.5 | 0.0 | 5.0 | 7.5 | 0.0 | 7.5 | 7.5 | 0.53 | 0.38 |
| | **Total** | 75.6 | 3.7 | 3.7 | 7.3 | 2.4 | 3.7 | 3.7 | 0.58 | 0.25 |
| | **Mean (± SE)** | 76.6±2.2 | 4.7±2.6 | 3.2±1.6 | 7.3±1.6 | 3.2±1.6 | 2.5±2.5 | 2.5±2.5 | 0.59±0.03 | 0.37±0.03 |

Table 2.4: Total percent parasitism of the *Trichoplusia ni* larval parasitoid assemblage species in tomato fields.

| Species | Year | |
|---|---|---|
| | **2005** | **2006** |
| *Campoletis sonorensis (Cameron)* | 12.75 | 17.26 |
| *Cotesia marginiventris* (Cresson) | 0.25 | 1.64 |
| *Cotesia plathypenae* (Muesebeck) | 0.25 | - |
| *Microplitis alaskensis* (Ashmead) | 0.25 | 0.55 |
| *Meteorus spp.* (Haliday) | - | 0.82 |
| Braconid not identified | 0.25 | - |
| *Copidosoma floridanum* (Ashmead) | 0.75 | 0.82 |
| *Euplectrus spp.* (Westwood) | 0.75 | 0.82 |
| *Diptera* | - | 0.82 |
| Total parasitism (%) | 15.25 | 22.73 |
| Total number of larvae | 400 | 365 |

Table 2.5: Overall total percent parasitism of *Trichoplusia ni* larval instars in tomato fields and greenhouses.

| System | Fields | | | | | | Greenhouses | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Year | 2005 | | | 2006 | | | 2005 | | 2006 | |
| Instar | Total number of larvae (#) | *Campoletis sonorensis* parasitism (%) | All other parasitoids parasitism (%) | Total number of larvae (#) | *Campoletis sonorensis* parasitism (%) | All other parasitoids parasitism (%) | Total number of larvae (#) | *Campoletis sonorensis* parasitism (%) | Total number of larvae (#) | *Campoletis sonorensis* parasitism (%) |
| 1 | 41 | 0.0 | 0.0 | 7 | 0.0 | 0.0 | 305 | 1.0 | 450 | 0.0 |
| 2 | 210 | 22.9 | 3.8 | 177 | 31.6 | 8.5 | 391 | 4.9 | 931 | 3.9 |
| 3 | 118 | 2.5 | 1.7 | 84 | 8.3 | 4.8 | 111 | 0.0 | 233 | 1.3 |
| 4 | 24 | 0.0 | 0.0 | 54 | 0.0 | 1.9 | 19 | 0.0 | 20 | 0.0 |
| 5 | 7 | 0.0 | 0.0 | 43 | 0.0 | 0.0 | 12 | 0.0 | 11 | 0.0 |
| Total | 400 | 12.75 | 2.5 | 365 | 17.3 | 5.5 | 838 | 2.6 | 1645 | 2.4 |

Table 2.6: Pearson Correlation of the number of second instar larvae of *Trichoplusia ni* and the number of larvae parasitised by *Campoletis sonorensis* in fields 2006.

| Field | Pearson Correlation | P-value | N |
|---|---|---|---|
| **1** | 0.664 | 0.336 | 4 |
| **2** | 0.929 | 0.0001 | 9 |
| **3** | 0.979 | 0.0001 | 9 |
| **Overall** | 0.946 | 0.0001 | 22 |

Table 2.7: Regression analysis of the second larval instar density of *Trichoplusia ni* and percent parasitism by *Campoletis sonorensis*. Samples from all dates were pooled by field and by year (Overall).

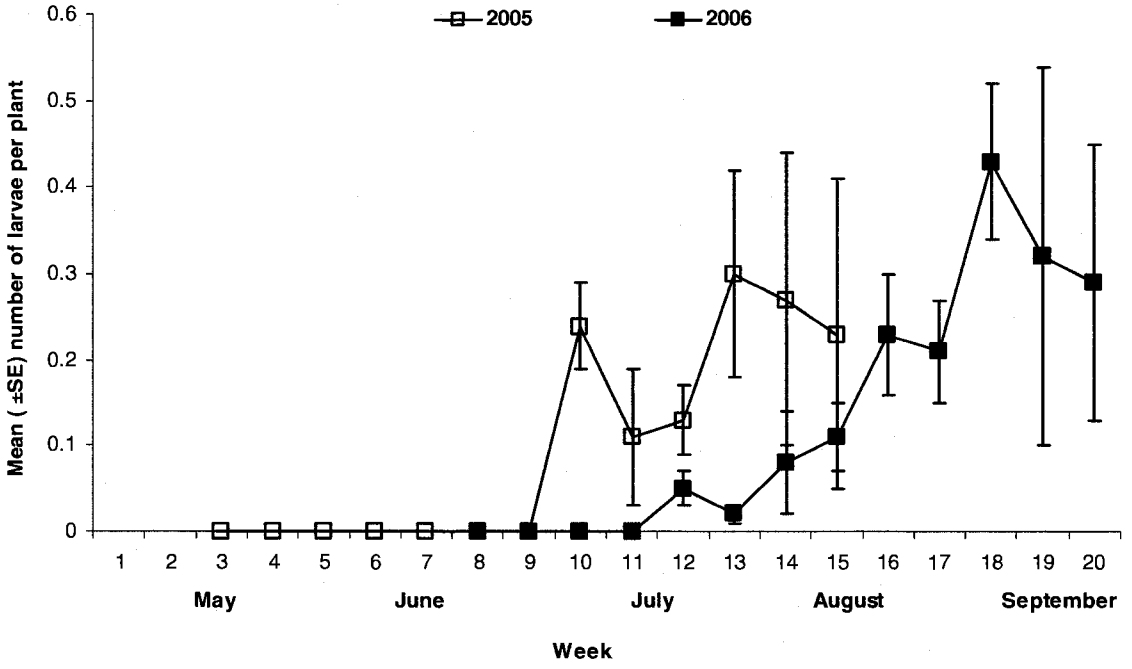
| 2006 | | | | | |
|---|---|---|---|---|---|
| **Field** | **Slope (b)** | **D.F.** | **$r^2$** | **F-value** | **P-value** |
| 1 | -0.686 | 1,3 | 0.705 | 4.782 | 0.160 |
| 2 | 0.444 | 1,3 | 0.224 | 2.015 | 0.199 |
| 3 | 0.388 | 1,3 | 0.428 | 5.241 | 0.056 |
| Overall | 0.322 | 1,3 | 0.182 | 4.4751 | 0.048 |

Table 2.8: Temporal relationship between second larval instar density of *Trichoplusia ni* and percent parasitism by *Campoletis sonorensis* in tomato fields 2006.

| Date / Week | Slope (b) | D.F. | $r^2$ | F-value | P-value |
|---|---|---|---|---|---|
| August 2 (week 8) | -0.397 | 1,1 | 0.386 | 0.628 | 0.572 |
| August 9 (Week 9) | 0.368 | 1,1 | 0.116 | 0.131 | 0.779 |
| August 17 (Week 10) | 1.331 | 1,1 | 0.905 | 9.558 | 0.199 |
| August 24 (Week 11) | 0.940 | 1,1 | 0.998 | 629.635 | 0.025 |

Figure 2.1: Mean (± SE) number of *Trichoplusia ni* larvae per plant.

A: Tomato Fields




B: Tomato greenhouses

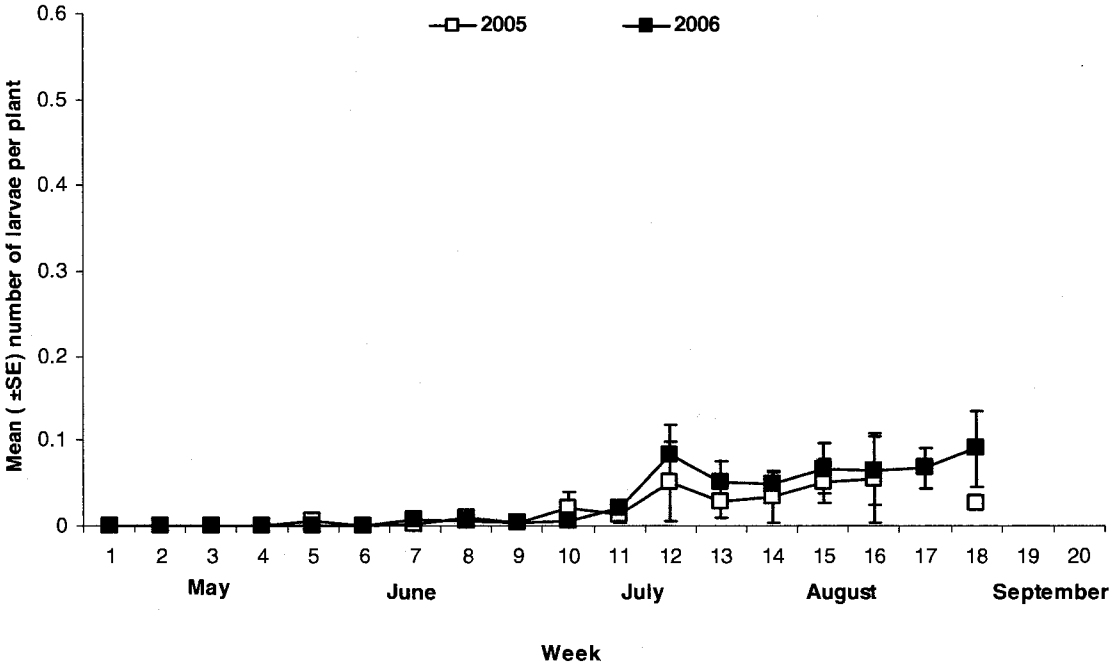
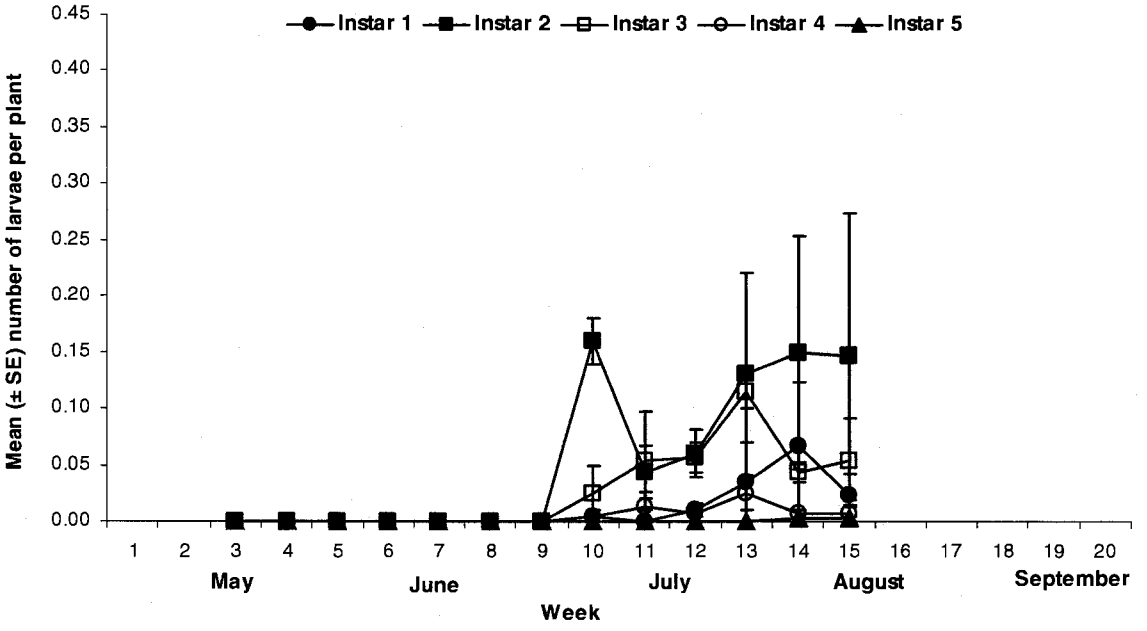
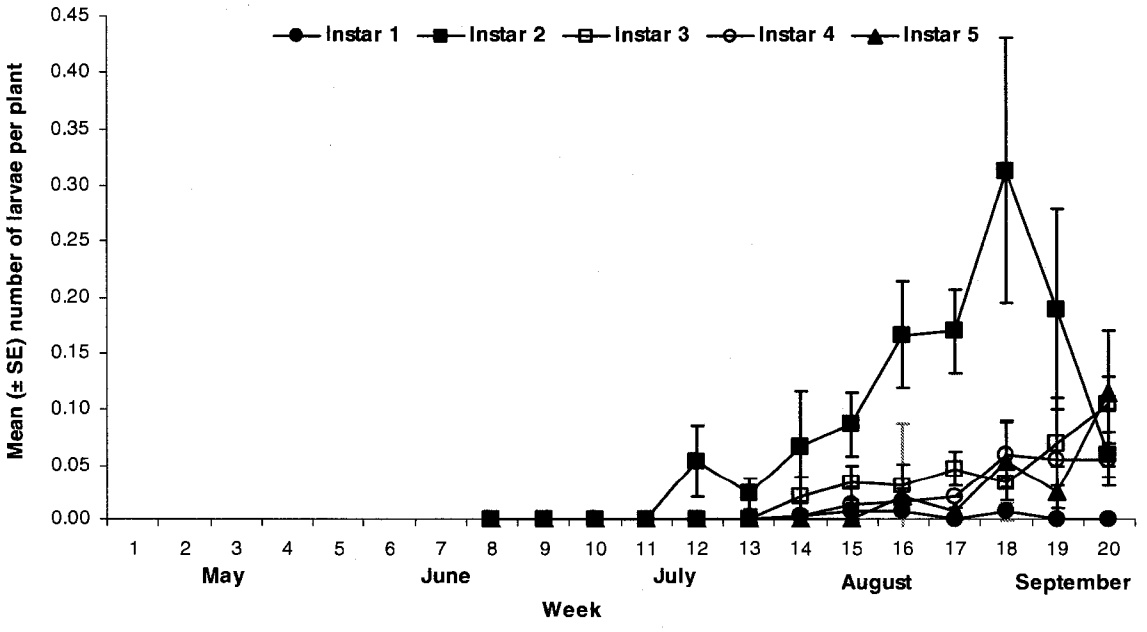


Figure 2.2: Mean (± SE) number of each larvae instar of *Trichoplusia ni* per plant.

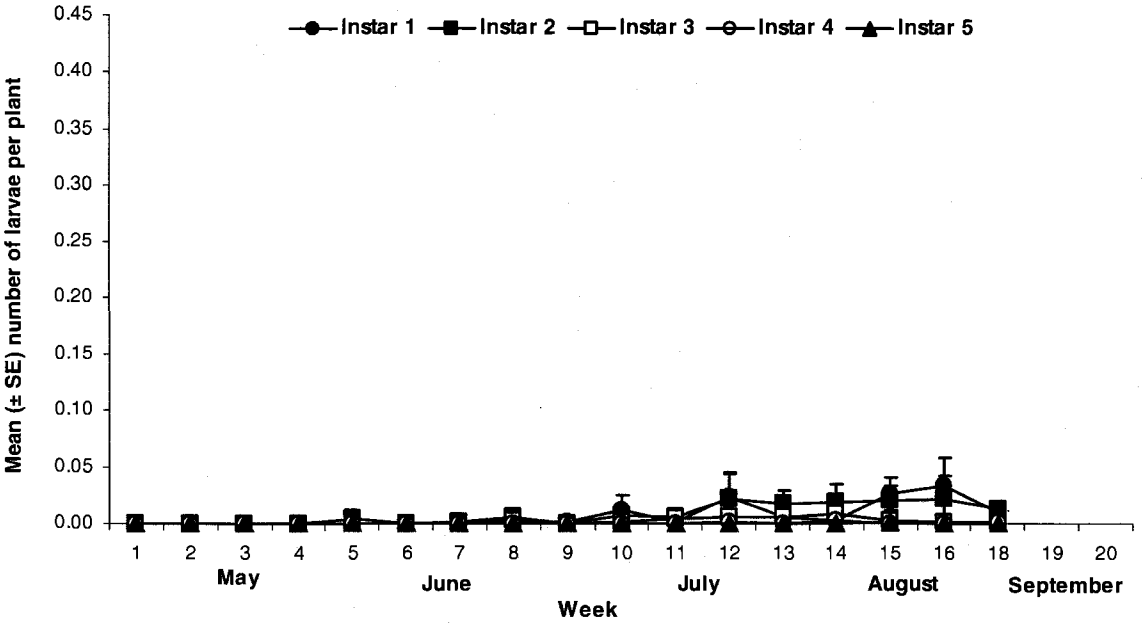
A. Within tomato fields in 2005




B. Within tomato fields in 2006



C. Within tomato greenhouses in 2005




D. Within tomato greenhouses in 2006

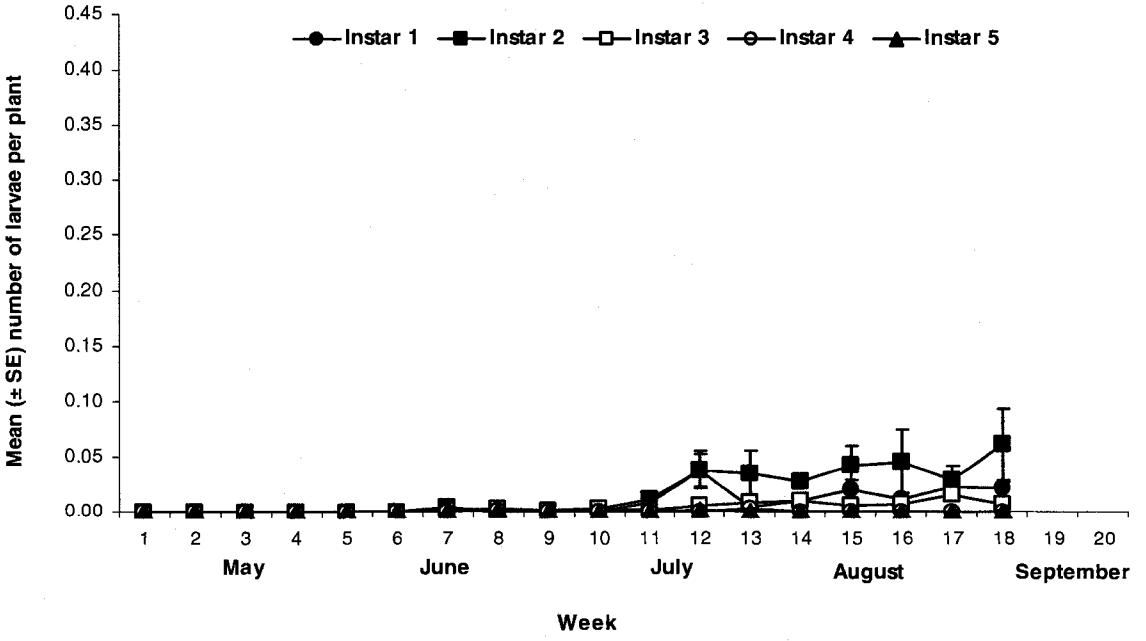
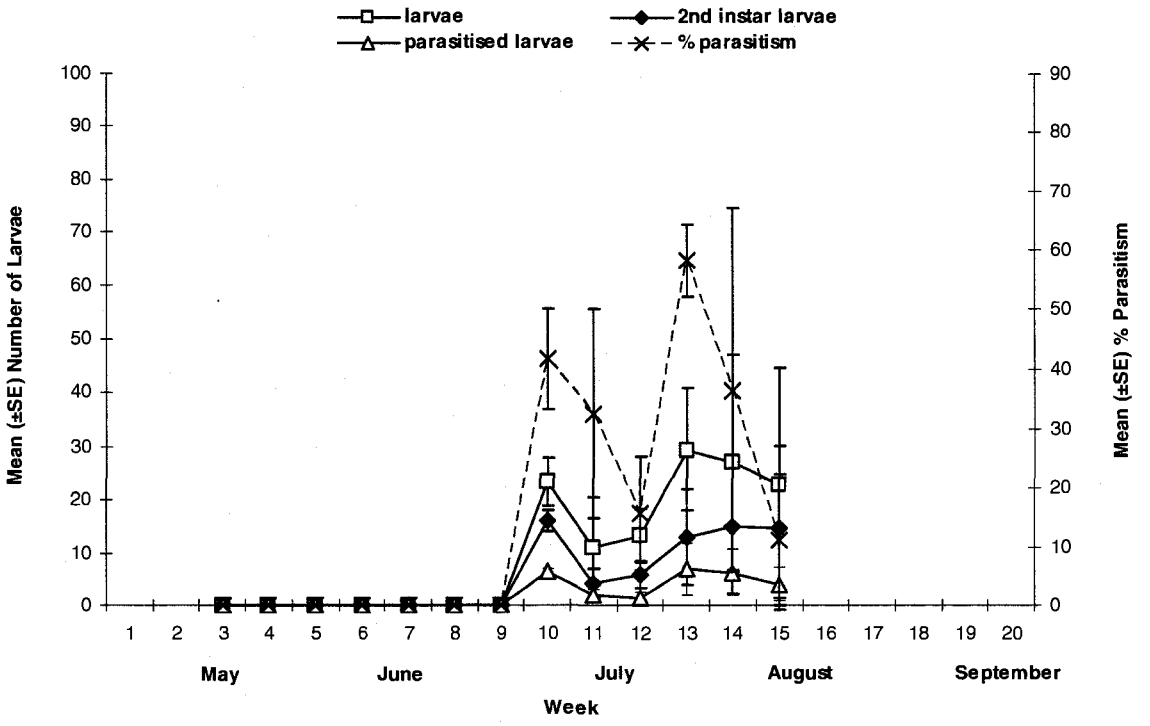
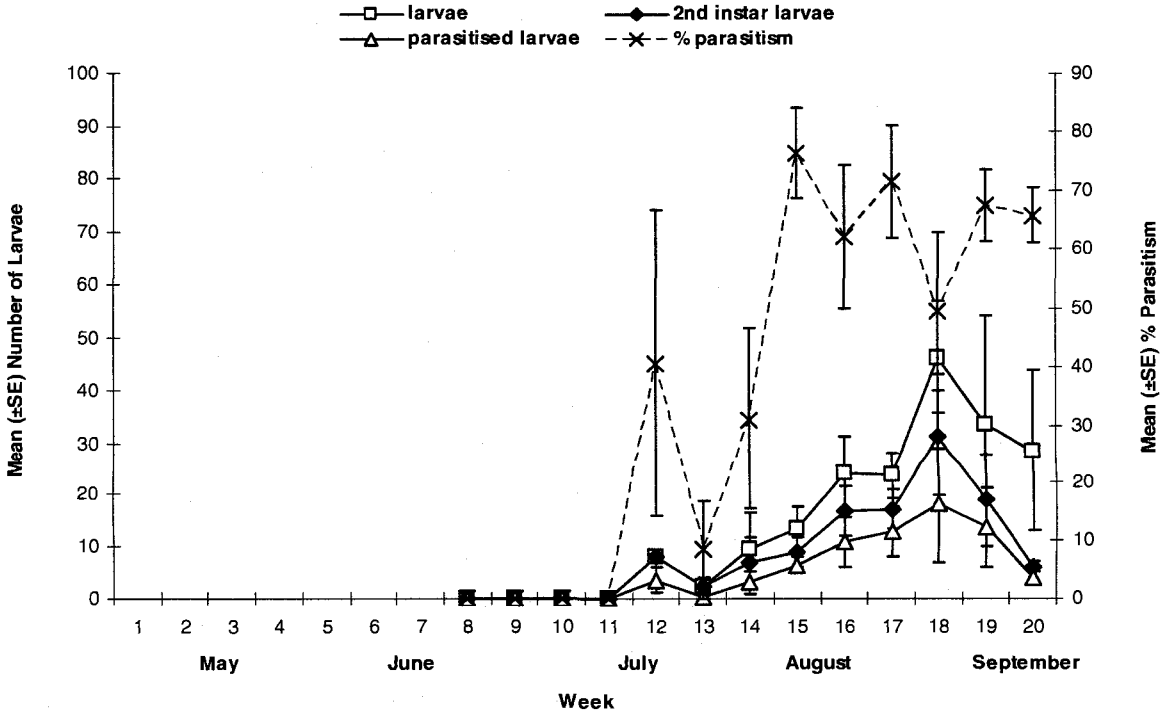


Figure 2.3: Mean (± SE) percent parasitism of the 2nd larval instar of *Trichoplusia ni* by *Campoletis sonorensis*

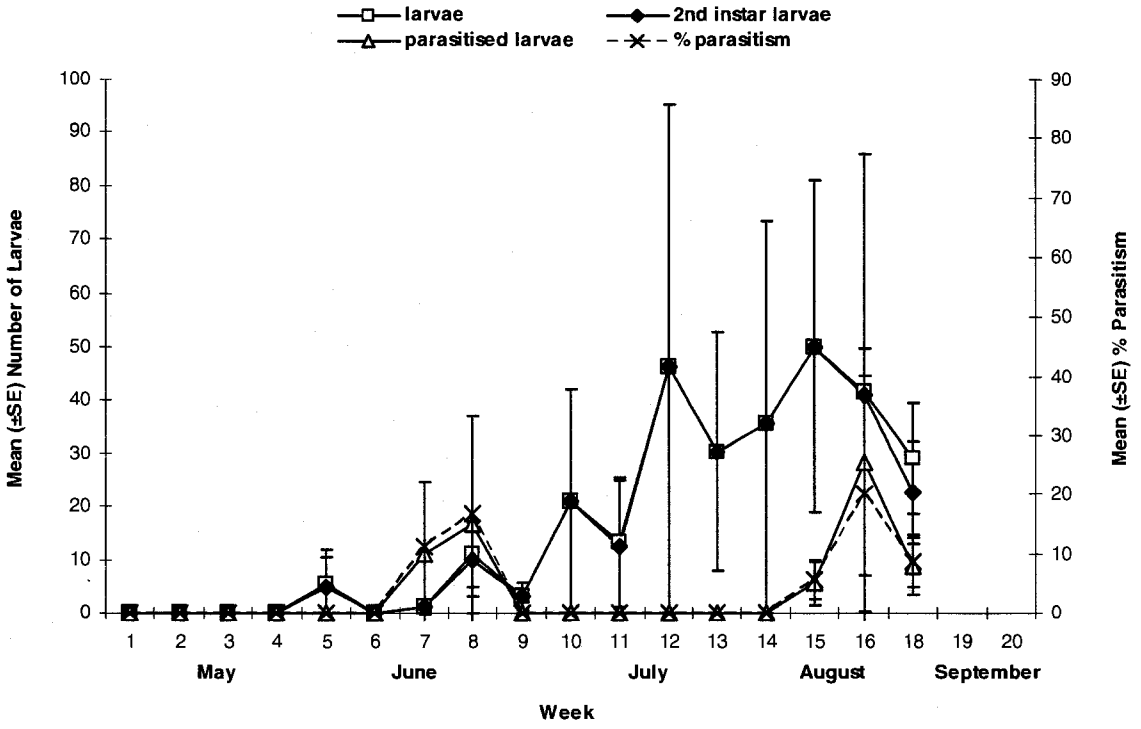
A. Within tomato fields in 2005



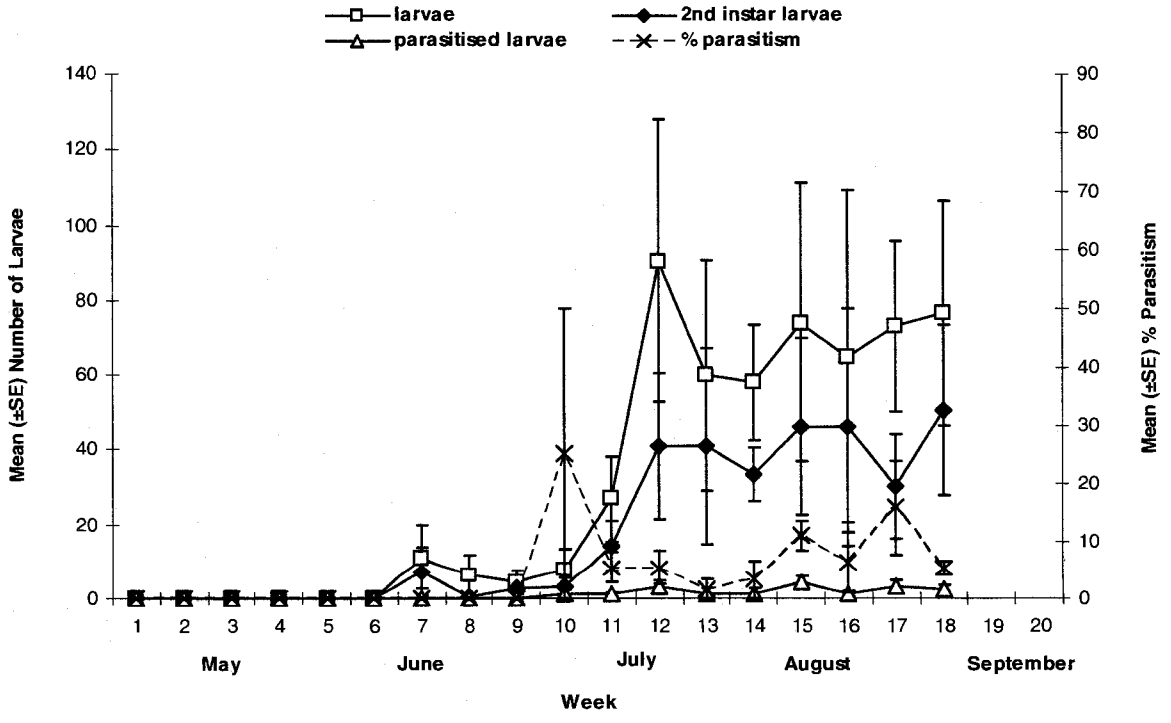

B. Within Tomato Fields in 2006



C. Within tomato greenhouses in 2005




D. Within tomato greenhouses in 2006



## Chapter 3

# Host preference and fitness-related proxies of *Campoletis sonorensis* (Hymenoptera: Ichneumonidae) as a Parasitoid of the Cabbage Looper, *Trichoplusia ni* (Lepidoptera: Noctuidae)

## Introduction

For insect parasitoids, the host represents the whole nutritional and physiological environment during immature development. Thus, host quality evaluation by female parasitoids plays a key role in host selection and the tradeoffs in fitness of the parasitoid because the host quality and the developmental requirements of the immature parasitoid may result in an increased or lowered gain (Vinson 1990; Godfray 1994; Harvey and Strand 2002; Beckage and Gelman 2004).

Koinobiont parasitoids, which allow the host to continue to feed and grow after parasitisation, have to cope with a higher degree of uncertainty regarding the resources available for their offspring as host quality varies during parasitoid development (Mackauer 1986). Thus, the relationship between host characteristics at oviposition and fitness gain of the parasitoid is not obvious and depends on a combination of factors such as (1) the physiology and behaviour of the host instars (Liu et al. 1984; Gerling et al. 1990; Weisser 1994; Jones and Greenberg 1998; Chau and Mackauer 2000; Lin and Ives 2003), (2) host-plant quality (Kouame and Mackauer 1991; Stadler and Mackauer 1996), (3) the feeding ecology of the host (Harvey and Strand 2002), and (4) rearing conditions (Roitberg et al. 2001; Hoelscher and Vinson 1971, Li and Mills 2004).

Parasitoid fitness is usually measured by life-history traits such as development time, survival, fecundity, sex ratio, and size (Godfray 1994; Roitberg et al. 2001) and although they are not true measures of fitness (Roitberg et al. 2001; van Baalen and Hemerik 2008), they can have direct or indirect contributions to it.

Several host quality models assume fitness as a relationship between the host size at oviposition and the emerging parasitoid size (Nicol and Mackauer 1999; Harvey et al. 2000; Chau and Mackauer 2001) such that when host size and quality vary, parasitoid wasps are expected to oviposit more females in high quality hosts, because the fitness of sons suffers less from being small than the fitness of the daughters, who will have to produce eggs (Charnov et al. 1981; Godfray 1994; VanLaerhoven and Stephen 2003).

*Trichoplusia ni* (Lepidoptera: Noctuidae), an important pest of crucifers and many other field crops in Ontario, is now a year-round pest in the vegetable greenhouse crops in Canada (Gillespie et al. 2002). Canadian populations of this insect pest are usually established through annual migration of adult moths from the south (Lafontaine and Poole 1991). The overwintering *T. ni* populations inside Canadian greenhouses have increased the development of resistance to *Bacillus thuringiensis var. kurstaki* (Janmaat and Myers 2003, 2006) which has resulted in increased use of chemical pesticides that are not compatible with other biocontrol agents and bumble bee pollinators.

*Campoletis sonorensis* (Hymenoptera: Ichneumonidae) is a solitary larval endoparasitoid that has been reported on about 30 Lepidoptera crop pests, primarily of the family Noctuidae (Lingren and Noble 1970; de Moraes et al. 1991; Machuca et al. 1989; CABI 2005). This generalist parasitoid has demonstrated potential to suppress populations of the tobacco budworm, *Helicoverpa virescens* (Fabricious) (Lepidoptera: Noctuidae), the corn earworm / tomato fruitworm, *Helicoverpa zea* (Boddie) and the fall armyworm *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae) in tobacco (*Nicotiana tabacum* L.)(Solanaceae), tomatoes (*Lycopersicon esculentum* Mill.)(Solanaceae), cotton (*Gossypium hirsutum* L.)(Malvaceae), corn (*Zea mays* L.)(Gramineae) and sorghum (*Sorghum bicolor* L.)(Poaceae) (Hoelscher and Vinson 1971; Lingren 1977; Isenhour 1986) and as reported in my previous study (Chapter 2), it has been

found to be a major factor in the regulation of *T. ni* populations in tomato fields in Southern Ontario.

The objectives of this study were to measure which larval stage of *T. ni* is the preferred host of the parasitoid *C. sonorensis*, and to measure the effect of different larval age classes of *T. ni* on parasitism, offspring sex ratio, mortality and development time parameters of *C. sonorensis*.

## Methods and Materials

### *Trichoplusia ni* rearing

The colony was maintained in an environmental chamber at 24°C, 60% RH and a photoperiod of 12:12 (L:D). Approximately 50 adults were kept in a 5 L plastic container. Adults were fed a 5% sugar solution and every other day the eggs were collected from paper towels used as the lid of the container and as oviposition substrate. The eggs were disinfected with a 0.5% solution of commercial bleach. Once the eggs hatched, larvae were reared on a pinto bean diet (Shorey and Hale 1965) in 12-oz Styrofoam containers. Larvae were moved into individual 1-oz transparent plastic cups (Solo Cup Company, Urbana, USA) once they developed to the second instar.

### *Campoletis sonorensis* rearing

The parasitoid colony was maintained under the same conditions as the *T. ni* colony, with 4 day-old *T. ni* larvae (early second larval instar) provided as hosts. In small plastic transparent cages (17 x 12 x 15 cm) on the same artificial diet as stated above, *T. ni* larvae were exposed to naïve mated *C. sonorensis* females for 24 h. Within each cage, there was a ratio of 20 larvae: 1 parasitoid female, with a total of up to 5 parasitoids/cage. Subsequently, each *T. ni* larva was placed into individual 1-oz plastic cups to allow the parasitoid to develop to adult. When *C. sonorensis* adults emerged, they were separated into cages by sex. After 24 h,

females were introduced into male cages to allow mating for 48 hours (ratio of 3 males: 1 female) (Isenhour 1986; Hoelscher and Vinson 1971)

**Fitness & Preference of *C. sonorensis* on *T. ni***

Larvae of *T. ni* were separated into 7 age class treatments based on date of eclosion (i.e. 2-8 day-old). The selection of age classes was based on the natural survey rearing results (Chapter 2) in which the 2$^{nd}$ larval instar of *T. ni* was the most frequent developmental stage parasitised by *C. sonorensis*. Under the rearing conditions described, *T. ni* larvae reached 2$^{nd}$ instar at 3-4 days and 3$^{rd}$ instar at 7-8 days. Twenty *T. ni* larvae of each age class were placed on tomato leaves in small transparent cages (17 x 12 x 15 cm). The tomato leaves chosen consisted of the three distal leaflets of a new side shoot, which were removed and kept in a plastic cup with wet cotton. One mated *C. sonorensis* female was introduced to the cage for 24 h. After exposure to the parasitoid, the *T. ni* larvae were placed individually in 0.5 oz cups (Solo Cup Company, Urbana, USA) with diet. Cups were checked daily and the time of formation of parasitoid cocoons was recorded until emergence of either adult *T. ni* or *C. sonorensis*. Upon emergence, the sex of each parasitoid was determined. Both the cages and the rearing cups were held in an environmental chamber set at 27°C, 60% RH and a photoperiod of 12:12 L:D. Each age class treatment was replicated 10 times.

The *C. sonorensis* fitness parameters measured were of four types: 1) parasitism ratio and success, 2) offspring sex ratio, 3) mortality, and 4) developmental time.

1. The parasitism ratio and success parameters consisted of: (a) parasitisation rate, (b) emergence rate, and (c) no emergence rate.
    a. Parasitisation rate was calculated from the proportion of the total number of hosts that produced parasitoid cocoons.
    b. Emergence rate was calculated from the proportion of parasitoids that emerged from the total number of cocoons.
    c. No emergence rate was calculated from the proportion of cocoons where adult parasitoids didn't emerge.

2. Offspring sex ratio parameters consisted of: (a) male rate, (b) female rate, and (c) overall sex ratio.
    a. Male rate was calculated from the proportion of male offspring.
    b. Female rate was calculated from the proportion of female offspring.
    c. Overall sex ratio was calculated from the proportion of male and female offspring.
3. Mortality parameters consisted of mortality rate, and corrected mortality rate, which were calculated as proportion of dead larvae, which was then corrected against that in the control for each host age according to Abbott (1925):

$$M_{corrected} = \frac{M_{treatment} - M_{control}}{100 - M_{control}} \times 100$$

4. Offspring development time parameters consisted of: (a) parasitisation to cocoon formation, (b) cocoon formation to adult emergence, and (c) parasitisation to adult emergence (or total development time). These parameters were calculated individually for males and females.

**Statistical Analysis**

The effect of different *T. ni* age classes on fitness parameters (except for developmental time) of *C. sonorensis* were analyzed using the Kruskal-Wallis test for nonparametric data, followed by Dunn's Multiple Comparison Test (Zar 1999) when significant differences were found between the host age classes. Pairwise comparisons to evaluate the effect of gender on emergence rate were analyzed with the Mann-Whitney U test. One-Sample sign test was used to compare the mean sex ratio of each age class with an equal mean sex ratio (0.5). ANCOVA was used to analyze a possible relationship between no emergence rate and parasitism rate through the age classes where no emergence rate was the dependent variable, age was the fixed factor and parasitism was the covariate. ANCOVA was also used to analyze a possible relationship between corrected

mortality rate and parasitism rate through the age classes where corrected mortality rate was the dependent variable, age was the fixed factor and parasitism rate was the covariate. The interactions of the different *T. ni* age classes and the *C. sonorensis* gender on each developmental time parameter was analyzed using a two-way ANOVA followed by Tukey's SHD Test at P=0.05 for means separation between the different age classes. The parameters parasitisation to cocoon formation, cocoon formation to adult emergence, and parasitisation to adult emergence (or total development time) were used as the dependent variable and sex and age were used as fixed factors. Pairwise comparisons to evaluate the effect of gender on each development parameter within each age classes were analyzed with independent samples T-test. These analyses were conducted in Minitab 15 (2006) and SPSS v.15 (2006)

**Results**

*Campoletis sonorensis* was able to parasitise and successfully develop to adult in all of the age classes provided (2 to 8 day-old larvae) (Figure 3.1). The percentage of hosts parasitised (parasitisation rate) differed between different host age classes (Kruskal-Wallis $X^2_6 = 27.47$, P=0.0001) such that the highest parasitism rate (53.0±5.7%), which occurred on 4 day-old hosts, did not differ from the parasitism rates on hosts of 3, 5 and 7 day-old, but it was higher than that on 2, 6 and 8 day-old hosts.

The percentage of parasitoids that successfully developed to adult (emergence rate) also differed between different host age classes (Figure 3.1; Kruskal-Wallis test: $X^2_6 = 27.89$, P=0.0001)). Similar to the parasitism rate, the highest emergence rate also occurred on 4 day-old hosts (44.0±5.5%) and it was not different from the emergence rates on hosts of 3, 5 and 7 day-old but it was higher than that on 2, 6 and 8 day-old hosts.

The percentage of parasitoids that were unsuccessful in developing to adult (no emergence rate) did not differ between different host age classes (Figure 3.1; Kruskal-Wallis test: $X^2_6$ = 10.18, P=0.117). The fluctuation in the no emergence rate is related to fluctuation in parasitisation rate (ANCOVA: $F_{1, 62}$=51.377, P=0.0001), not host age (ANCOVA: $F_{6, 62}$= 1.086, P = 0.381).

The offspring sex ratio was equal between males and females from all host age classes (Figure 3.2) and did not differ between different host age classes (Kruskal-Wallis test: $X^2_6$=3.22, P=0.781)). There was no difference in emergence rates of male compared to female parasitoids from different host age classes (Table 3.1).

Emergence rate of males differed between host age classes (Figure 3.3; $X^2_6$ = 21.84, P=0.001).The highest male mean emergence (22.0±3.9%) was from 4 day-old hosts, which did not differ from emergence from 3, 5 and 7 day-old hosts, but was higher than that from 2, 6, 8 day-old hosts. Emergence rate of females differed between host age classes ($X^2_6$=21.33, P=0.002). The highest mean female emergence rate, 22.0±4.8%, was from 4 day-old hosts, which did not differ from emergence from 3, 5, 6, and 7 day-old hosts, but was higher than that from 2 and 8 day-old hosts.

Both mortality rate and corrected mortality rate differed between host age classes (Figure 3.4; $X^2_6$=33.04, P=0.0001; $X^2_6$ = 68.01, P=0.0001). Both mortality rate and corrected mortality rate were highest in 2 day-old hosts, 39.0±5.3% and 31.7±5.7%, respectively. The mortality rates decreased with host age such that the lowest mortality rates were of 5-8 day-old larvae (mortality rate) or 6-8 day-old larvae (corrected mortality rate). The rate of parasitism on dead larvae was not measured, however most of the dead larvae that were examined under the stereoscope showing possible signals of parasitism (scars) and/or parasitoid eggs inside the bodies were 2 -3 day-old hosts. It could be that they were killed by the oviposition of the parasitoid as the corrected mortality was only marginally

related to the parasitisation rate (ANCOVA: $F_{1,62}$=3.665, P=0.060) but was related to the age of the host (ANCOVA: $F_{6,62}$=6.096, P=0.0001).

The development time from parasitisation to cocoon formation differed overall between host age classes (ANOVA: $F_{6,254}$=22.718, P=0.0001) and between sexes (ANOVA: $F_{1,254}$=7.111, P=0.008) but there was no interaction between age class and sex (ANOVA: $F_{6,254}$=1.360, P=0.231). Parasitoids developed faster to cocoon formation on 5-8 day-old hosts than on younger hosts (Table 3.2). In general, the development time from parasitisation to cocoon formation was shorter for males and it just differed from that on females on 3, 5, and 7 day-old hosts (Table 3.3a).

Development time from cocoon formation to adult emergence differed between host age classes (ANOVA: $F_{6,254}$=2.552, P=0.020) but not between sexes (ANOVA: $F_{1,254}$=0.270, P=0.604). There was no interaction between age class and sex (ANOVA: $F_{6,254}$=1.166, P=0.325). Parasitoids developed faster from cocoon formation to adult emergence on 7 day-old hosts than on 2 day-old hosts (Table 3.2) and it took the same amount of time in both sexes within each age host class (Table 3.3b).

Total development time (parasitisation to adult emergence) differed between host age classes (ANOVA: $F_{6,254}$=26.091, P=0.0001) and between sexes (ANOVA: $F_{1,254}$=5.515, P=0.020) but there was no interaction between age class and sex (ANOVA: $F_{6,254}$=1.600, P=0.148). Total developmental time was faster on 5-8 day-old hosts than on younger hosts (Table 3.2). These results are similar to the results for the development time from parasitisation to cocoon formation described above. Total developmental time was shorter for males than females on 3, 4 and 5, day-old hosts (Table 3.3c).

## Discussion

The suitability of the seven age-classes of *T. ni* larvae evaluated in this study as hosts of *C. sonorensis* indicates that 3-5 day-old larvae (early second larval instar) are the preferred stage of this host for parasitisation and provide the highest degree of fitness, although the parasitoid was able to develop to adult in all seven age-classes. These results agree with the results of Lingren et al. (1970) who studied the preference of *C. sonorensis* in ten different Lepidoptera hosts and reported that the suitability of these hosts depended on the age of the host species. In their study, they found that *C. sonorensis* was able to develop to adult on 2-8 day-old *T. ni* larvae. However, they reported that the parasitoid preferred 2-4 day-old larvae instead of the 3-5 day-old larvae preferred in the current study. They used a temperature of 29.5°C whereas I used 27°C, which may make a difference due to temperature effects on development rate. Likely, 2-4 day-old larvae at 29.5°C are the same size as 3-5 day-old larvae at 27°C. Although they used 2 mated parasitoid females per enclosure, the number of parasitised larvae was lower than the number I found in the current study. With a 24 hour exposure time, from 100 3-day-old larvae they reported a mean of 7.4 parasitised larvae, (3.7 per female) but from 20 4-day-old larvae, I found a mean of 10.6±1.1 parasitised larvae per female. Although it appears to be different, it is impossible to make a direct comparison because there is no measure of variation associated with their mean.

There are multiple factors identified that affect the parasitisation rate on different host age classes and these can be divided into two groups: 1) internal factors, including a) physiological and nutritional compatibility between the host and the immature parasitoid (Harvey et al. 2004), b) disruption of the parasitoid oviposition behaviour (Schmidt 1974; Bigornia 1956), c) failing of the parasitoid larvae to egress from older hosts or lack of a trigger from the host to initiate parasitoid egression (Gunasena et al. 1989a), and d) host mortality before parasitoid egression mostly from hosts parasitised at early age (Jenner and

Kuhlmann 2006); and 2) external factors, such as a) host food (Campbell and Duffey 1979; Gunasena et al. 1989b; Fox et al. 1990; Romeis et al. 2005), b) parasitoid parental aging (Hoelscher and Vinson 1971; Matos et al. 2005; Pandey et al. 2007), c) interference between females (Lingren and Noble 1970; Pandey et al. 2004), d) oviposition enclosure (Lingren and Noble 1972), and e) environmental conditions such as temperature and photoperiod (Hoelscher and Vinson 1971). Differences in these external factors between the ones in the current study and those of Lingren et al (1970), which were not fully specified, may explain the difference in parasitisation levels of *C. sonorensis* on *T. ni* observed between the two studies.

The difference on the parasitisation rate and on the emergence rate between the different age classes is due to two types of mortality: 1) mortality of host larvae prior to parasitoid cocoon formation, and 2) mortality of parasitoid prior to emergence. Many factors could explain this mortality. For example, superparasitism is a possible explanation. Although it was not quantified in this study, superparasitism has been found to be common under the conditions that *C. sonorensis* is reared in our lab (unpublished data).

Another mortality factor could be host age because in young larvae, the resource for the parasitoid development may be insufficient such that the parasitoid fails to mature and dies (Godfray 1994) and that young hosts are more susceptible to lethal injury during parasitoid oviposition by stinging, by the polydnavirus-venom injection or both. This mortality was indirectly measured by the corrected mortality rate as it provides a measure of the background level of mortality of hosts in the absence of parasitism. *Campoletis sonorensis* injects a polydnavirus into its hosts during oviposition which induces immunosuppression, host developmental arrestment, and in some cases, the death of the host (Norton and Vinson 1977; Webb and Summers 1990; Vinson and Stoltz 1986). Lingren et al. (1970) concluded that the higher mortality in 2-3 day-old larvae of *T. ni* exposed to *C. sonorensis* was due to abortive parasitism, however as they did not explain what

they meant by it, I assume that it could have been induced by all the factors mentioned previously. On the other hand, the mortality was reduced in the older host larvae, probably as a result of the larval defensive behavioural response (Bigornia 1956; Noble and Graham 1966), or to a stronger immune response to parasitism (Salt 1968; Vinson 1990), or both.

The proportion of parasitoid cocoons that did not emerge as adults was related to the increase in the parasitisation rate but not to the host age, probably a matter of the sample size which was too small to show any relationship.

Hoelscher and Vinson (1971) and Lingren et al. (1970) reported that the proportion of males is usually greater than that of females in field-collected and laboratory-reared *C. sonorensis*. In current study, the offspring sex ratio was not dependent on the host age. Lingren et al. (1970) reported sex ratio from 2-8 day-old larvae of 5 different Lepidoptera host species including *T. ni*, and found a female-biased sex ratio in *C. sonorensis* reared from 2 and 3 day-old larvae of *S. frugiperda* and *S. eridania* (Cramer), respectively. In the current study, an equal sex ratio was obtained from all the different age classes. Noble and Graham (1966) reported a higher ratio of adult females to males in older hosts. In the reproduction rate and life table study of *C. sonorensis* (Chapter 4), I reported a mean female-biased sex ratio on 4 day-old larvae of *T. ni*.

The sex ratio of the parasitoid progeny can be affected by multiple factors including: 1) photoperiod and female age, 2) host species, 3) female parasitoid density, and 4) host plant and/or diet quality. Hoelscher and Vinson (1971) reported that a 12:12 (L:D) photoperiod and 4 day-old females produced offspring with the greatest proportion of females, although the sex ratio was always male-biased. Lingren et al. (1970) found that *S frugiperda* and *S. eridania* were the only hosts that provided female-biased sex ratios for *C. sonorensis*, whereas parasitoid offspring from *T. ni* were always male-biased. Pandey et al. (2004) reported that with an increase in female parasitoid density, the proportion of male

progeny increased significantly when they used 1, 2, 4 and 8 females of *C. chlorideae* per cage. In the studies of Hoelscher and Vinson (1971) and Lingren et al. (1970), two to three female parasitoids were used per cage with *T. ni* and *H. virescens* as hosts and these studies had a male-biased *C. sonorensis* progeny sex ratio. I used 1 female per cage and obtained female-biased progeny sex ratios. Multiple lab and field-based studies support the idea that the progeny sex ratio of parasitoids is affect by the host plant and/or diet quality (Kumar and Tripathi 1987; Fox et al. 1990; Jansson 2003; Weathersbee III et al. 2004; Sétamou et al. 2005; Onagbola et al. 2007; Lentz and Kester 2008). In the current study, 4 day-old *T. ni* larvae were exposed to *C. sonorensis* females on tomato seedlings and in the reproduction rate and life table study (Chapter 4), the larvae were exposed on pinto bean diet. This may be affecting the progeny sex ratio which was equal for males and females in the current study and female-biased in the subsequent study (Chapter 4).

The development time of *C. sonorensis* from parasitism to cocoon formation was longer in young *T. ni* larvae and shorter for older host ages. Development time from cocoon formation to adult emergence is dependent on the environmental conditions during which the cocoons are exposed. Gunasena et al. (1989a) and Noble and Graham (1966) reported that the time to cocoon formation and adult emergence of *C. sonorensis* was not affected by the instar stage of *Heliothis virescens* attacked at 28°C and 36°C, respectively. Gunasena el al. (1989a) reported that males and females formed cocoons at approximately the same time, but the mean developmental time was longer for females. These results are in part contrary to the results of the current study because, for both parameters, the development time was longer for females. In contrast, Isenhour's (1986) results demonstrated the same relationship with *C. sonorensis* on *S. frugiperda* at 20°C as I did in the current study. As found by Isenhour (1986), temperature seems to be a major factor influencing these results because he did not find dependence of the development time of *C. sonorensis* from *S. frugiperda* at 15, 25 and 30°C but it has been reported in other parasitoids such as *Encarsia*

*formosa* (Gahan)(Hymenoptera: Aphelinidae) (Hu et al. 2002, 2003) and in *Aphidius ervi* (Haliday)(Hymenoptera: Aphelinidae) (Colinet et al. 2005). The longer development time observed in parasitoids in young host stages may be associated with the existence of a critical host size required for successful parasitoid development. In younger host stages that have fewer resources available, the immature parasitoid may need to slow down its development until the host has reached a sufficient size (Colinet et al. 2005). The developmental times of between 13 to 17.2 days for *C. sonorensis* on 1-8 day-old larvae of *T. ni* at 27°C found in the current study were very similar and followed the same trend through the age classes as development times from 14.5 to 16.8 days on 1-5 day-old larvae of *H. virescens* at 36°C found by Noble and Graham (1966).

In summary, the early 2$^{nd}$ larval instar (3-5 day-old larvae) of *T. ni* represents the most preferred host stage of the larval endoparasitoid *C. sonorensis*. The higher suitability of this host stage results in more parasitised larvae, a higher rate of successful parasitoid emergence, a higher rate of female emergence, and lower rate of immature parasitoid mortality. The fitness gain of *C. sonorensis* on late 1$^{st}$ larval instar (2 day-old larvae) and late 2$^{nd}$ larvae instar (6-8 day-old larvae) stages of *T. ni* is negatively affected by the trade-offs between the different physiological and behavioral characteristics influencing their suitability as hosts of *C. sonorensis*. Although the use of these suboptimal hosts results in a lower parasitisation rate, lower adult parasitoid emergence rate, lower female parasitoid rate, and higher mortality of immature parasitoids rate, the female parasitoids will probably use them when their availability, either in terms of accessibility or abundance, makes them profitable even though parasitoid fitness is diminished compared to other host stages (Colinet et al. 2005). Here, I clearly show why in the study of the host–parasitoid interactions, it is important to include multiple trade-offs between the parasitoid fitness-related proxies and that the physiological and behavioral characteristics of the host can influence the prediction of the interactions.

## References

Beckage NE, Gelman DB (2004) Wasp parasitoid disruption of host development: implications for new biologically based strategies for insect control. Annual Review of Entomology 49, 299–330.

Bigornia AE (1956) Studies on the biology and morphology of *Campoletis* perdistinctus (Viereck), a parasite of the Tobacco Budworm, *Heliothis virescens* (F.) MSc thesis. North Carolina State College, Raleigh.

Brown JR, Phillips JR (1990) *Microplitis croceipes* (Hymenoptera: Braconidae) diapause response to insectary conditions. The Florida Entomologist 73: 508-509.

CAB International (2005) Crop Protection Compendium. CABI Publishing. Wallingford, Oxfordshire. UK.

Campbell BC, Duffey SF (1979) Tomatine and parasitic wasps: potential incompatibility of plant antibiosis with biological control. Science 20: 700-702.

Charnov EL, Los-den Hartogh RL, Jones WT, van Den Assem J (1981) Sex ratio evolution in a variable environment. Nature 289: 28–33.

Chau A, Mackauer M (2000) Host-instar selection in the aphid parasitoid *Monoctonus paulensis* (Hymenoptera: Braconidae, Aphidiinae): a preference for small pea aphids. European Journal of Entomology 97: 347–353.

Chau A, Mackauer M (2001) Host-instar selection in the aphid parasitoid Monoctonus paulensis (Hymenoptera: Braconidae, Aphidiinae): assessing costs and benefits. Canadian Entomologist 133: 549-564.

Colinet H, Salin C, Boivin G, Hance Th (2005) Host age and fitness-related traits in a koinobiont aphid parasitoid. Ecological Entomology 30: 473-479.

Danks HV, Rabb RL, Southern PS (1979) Biology of insect parasites of *Heliothis* in North Carolina. Journal of the Georgia Entomological Society 14: 36-64.

de Moraes RR, Loeck AE, Belarmino LC (1991) Natural enemies of *Rachiplusia nu* (Guenée, 1852) and *Pseudoplusia includens* (Walker, 1857) (Lepidoptera: Noctuidae) on soybean in Rio Grande do Sul. [In Portuguese.] Pesquisa Agropecuária Brasileira 26: 57–64.

Fox LR, Etourneau DKL, Isenbach JE, Ann Ouhuys SV (1990) Parasitism rates and sex ratios of a parasitoid wasp: effects of herbivore and plant quality. Oecologia 83: 414-419.

Gerling D, Orion T, Yaakov D (1990). *Eretmocerus* penetration and immature development: A novel approach to overcome host immunity. Archives of Insect Biochemistry and Physiology 13:247–253.

Gillespie DR, Raworth DA, Shipp JL (2002) *Trichoplusia ni* Hübner, Cabbage Looper (Lepidoptera: Noctuidae). In: Mason PG, Huber JT (eds) Biological Control Programmes in Canada, 1981-2000. CABI Publishing. New York. NY, pp. 269-271.

Godfray HCJ (1994) Parasitoids behavioral and evolutionary ecology. Princeton University Press, Princeton, NJ

Gunasena GH, Vinson SB, Williams HJ (1989a) Interrelationships between growth of *Heliothis virescens* (Lepidoptera: Noctuidae) and that of its parasitoid, *Campoletis sonorensis* (Hymenoptera: Ichneumonidae). Annals of the Entomological Society of America 82: 187-191.

Gunasena GH, Vinson SB, Williams HJ, Stipanovic RD (1989b) Development and survival of the endoparasitoid *Campoletis sonorensis* (Hymenoptera: Ichneumonidae) reared from gossypol-exposed *Heliothis virescens* (F.) (Lepidoptera: Noctuidae). Environmental Entomology 18: 886-891.

Harvey JA, Kadash K, Strand MR (2000) Differences in larval feeding behavior correlate with altered developmental strategies in two parasitic wasps: implications for the size–fitness hypothesis. Oikos 88: 621-629.

Harvey JA, Strand MR (2002) The developmental strategies of endoparasitoid wasps vary with host feeding ecology. Ecology 83: 2439-2451.

Harvey JA, Bezemer TM, Elzinga A, Strand MR (2004) Development of the solitary endoparasitoid *Microplitis demolitor*: host quality does not increase with host age and size. Ecological Entomology 29: 35-43.

Herbert DA Jr, Zehnder GW, Speese J, Powell JE (1993) Parasitization and timing of diapause in Virginia *Microplitis croceipes* (Hymenoptera: Braconidae): implications for biocontrol of *Helicoverpa zea* (Lepidoptera: Noctuidae) in soybean. Environmental Entomology 22: 693-698.

Hoelscher CE, Vinson SB (1971) The sex ratio of a Hymenopterous parasitoid, *Campoletis perdistinctus*, as affected by photoperiod, mating, and temperature. Annals of the Entomological Society of America 64: 1373-1376.

Hu JS, Gelman DB, Blackburn MB (2002) Growth and development of *Encarsia formosa* (Hymenoptera: Aphelinidae) in greenhouse whitefly, *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae): effect of host age. Archives of Insect Biochemistry and Physiology 49: 125-136.

Hu JS, Gelman DB, Blackburn MB (2003) Age-specific interaction between the parasitoid, *Encarsia formosa* and its host, the silverleaf whitefly, *Bemisia tabaci* (strain B). Journal of Insect Science 3: 1-10.

Isenhour DJ (1986) Developmental time, adult reproductive capability, and longevity of *Campoletis sonorensis* (Hymenoptera: Ichneumonidae) as a parasitoid of fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae). Annals of the Entomological Society of America 79: 893-897.

Janmaat AF, Myers JH (2003) Rapid evolution and the cost of resistance to *Bacillus thuringiensis* in greenhouse populations of cabbage looper, *Trichoplusia ni*. Proceedings of the Royal Society of London *B.* 270: 2263-2270.

Janmaat AF, Myers JH (2006) The influences of host plant and genetic resistance to *Bacillus thuringiensis* on trade-offs between offspring number and growth rate in cabbage loopers, *Trichoplusia ni.* Ecological Entomology 31: 172–178.

Jansson J (2003) The influence of plant fertilization regime on plant-aphid-parasitoid interactions. Doctoral thesis. Department of Entomology, Swedish University of Agricultural Sciences. Uppsala.

Jenner W, Kuhlmann U (2006) Significance of host size for a solitary endoparasitoid: A trade-off between fitness parameters. Basic and Applied Ecology 7: 461-471.

Jones WA and Greenberg SM (1998) Suitability of *Bemisia argentifolii* (Homoptera: Aleyrodidae) instars for the parasitoid *Eretmocerus mundus* (Hymenoptera: Aphelinidae). Biological Control 27: 1569-1573.

Kouame KL and Mackauer M (1991) Influence of aphid size, age and behaviour on host choice by the parasitoid wasp *Ephedrus californicus* – a test of host-size models. Oecologia 88: 197-203.

Kumar A, Tripathi CPM (1987) Parasitoid host relationship between *Trioxys* (*Binodoxys*) *indicus* Subba Rao and Sharma (Hym., Aphidiidae) and *Aphis craccivora* Koch, (Hem., Aphididae). IV. Effect of host plants on the sex ratio of the parasitoid. Entomon 12: 96-97.

Lafontaine JD, Poole RW (1991) Noctuoidea, Noctuidae (part) – Plusiinae. Fascicle 25.1. In: Hodges RW, Davis DR, Dominick T, Ferguson DC, Franclemont JG, Hodges RW, Munroe EG (Eds.) The Moths of America North of Mexico, fascicle 25.1: 1-182, The Wedge Entomological Research Foundation, Washington, D.C.

Lentz AJ, Kester KM (2008) Postemergence experience affects sex ratio allocation in a gregarious insect parasitoid. Journal of Insect Behavior 21: 34-45.

Li B, Mills N (2004) The influence of temperature on size as an indicator of host quality for the development of a solitary koinobiont parasitoid. Entomologia Experimentalis et applicata 110: 249-256.

Lin LA, Ives AR (2003) The effect of parasitoid host-size preference on host population growth rates: an example of *Aphidius colemani* and *Aphis glycines*. Ecological Entomology 28: 542-550.

Lingren PD (1977) *Campoletis sonorensis*: maintenance of a population on tobacco budworms in a field cage. Environmental Entomology 6: 72-76.

Lingren PD, Guerra RF, Nickelsen JW, White C, 1970. Hosts and host-age preference of *Campoletis perdistinctus*. Journal of Economic Entomology 63: 518–522.

Lingren PD, Noble LW (1972) Preference of *Campoletis perdistinctus* for certain Noctuidae larvae. Journal of Economic Entomology 65: 104-107.

Liu SS, Morton R, Hughes RD (1984) Oviposition preference of a hymenopterous parasite for certain instars of its aphid host. Entomologia Experimentalis et Applicata 35: 249–254.

Machuca Jr, Arretz P, Araya J (1989) Presencia de *Campoletis sonorensis* (Cameron, 1886) (Hymenoptera: Ichneumonidae) en Chile. Acta Entomologica Chilena, 15: 269-270.

Mackauer M (1986) Growth and developmental interactions in some aphids and their hymenopterous parasites. Journal of Insect Physiology 32: 275–280.

Matos NFC, Zanuncio JC, Cruz I, Guedes RNC, Picanco MC (2005) Progeny production and parasitism by *Campoletis flavicincta* (Hym.: Ichneumonidae) as affected by female ageing. Biological Agriculture and Horticulture 22: 369-378.

Minitab for Windows, Rel. 15.1.1.0. (2006) State College, PA: Minitab Inc.

Nicol CMY, Mackauer M (1999) The scaling of body size and mass in a host parasitoid association: influence of host species and stage. Entomologia Experimentalis et Applicata 90: 83–92.

Noble and Graham (1966) Behavior of *Campoletis perdistinctus* (Viereck) as a parasite of the Tobacco budworm. Journal of Economic Entomology 59: 1118-1120.

Norton WN, Vinson SB (1977) Encapsulation of a parasitoid egg within its habitual host: an ultrastructural investigation. Journal of Invertebrate Pathology 30: 55-67.

Onagbola EO, Fadamiro HY, Mbata GN (2007) Longevity, fecundity, and progeny sex ratio of *Pteromalus cerealellae* in relation to diet, host provision, and mating. Biological Control 40: 222-229.

Pandey P, Kumar N, Tripathi CPM (2004) Impact of males on the progeny sex ratio of *Campoletis chlorideae* Uchida (Hym., Ichneumonidae), a parasitoid of *Helicoverpa armigera* (Hübner) (Lep.,Noctuidae). Journal of Applied Entomology 128: 254-257.

Pandey AK, Tripathi S, Tripathi CPM (2007) Effects of parental age at mating on the fecundity and progeny sex ratio of *Campoletis chlorideae*, an endolarval parasitoid of the pod borer, *Helicoverpa armigera.* Biocontrol. DOI 10.1007/s10526-007-9149-2

Quicke DLG (1997) Parasitic wasps. Chapman and Hall, London.

Roitberg BD, Boivin G, Vet LEM (2001) Fitness, parasitoids, and biological control: an opinion. Canadian Entomologist, 133: 429–438.

Romeis J, Babendreier D, Wäckers FL, Shanower TG (2005) Habitat and plant specificity of *Trichogramma* egg parasitoids-underlying mechanisms and implications. Basic and Applied Ecology 6: 215-236.

Salt G (1968) The resistance of insect parasitoids to the defence reactions of their hosts. Biological Reviews 43: 200-232.

Sétamou M, Jiang N, Schulthess F (2005) Effect of different host plants on the survivorship of *Chilo partellus* and performance of its larval parasitoid *Cotesia flavipes*. Biological Control 32: 183–190.

Shorey HH, Hale RL (1965) Mass-rearing of the larvae of nine noctuid species on a single artificial medium. Journal Economic Entomology 58: 522-524.

Schmidt GT (1974) Host-acceptance behaviour of *Campoletis sonorensis* toward *Heliothis zea*. Annals of the Entomological Society of America 67: 835-844.

SPSS for Windows, Rel. 15.0.0. (2006) Chicago, IL: SPSS Inc.

Stadler B, Mackauer M (1996) Influence of plant quality on interactions between the aphid parasitoid *Ephedrus californicus* (Hymenoptera: Aphidiidae) and its host, *Acyrthosiphon pisum* (Homoptera: Aphididae). Canadian Entomologist 128: 27-39.

Tauber MJ, Tauber CA, Masaki S (1986) Seasonal Adaptations of Insects. Oxford University Press, USA.

van Baalen, M. and L. Hemerik (2008). Parasitoid fitness: from simple idea to intricate concept. in Wajnberg E, Bernstein C, van Alphen J (eds). Behavioural Ecology of Insect Parasitoids. Blackwell, Oxford, pp. 31-50.

VanLaerhoven, SL; Stephen, FM (2003) Host species influences body size and egg load of the bark beetle (Coleoptera: Scolytidae) parasitoid, *Roptrocerus xylophagorum* Ratzeburg (Hymenoptera: Pteromalidae). The Canadian Entomologist 135: 737-740.

Vinson SB (1990) Physiological interactions between the host genus *Heliothis* and its guild of parasitoid. Archives of Insect Biochemistry and Physiology 13: 63-81.

Vinson SB, Stoltz DB (1986) Cross-protection experiments with two parasitoid (Hymenoptera: Ichneumonidae) viruses. Annals of the Entomological Society of America 79: 216-218.

Weathersbee III AA, Mckenzie CL, Tang YQ (2004) Host plant and temperature effects on *Lysiphlebus testaceipes* (Hymenoptera: Aphidiidae), a native parasitoid of the exotic Brown Citrus Aphid (Homoptera: Aphididae). Annals of the Entomological Society of America 97: 476-480.

Webb BA, Summers MB (1990) Venom and viral expression products of the endoparasitic wasp *Campoletis sonorensis* share epitopes and related sequences. Procedings of the National Academy of Science Microbiology 87: 4961-4965.

Weisser WW (1994) Age-dependent foraging behaviour and host instar preference of the aphid parasitoid *Lysiphlebus cardui*. Entomologia Experimentalis et Applicata 70: 1-10.

Zar JH (1999) Biostatistical Analysis. Fourth Edition. Prentice Hall, New Jersey.

Table 3.1: Comparison of male versus female *Campoletis sonorensis* offspring emergence rates from each age class of *Trichoplusia ni* larvae. Means with the same letter are not significantly different (Mann-Whitney U test, P>0.05)

| Host age (Day-old) | Mean±SE emergence rate | |
|---|---|---|
| | Male percentage (%) | Female percentage (%) |
| 2 | 4.5±2.5a | 2.5±1.1a |
| 3 | 10.0±3.7a | 10±4.3a |
| 4 | 22.0±3.9a | 22.0±4.8a |
| 5 | 15.0±4.9a | 9.0±1.8a |
| 6 | 4.0±1.2a | 11.5±3.3a |
| 7 | 9.5±2.3a | 5.5±1.6a |
| 8 | 5.0±2.2a | 2.0±0.8a |

Table 3.2: Development time parameters of *Campoletis sonorensis* offspring by host age classes. Means within the same response variable followed by the same letter are not significantly different (Tukey's Multiple Comparison Test, P>0.05)

| Host Age (day-old) | Parasitism to cocoon formation (days) | Cocoon formation to adult emergence (days) | Parasitism to adult emergence (days) |
|---|---|---|---|
| | Mean±SE | Mean±SE | Mean±SE |
| 2 | 11.1±0.5b | 5.7±0.2b | 16.8±0.5b |
| 3 | 11.4±0.3b | 5.6±0.1ab | 17.0±0.3b |
| 4 | 10.2±0.2b | 5.4±0.1ab | 15.6±0.2b |
| 5 | 8.0±0.2a | 5.3±0.1ab | 13.4±0.2a |
| 6 | 7.6±0.2a | 5.1±0.1ab | 12.7±0.2a |
| 7 | 8.3±0.4a | 5.0±0.1a | 13.3±0.5a |
| 8 | 7.71±0.2a | 5.3±0.2ab | 13.0±0.4a |

Table 3.3: Development time parameters of *Campoletis sonorensis* offspring by sex within host age classes. Means with the same letter are not significantly different (Independent samples T-test, P>0.05)

a. Parasitism to cocoon formation

| Host Age (day-old) | Mean±SE development time from parasitism to cocoon formation (Days) | | |
|---|---|---|---|
| | Male | Female | T-test |
| 2 | 11.4±0.5a | 10.4±0.9a | $t_{1,12}$=1.122, P=0.284 |
| 3 | 10.6±0.3a | 12.3±0.6b | $t_{1,38}$=-2.736, P=0.009 |
| 4 | 9.8±0.3a | 10.6±0.3a | $t_{1,89}$=-1.800, P=0.075 |
| 5 | 7.6±0.1a | 8.7±0.3b | $t_{1,46}$=-3.996, P=0.0001 |
| 6 | 7.3±0.4a | 7.7±0.2a | $t_{1,29}$=-1.061, P=0.297 |
| 7 | 7.6±0.4a | 9.5±0.9b | $t_{1,28}$=-2.252, P=0.032 |
| 8 | 7.6±0.2a | 8.0±0.7a | $t_{1,12}$=-0.726, P=0.482 |

b. Cocoon formation to adult emergence

| Host Age (day-old) | Mean±SE development time from cocoon formation to adult emergence (Days) | | |
|---|---|---|---|
| | Male | Female | T-test |
| 2 | 5.8±0.4a | 5.6±0.2a | $t_{1,12}$=3.37, P=0.742 |
| 3 | 5.5±0.1a | 5.7±0.3a | $t_{1,38}$=-0.677, P=0.503 |
| 4 | 5.2±0.1a | 5.6±0.1b | $t_{1,89}$=-2.443, P=0.017 |
| 5 | 5.4±0.1a | 5.3±0.2a | $t_{1,46}$=0.408, P=0.685 |
| 6 | 2.3±0.3a | 5.0±0.2a | $t_{1,29}$=-0.631, P=0.533 |
| 7 | 5.1±0.1a | 4.9±0.2a | $t_{1,28}$=0.639, P=0.528 |
| 8 | 5.4±0.2a | 5.0±0.4a | $t_{1,12}$=0.926, P=0.373 |

c. Parasitism to adult emergence

| Host Age (day-old) | Mean±SE development time from parasitism to adult emergence (Days) | | |
|---|---|---|---|
| | Male | Female | T-test |
| 2 | 17.2±0.5a | 16.0±1.0a | $t_{1,12}$=1.239, P=0.239 |
| 3 | 16.1±0.3a | 18.0±0.6b | $t_{1,38}$=-3.109, P=0.004 |
| 4 | 15.0±0.3a | 16.2±0.3b | $t_{1,89}$=-2.616, P=0.010 |
| 5 | 13.0±0.2a | 14.0±0.3b | $t_{1,46}$=-3.011, P=0.004 |
| 6 | 12.5±0.3a | 12.7±0.2a | $t_{1,29}$=-0.551, P=0.586 |
| 7 | 12.6±0.4a | 14.4±1.0a | $t_{1,28}$=-1.808, P=0.081 |
| 8 | 13.0±0.4a | 13.0±1.0a | $t_{1,12}$=0.000, P=1.000 |

Figure 3.1: Mean (± SE) parasitisation rate (percent of parasitised hosts), parasitoid emergence rate (percent of parasitoids successfully developing to adult), and no emergence rate (percent of parasitoids not successfully developing to adult) of *Campoletis sonorensis* on each *Trichoplusia ni* age class. Means within the same response variable followed by the same letter are not significantly different (Dunn's Multiple Comparison Test, P>0.05)

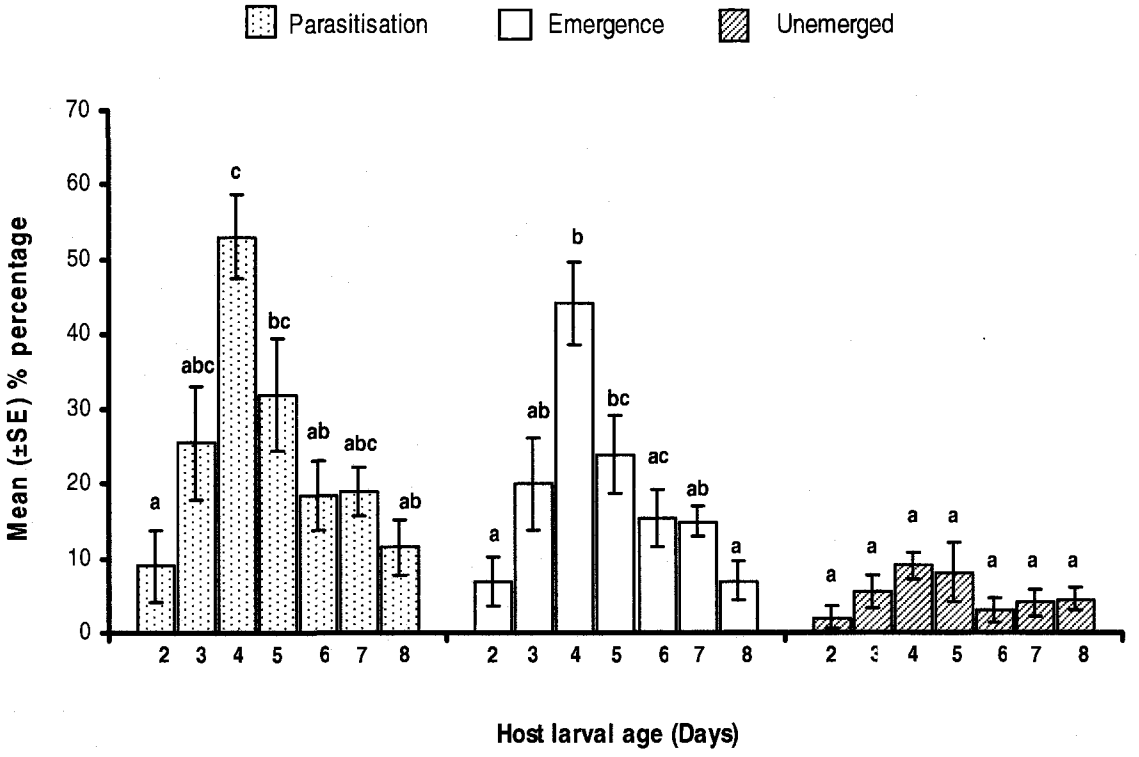


Figure 3.2: Mean (± SE) offspring sex ratio of *Campoletis sonorensis* emerging from different *Trichoplusia ni* age classes. Means with the same letter are not significantly different between them (Dunn's Multiple Comparison Test, P>0.05) and from a mean sex ratio of 0.5 (One-Sample sign test, P>0.05)

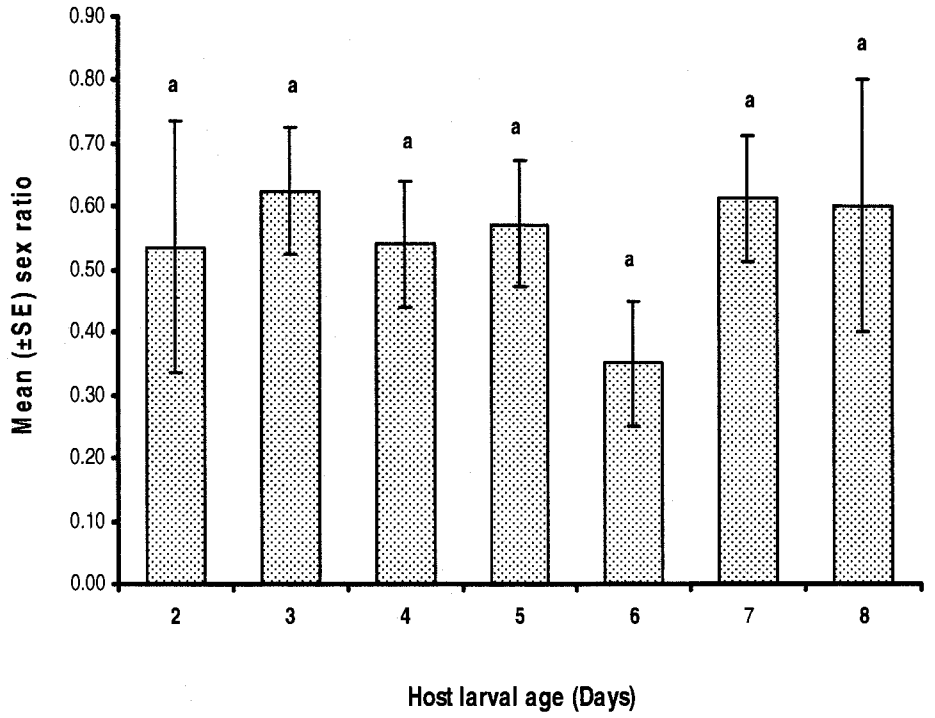


Figure 3.3: Mean (± SE) percentage of male or female *Campoletis sonorensis* offspring emerging from different *Trichoplusia ni* age classes (*T. ni* larvae reached 2nd instar at 3-4 days and 3rd instar at 7-8 days). Means within the same response variable followed by the same letter are not significantly different (Dunn's Multiple Comparison Test, P>0.05)

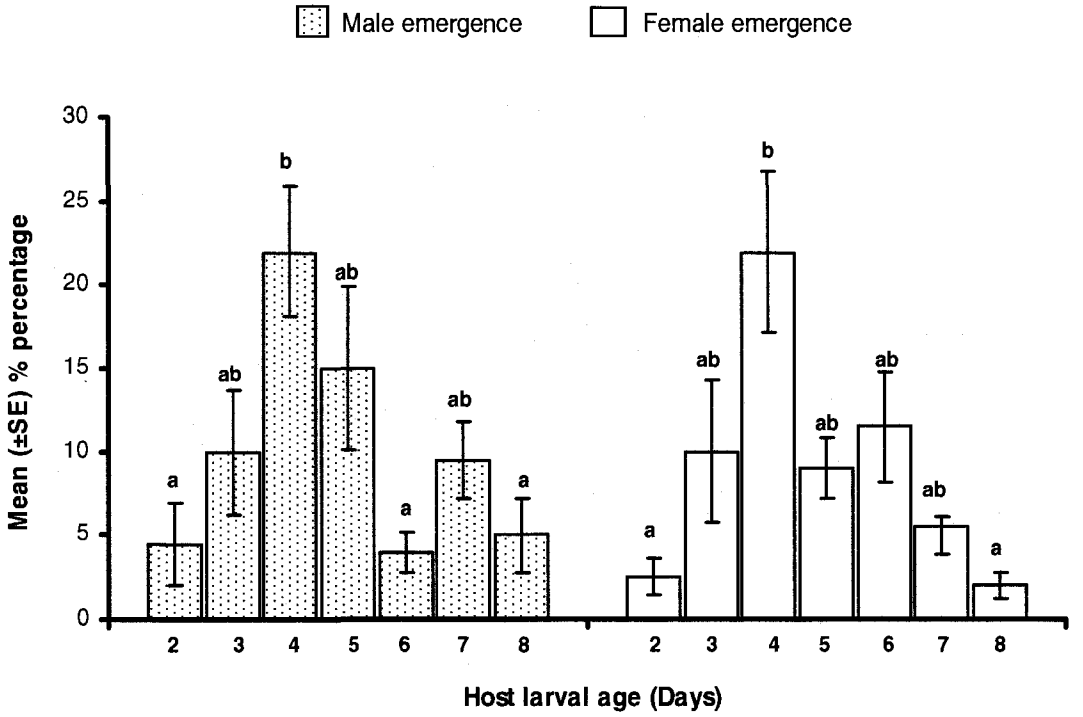
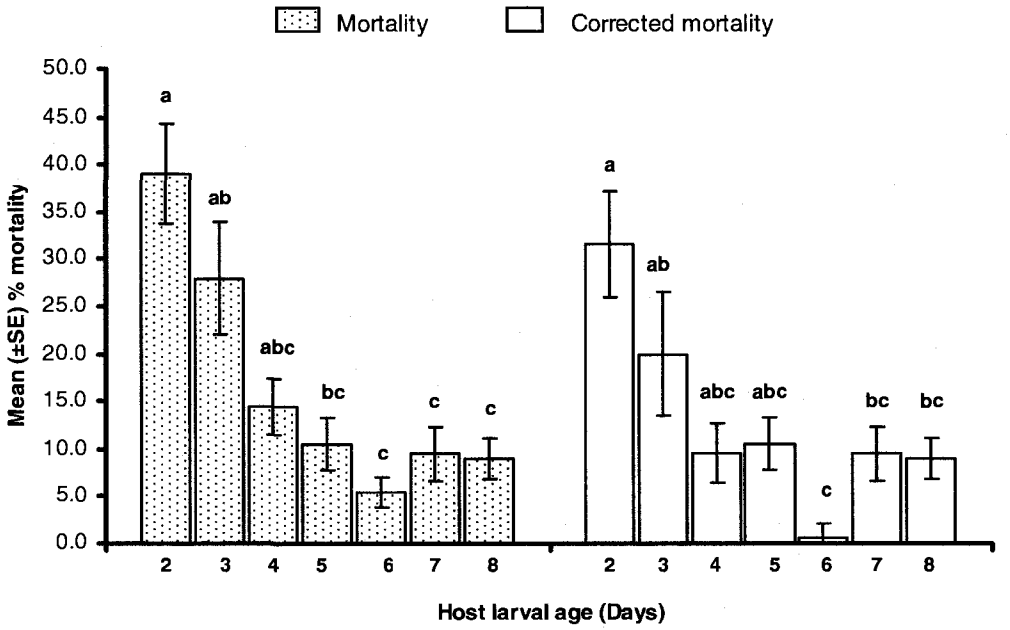


Figure 3.4: Mean (± SE) percent mortality and corrected mortality of different *Trichoplusia ni* age classes parasitised by *Campoletis sonorensis.* Means within the same response variable followed by the same letter are not significantly different (Dunn's Multiple Comparison Test, P>0.05)



## Chapter 4

## Reproduction of *Campoletis sonorensis* (Hymenoptera: Ichneumonidae), an Endoparasitoid of the Cabbage Looper *Trichoplusia ni* (Lepidoptera: Noctuidae) under laboratory conditions

### Introduction

The term fecundity refers to an animal's reproductive output, in terms of the total number of eggs produced or laid over a specified period, and should be distinguished from fertility, which refers to the number of viable progeny that ensue. From the standpoint of population dynamics, fertility is the more important parameter, as it is the number of progeny entering the next generation. A species' potential fecundity is usually taken to be the maximum number of eggs that can potentially be laid by females and the realised fecundity as the number of eggs actually laid over the life-span (Jervis et al. 2005)

Fecundity is a variable feature of a species, influenced by a range of intrinsic and extrinsic (physical and biotic) factors. The evaluation of a natural enemy for biological control requires a study of the influence of these factors and possible interaction effects between certain factors on potential and realised fecundity, and if possible, fertility (Jervis et al. 2005 ). The life table analysis is the most reliable method to account for survival and reproduction of a population, which is vital to the description and understanding of the population dynamics of a species (Andrewartha and Birch 1966; Southwood 1978). Biological parameters, such as the duration of developmental stages and population growth obtained from fertility life tables, are important for that knowledge. The main parameters associated with a fertility life table are the net reproductive rate (***Ro***), intrinsic rate of increase ($r_m$ ), mean generation time (***T***), finite rate of increase (***l***) and the doubling time (***D***). Rate of increase ($r_m$) or growth potential of a population under specified physical conditions in an unlimited environment where the effects of increasing

density do not need to be considered (Birch 1948) is one of the key criteria in the process of selecting parasitoids as a biological control agents (van Lenteren 1986)

*Trichoplusia ni* (Hübner) (Lepidoptera: Noctuidae), an important pest of crucifers and many other field crops in Ontario, is now a year-round pest in vegetable greenhouse crops in Canada (Gillespie et al. 2002). In the past, Canadian populations of this insect pest were usually established through annual migration of adult moths from the south (Lafontaine and Poole 1991) but recently, *T. ni* has been found overwintering inside Canadian vegetable greenhouses, which has required increased insecticide sprays of *Bacillus thuringiensis var. kurstaki* and lead to the development of resistance to Btk in populations of *T. ni* (Janmaat and Myers 2003, Janmaat et al. 2004).

*Campoletis sonorensis* (Cameron)(Hymenoptera: Ichneumonidae) is an arrenotokous, solitary, endoparasitoid of lepidopterans, including several major pest species (Townes and Townes 1951, Lingren et al. 1970; de Moraes et al. 1991; Machuca et al. 1989; CABI 2005). This generalist parasitoid has demonstrated potential to suppress populations of the tobacco budworm, *Helicoverpa virescens* (Fabricious) (Lepidoptera: Noctuidae), the corn earworm / tomato fruitworm, *Helicoverpa zea* (Boddie) and the fall armyworm *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae) in tobacco (*Nicotiana tabacum* L.)(Solanaceae), tomatoes (*Lycopersicon esculentum* Mill.)(Solanaceae), cotton (*Gossypium hirsutum* L.)(Malvaceae), corn (*Zea mays* L.)(Gramineae) and sorghum (*Sorghum bicolor* L.)(Poaceae) from USA to Chile (Hoelscher and Vinson 1971; Isenhour 1985, Carlson 1972; Machuca et al. 1989) but is a rare parasitoid of *T. ni* (Carlson 1972; Waterhouse 1998). However, in Southwestern Ontario vegetable fields and greenhouses, *T. ni* seems to be an important host for *C. sonorensis* for the first time recorded (Chapter 2). Thus, more knowledge about this parasitoid-host relationship is required in order to evaluate the potential of this parasitoid as a biocontrol agent of *T. ni*. This study measured the realised

fecundity and fertility parameters of *C. sonorensis* as an endoparasitoid of *T. ni* and calculated parasitoid life table statistics.

## Materials and Methods

### *Trichoplusia ni* rearing

The colony was maintained in an environmental chamber at 24°C, 60% RH and a photoperiod of 12:12 (L:D). Approximately 50 adults were kept in a 5 L plastic container. Adults were fed a 5% sugar solution and every other day the eggs were collected from paper towels used as the lid of the container and as oviposition substrate. The eggs were disinfected with a 0.5% solution of commercial bleach. Once the eggs hatched, larvae were reared on a pinto bean diet (Shorey and Hale 1965) in 12-oz Styrofoam containers. Larvae were moved into individual 1-oz transparent plastic cups (Solo Cup Company, Urbana, USA) once they developed to the second instar.

### *Campoletis sonorensis* rearing

The parasitoid was maintained under the same conditions as the *T. ni* colony, with 4 day-old *T. ni* larvae (early second larval instar) provided as hosts. In small plastic transparent cages (17 x 12 x 15 cm) on the same artificial diet as stated above, *T. ni* larvae were exposed to mated *C. sonorensis* females for 24 h. Within each cage, there was a ratio of 20 larvae: 1 parasitoid female, with a total of up to 5 parasitoids / cage. Subsequently, each *T. ni* larva was placed into individual 1-oz plastic transparent cups to allow the parasitoid to develop. When *C. sonorensis* wasps emerged, they were separated into cages by sex. After 24 h, females were introduced into male cages to allow mating for 48 hours (ratio of 3 males: 1 female) (Hoelscher and Vinson 1971; Isenhour 1986)

### Fecundity and life table experiment

Using a fine paint brush, thirty 4 day-old *T. ni* larvae were placed in a plastic Petri dish (12 cm diameter) with a 2x2 cm piece of diet (Shorey and Hale 1965) inside

a cage (17x12x15 cm) with one mated female *C. sonorensis.* After 24 h, the *T. ni* larvae were removed and another set of 30 *T. ni* larvae were placed in the cage with the parasitoid. This was continued until the parasitoid died. After exposure to the parasitoid, the *T. ni* larvae were placed individually in small cups (1 oz) with diet and checked daily until adult emergence of either a parasitoid or a moth. Twelve parasitoid females were used. The experiment was conducted in environmental chambers set at 24°C, 60% RH and a photoperiod of 12:12 Light: Dark.

The parasitoid life span was measured and divided into an **oviposition period** and a **post-oviposition period**. The oviposition period was divided in two as follows: the constant oviposition period which refers to the number of sequential days that hosts were successfully parasitised (resulting in cocoon or adult offspring) and total oviposition period as the total number of days that hosts were successfully parasitised. The post-oviposition period refers to the time when a parasitoid ceased to parasitise hosts until death of the parasitoid. Two fecundity parameters were calculated, **realised fecundity** as the number of parasitised larvae that developed in a cocoon (whether it developed into an adult parasitoid or not) over the life-span of the parasitoid, and **fertility** as the number of parasitised larvae laid by a parasitoid that developed into adult parasitoids. The mean sex ratio was calculated as the proportion of males.

**Statistical Analysis**

Realised fecundity and fertility were compared using repeated measures ANOVA. The comparison between the daily fertility values for the oviposition period was tested using Kruskal Wallis test, followed by Dunn's multiple comparison test for means separation as ANOVA could not be used because normality and equal variances assumptions were not met by these data. One sample t-test was used to compare the mean daily sex ratio with the mean equal sex ratio, 0.5. All analyses were conducted in SPSS v.15 (2006) and Minitab 15 (2006).

Life table statistics

The life table statistics and the intrinsic rate of natural increase of *C. sonorensis* were calculated from the previous parameters as follows:

The **intrinsic rate of natural increase** $r_m$ was calculated by iteratively solving the following equation (Birch 1948):

$$\sum_{X=0}^{n} e^{-r_m x} l_x m_x = 1$$

Where **x** is the mid-point of age intervals in days, $l_x$ is the fraction of females surviving to the pivotal age **x** (the probability of a female surviving to age x), $m_x$ is the mean number of female 'births' during age interval x per female aged **x**, and e is the base of natural logarithms. Trial $r_m$ values are substituted into the above expression until the left hand side is (arbitrarily) close to 1. $l_x$ and $m_x$ were calculated by tabulating (Table 4.2) age-specific fertility and age-specific survival (Jervis et al. 2005)

Once the values for $l_x$ and $m_x$ were calculated, then the following population statistics were also calculated (Messenger 1964):

1. The **gross reproductive rate**: the mean total number of eggs produced by female over the lifetime; measured in female/female/generation.

   **GRR = Σ $m_x$.**

   In this study the mean number of parasitoid progeny that developed up to cocoon (for realised fecundity) and the mean number of parasitoid progeny that developed up to adult (for fertility) were used instead of the mean number of eggs produced by female over the lifetime.

2. The **net reproductive rate**: the number of times a population will multiply per generation; measured in female/female/generation.

$$R_o = \Sigma\, l_x m_x$$

3. The **finite capacity for increase**: the number of times the population will multiply itself per unit of time; measured in female/female/day.

$$\lambda = e^{r_m}$$

4. The **mean generation time**: the mean time, measured in days, required for a given parasitoid cohort to develop from egg to adult.

$$T = (\log_e R_o) / r_m$$

5. The **doubling time**: the time, measured in days, required for a given population to double its numbers.

$$DT = \log_e 2 / r_m$$

6. The **capacity for increase**: approximation of $r_m$ but is more useful than $r_m$ for consideration of the relation between the capacity for increase and life-history parameters such as generation time (Laughlin 1965; May 1976).

$$r_c = \frac{\log_e R_o}{T_c}$$

7. The **cohort generation time**: the mean age of maternal parents in the cohort at birth of female offspring (Laughlin 1965; May 1976).

$$T_c = \sum_x l_x m_x / \underline{R_o}$$

## Results

### Fecundity parameters

The mean (±SE) longevity of the 12 *C. sonorensis* females used in this study was 34.5±2.8 days, with a range of 21 to 46 days. The mean (±SE) oviposition period was 22.7±1.9 days, with a range of 15 to 35 days. The mean (±SE) constant oviposition period and the mean (±SE) post-oviposition period were 15.9±1.3 and 11.9±2.2 days, respectively. Ninety two percent of the *C. sonorensis* females survived up to the end of the oviposition period (Figure 4.1)

The mean (±SE) realised fecundity and the mean (±SE) fertility differed significantly (rmANOVA: $F_{1,11}$=67, P=0.001) at 66.9±7.8 and 60.4±7.8 parasitoids per female, respectively.

The mean (±SE) daily realised fecundity and mean (±SE) daily fertility calculated for total oviposition period were 3.1±0.4 and 2.8±0.4 parasitoids per female, respectively. During just the constant oviposition period, the mean (±SE) daily realised fecundity and mean (±SE) daily fertility were 4.3±0.4 and 3.8±0.4, respectively.

Mean daily fertility values for the first 23 days (the mean oviposition period) differed between days (Kruskal Wallis: $H_{1,9}$ = 78.64, P = 0.0001). Mean daily fertility did not differ between day 4 to day 18, however, days 8-10 and 12 were higher than that of days 19-23 (Table 4.1). The mean daily fertility values for realised fecundity and fertility increase from day 4 to day 8, at which point the highest number of offspring were deposited (Table 4.1). After day 8, the daily values decreased until day 24 when intermittent parasitisation occurred at the

lowest mean daily values. Day 22 had the lowest mean daily fertility during the mean oviposition period.

The mean (±SE) sex ratio for the mean oviposition period (23 days) was 0.13±0.07, indicating a highly female biased ratio (Table 4.1). The mean daily sex ratios were different from a sex ratio equal to 0.5 at 19 and 21 day-old parasitoid probably due to the small number of samples.

**Life table parameters**

The life table of the *C. sonorensis* cohort is presented in Table 4.2. Fertility and realised fecundity parameters were calculated from the life table, and presented in Table 4.3.

**Discussion**

**Fecundity parameters**

Both Isenhour (1986) and Nobel and Graham (1966) conducted studies on the reproductive capacity of *C. sonorensis*, however, these two studies had very different results. Isenhour (1986) reported that *C. sonorensis* females produce a mean of 222.45 progeny when held at 30°C and provided with 40 *S. frugiperda* larvae every 24 hours whereas Noble and Graham (1966) reported a mean of 27.2 progeny per female at 36°C and provided with 15 to 20 larvae of *H. virescens*. Although the studies utilized different hosts, Isenhour (1986) concluded that the increase in temperature and host density resulted in increased progeny for *C. sonorensis*. Subsequently, Hu and Vinson (2000) reported that the egg production estimate of *C. sonorensis* was 88.27 eggs from parasitoids developed from the third instar larvae of *H. virescens* at 28°C and that in younger hosts, parasitoids produced a significantly reduced body length, weight, longevity, and egg production estimate. Although the authors did not specify how many eggs were actually laid per female parasitoid, they reported a 77.7% adult parasitoid emergence. Thus, if all 88.27 eggs were laid, 68.6 progeny would be

the mean total fertility of *C. sonorensis*. In comparison, I had a slightly lower mean total fertility value of 60.4 progeny per female parasitoid. I have several ideas to explain the discrepancy between the studies, including host size, host density, incidence of superparasitism, host species, parasitoid age, venom production and misidentification of parasitoid species, which I have discussed further below.

Although Isenhour (1986) concluded that increases in temperature and in host density were the factors that increased the total progeny production of *C. sonorensis,* Hu and Vinson (2000)'s results also indicate that host stage (size) is important. This was also demonstrated by Gunasena et al. (1989), who showed that the reproductive potential of *C. sonorensis* was higher when females were reared from larger host sizes because the females themselves were larger. In laboratory and field studies, fecundity as the most direct measure of parasitoid fitness is found to be positively correlated with the size of solitary female parasitoids (VanLaerhoven and Stephen 2003; Roitberg et al. 2001; Charnov et al. 1981; Godfray 1994; Visser 1994; van dem Assem et al. 1989; Ellers et al. 1998).

Although I used a host density intermediate between Isenhour (1986) and Nobel and Graham's (1966) studies (30 *T. ni*), the temperature I conducted the current study at was lower than both of the studies (24°C) but I still had a higher mean realised fecundity (66.9) per female than Noble and Graham (1966) with their lower host density. Perhaps host density is more important than temperature in determining mean progeny in *C. sonorensis*.

Related to host density, superparasitism by *C. sonorensis* is common when low host densities are provided to our lab colony. Although the level of superparasitism have been not quantified, some superparasitism with densities of 40 *T. ni* larvae have been observed. At 24 hours of host exposure intervals, 15-20 larvae were used by Noble and Graham (1966), 30 larvae in the current

studies and 40 larvae by Isenhour (1986). In view of this, it may have been that the superparasitism was higher in the study of Noble and Graham (1966), explaining their lower parasitoid progeny. Bigornia (1956) reported superparasitism of *H. virescens* also under field conditions by *C. perdistinctus*, a misidentification of *C. sonorensis* (Carlson 1972). Superparasitism must be considered as an important factor in the final progeny number of *C. sonorensis* mostly because some parasitoids are not able to develop on superparasitised hosts as reported by Patel and Habib (1987) for *C. flavicincta* on superparasitised *S. frugiperda* larvae.

Isenhour (1986) did not consider host species by itself as a factor in the increased number of progeny of *C. sonorensis. Spodoptera frugiperda* may induce a higher reproductive capability on *C. sonorensis* than other insect hosts. Lingren et al (1970) concluded that *S. frugiperda* was the best host for mass rearing *C. sonorensis* when it was compared to 10 other potential host species that included *H. zea*, *H. virescens* and *T. ni.* In a later study using the same host species, Lingren and Noble (1972) found out that *H. zea* and *S. frugiperda* were the most preferred hosts and *T. ni* was the least preferred host. The fecundity and other components of the fitness of parasitoid progeny may vary with host species (Fellowes et al. 2005, VanLaerhoven and Stephen 2003; Lingren and Noble 1972) and according to the optimal host selection theory, female parasitoids choose hosts in a way which maximizes the expected fitness of progeny (Iwasa et al. 1984).

The age of parasitoid females can influence fertility and sex-ratio. Matos et al. (2005) found out that when 24, 3-4 day-old larvae of *S. frugiperda* were exposed to 4 day-old *C. flavicincta* at 25°C, the number of parasitised larvae over a female's lifespan was 170.25, whereas with 1-3 and 5 day-old females, it was lower. Hoelscher and Vinson (1971) found that when 33 hour-old mated females were used, the most favorable offspring female: male ratio was produced.

Bezemer et al. (2005) reported that other factors such as parasitoid venom production may be more important in limiting reproduction than egg availability. In order to facilitate protection against the host immune defenses *C. sonorensis* injects a polydnavirus and venoms when it oviposits into a host (Dover and Vinson 1990; Webb and Summers 1990, Summer and Dib-Hajj 1995). Bezemer et al. (2005) concluded that the production of venoms limits reproduction in parasitoids after observing mature eggs present in the ovarioles of dissected females of *Mastrus ridibundus* (Hymenoptera: Ichneumonidae) with a post-oviposition period of at least 5–6 days. There are three possible ways in which these venoms and polydnavirus could have affected the final progeny number of *C. sonorensis* in the current study: 1) the female parasitoids still had some mature eggs in their ovarioles during the long post-reproductive period but they were not used due to a depletion in the production of the polydnavirus and venoms (Bezemer et al. 2005); 2) The eggs were laid but the injection of the polydnavirus at the time of oviposition was either not done, or was not enough to provide long-term suppression of host immunity and the parasitised host survived (Cui et al. 2000); and 3) the host died before the parasitoid completed development (Vinson and Stoltz 1986). Vinson and Stoltz (1986) concluded that whether *T. ni* was naturally parasitised by *C. sonorensis,* or injected with *C. sonorensis* calyx fluid, or purified virus, the *T. ni* died in 4-8 days resulting in the death of the parasitoid larvae within the host.

Finally, Isenhour (1986) could have misidentified *C. flavicincta* with *C. sonorensis*. As stated by Carlson (1972), the misidentification of these two species has been common. Matos et al. (2005) recorded that *C. flavicincta* parasitised up to 170.25 *S. frugiperda* larvae throughout its lifespan at 25°C. This value is closer to the 222.45 found by Isenhour (1986), especially when we consider that Matos et al. (2005) used a lower temperature and lower host density than Isenhour (1986). *Campoletis flavicincta* prefers corn fields more than *C. sonorensis* (Carlson 1972) and parasitises *S. frugiperda* more frequently in corn fields than *C. sonorensis* (Matos et al. 2005; Ashley 1986; Molina et al.

2004; Hogg et al. 1982; Cruz et al. 1997), making if possible that Isenhour (1986) misidentified *C. sonorensis* when he collected it from *S. frugiperda* in corn fields for his research.

**Parasitoid longevity and oviposition period**

According to the literature, the longevity of *C. sonorensis* depends on temperature such that as temperature increases, longevity decreases. For *C. sonorensis* mated females, Noble and Graham (1966) recorded a mean longevity of 4.6 days at 36°C, whereas Isenhour (1986) reported 11.4 days at 25°C and 26.8 days at 20°C for unmated females. Although the temperature I used was only 1°C higher than that of Isenhour (1986), I recorded mean longevity as 34.5 days for mated females, which usually live a shorter time than unmated females. There are two reasons that I think may explain the difference between the results in the current study and Isenhour (1986). The first could be the number of samples as Isenhour (1986) used 21 mated females and I used 12. The second could be differences in the experimental methods. Isenhour (1986) fed them with 10% honey solution, newly emerged male and female parasitoids were paired, and male parasitoids were present all the time. Isenhour (1986) used a photoperiod of 14:10 (L:D), 70% RH. In contrast, I fed them with 100% honey, male and female parasitoids were paired after one day and left together only for 48 hours. I used a 12:12 (L:D) photoperiod with 60% RH as per Hoelscher and Vinson's (1971) recommendations. In both the current study and Isenhour's (1986), the time of oviposition exposure was 24 hours. Pandey et al (2004) reported that the presence of male parasitoids in the parasitisation cages affected the progeny sex ratio by decreasing the number of females in the offspring population in *C. chlorideae*, demonstrating that the presence of male parasitoids can affect female biology.

Daily oviposition, oviposition period and post-oviposition period of *C. sonorensis* also depend on temperature, as well as the age of parasitoid. The results in the current study for daily progeny were considerably smaller than that of Isenhour

(1986) (2.8 versus 11.7-23.7). Perhaps the sample size and experimental methods in the current study explain this large difference. Isenhour (1986) and Noble and Graham (1966) did not discuss a post-oviposition period for *C. sonorensis*, but using their data I was able to calculate their post-oviposition period of 1 day (Noble and Graham 1970) and 0.4-4.2 days (Isenhour 1986), compared to 11.9 days in the current study. Noble and Graham (1970) reported a mean oviposition period of 3.3 days, and I calculated a mean oviposition period of 8.4-11 days from Isenhour (1986), compared to 22.7 days in the current study. Although these post-oviposition periods are much shorter than in the current study, they are still a considerable amount of time compared to the short longevity values reported in those studies. Even though long post-oviposition periods are reported frequently in parasitoid reproductive laboratory studies (Kopelman and Chabora 1992; James 1993; Awadalla 1996; Babendreier 2000; Harvey et al. 2001, Loomans AJM 2003; Bezemer et al. 2005; Kivan and Kilic 2005), they have been disregarded from some of these studies because they are considered to be a laboratory artifact (Jervis et al. 2001). Under laboratory conditions with constant access to hosts, parasitoid wasps such as *Venturia canescens* Gravenhorst (Hymenoptera: Ichneumonidae), *Leptopilina boulardi* (Barbotin et al.)(Hymenoptera: Eucoilidae) and *Dicondylus indianus* Olmi (Hymenoptera: Dryinidae) experienced longer periods of post-reproductive survival than conspecific wasps with limited host access (Sahragard et al. 1991; Kopelman and Chabora 1992; Harvey et al. 2001). Whether the phenomenon is simply a laboratory artifact is something that requires further study in field situations (Jervis et al. 1994). In most laboratory studies, the parasitoids have been provided with a surfeit of hosts and food, which may not accurately reflect the heterogeneity of natural systems where resources are likely to be limiting (Harvey et al. 2001).

**Parasitoid sex ratio**

The highly female-biased sex ratio obtained in the current study differed from the male- biased sex ratio reported by Hoelscher and Vinson (1971) and Lingren et al

(1970) but agrees with the one obtained from 6 day-old larvae in the host preference and fitness of *C. sonorensis* study (Chapter 3) and with the higher ratio of adult females to males in older larvae reported by Noble and Graham (1966). Hoelscher and Vinson (1971) and Lingren et al (1970) reported that the proportion of males is usually greater than that of females in field-collected and laboratory-reared *C. sonorensis*. Photoperiod and female age were the most important factor affecting progeny sex ratio (Hoelscher and Vinson, 1971), with a 12:12 (L:D) photoperiod and 4 day-old females producing offspring with the greatest percentage of females (0.66), which was still male-biased and very different from the mean female-biased value of 0.13 obtained in the current study. Although Hoelscher and Vinson (1971) found that the temperature influenced the sex ratio of *Campoletis sonorensis,* they did not considered it as a major factor as did Pandey and Tripathi (2007), who observed that the sex ratio of *Campoletis chlorideae* was female-biased at temperatures of 17-27°C when using different constant temperatures from 12 to 37°C

Age of host larvae was stated to influence *C. sonorensis* sex ratio (Lingren et al. 1970) When they used 2 to 8 day-old larvae of five Lepidoptera species including *T. ni*, female sex ratios just occurred in the progeny of parasitoid reared on 2 and 3 day-old larvae of *S. frugiperda* and *Spodoptera eridania* (Cramer), respectively. In contrast, Noble and graham (1966) reported female-biased sex ratios in 3-5 day-old larvae.

When evaluating the progeny sex ratio of *C. sonorensis* on 6 different Lepidoptera species, Lingren et al (1970) found that under the same conditions, *S. frugiperda* and *S. eridania* were the only insect hosts that provided female-biased sex ratios of the *C. sonorensis*, whereas parasitoid offspring from *T. ni* were always male-biased. Thus, I conclude that in addition to other factors the host species also may influences parasitoid sex ratio in *C. sonorensis.*

Female parasitoid density may affect sex ratio in *C. sonorensis*. Pandey et al. (2004) reported that with an increase in female parasitoid density, the proportion of male progeny increased significantly when they used 1, 2, 4 and 8 females of *C. chlorideae* per cage. In the studies of Hoelscher and Vinson (1971) and Lingren et al. (1970), two to three female parasitoids were used per cage with *T. ni* and *Helicoverpa virescens* as hosts and these studies had a male-biased *C. sonorensis* progeny sex ratio. I used 1 female per cage and had a mean female-biased progeny sex ratio.

Multiple lab and field-based studies support the idea that host plant and/or diet quality affect the progeny sex ratio of parasitoids (Kumar and Tripathi 1987; Fox et al. 1990; Jansson 2003; Weathersbee III et al. 2004; Sétamou et al. 2005; Onagbola et al. 2007; Lentz and Kester 2008). In the host preference and fitness of *C. sonorensis* study (Chapter 3), 4 day-old *T. ni* larvae were exposed to *C. sonorensis* females on tomato seedlings and in the current study, they were exposed on pinto bean diet. This may be affecting the progeny sex ratio which was equal for females and males in the first study and female-biased in the second study.

**Potential for mass rearing**

The realised fecundity, fertility, oviposition period and sex ratio are important factors in the population dynamics of a species and in this case, for a parasitoid that is intended as biocontrol agent for augmentatives releases, and they are also important for starting a mass rearing system for the parasitoid. The highly significant difference between realised fecundity and fertility found for *C. sonorensis* due to pupal cocoons that do not develop to adult in this study indicates that reduction of this mortality could be a key challenge in achieving a higher number of progeny for subsequent generations. Although diapause has not been reported for *C. sonorensis*, I believe that the non-hatching cocoons are entering diapause in response to the 12:12 photoperiod of the experiment, as

photoperiod is one of the most common diapausing-stimulus among parasitoids (Tauber et al. 1986; Quicke 1997).

The high survivorship rate of 92% of *C. sonorensis* female adults to the end of the oviposition period allows this parasitoid to reach its maximum reproductive potential under lab conditions. The drop in mean daily fertility after 18 days indicates that for a mass rearing system of *C. sonorensis* under the conditions described here, it will not be worth keeping female parasitoids for more than 18 days due to the labor required for rearing. Also, I would recommend using a temperature of 28°C as was done by Hu and Vinson (2000) to get the same number of progeny in a shorter time.

Pandey and Tripathi (2007) conducted a life table analysis for *Campoletis chlorideae*, which is an Asiatic species that is an important natural control of Asiatic *Helicoverpa* species and other Noctuidae species (WanXue et al. 2004, Gupta and Nirmala 2004; Yan et al. 2005) as *C. sonorensis* is in America (Carlson 1972; Townes and Townes 1951; Lingren et al. 1970; de Moraes et al. 1991; Machuca et al. 1989; CABI 2005). *Campoletis chlorideae* is being developed as a commercial biocontrol agent in India, Korea and China against *Helicoverpa armigera* (Yan et al. 2005, Pandey et al. 2004). In a single generation, the intrinsic rate of increase of *C. sonorensis* was 0.24 per female per day, doubling time was 2.9 days and the mean generation time was 17.1 days in the current study. For *C. chlorideae*, at 22°C, the intrinsic rate of increase was 0.25 per female per day, doubling time was 2.73 days, and the mean generation time was 17.70 (Pandey and Tripathi 2007). Although the life table parameters in this study are in accordance with the observations of Pandey and Tripathi (2007), the progeny value of 137.3 per female they found is very high when it is compared the 60.4, which I observed. I propose that the similar results obtained in the life table parameters are probably due to the difference in the female parasitoid longevity which was 22.9 days shorter in Pandey and Tripathi (2007).

For *Campoletis* species that are specialists on Lepidoptera Noctuidae, such as *C. sonorensis, C. flavicincta* and *C. chlorideae*, certain *Spodoptera* species are likely the best hosts in terms of progeny production and mass production of these parasitoids because among a selection of Noctuidae species, Lingren et al (1970) reported *Spodoptera frugiperda* as the best host for *C. sonorensis* in USA, Carlson (1972) and Molina et al (2001) reported *Spodoptera frugiperda* and *S. ornithogalli* as frequent and important hosts of *C. flavicincta* in USA and Mexico, Matos et al. (2005) has identified this parasitoid as a potential biocontrol agent of *S. frugiperda* in Brazil, WanXue et al (2004) reported *Spodoptera litura* as the best host for *C. chlorideae* in China, and at the University of Neuchâtel (Switzerland), Laboratory of evolutionary entomology, *Spodoptera littoralis* has been chosen as the best host for the continues mass production of *C. sonorensis* (Jourdie V., personal communications). Although *S. frugiperda* was considered as the best host for mass rearing *C. sonorensis* by Lingren et al (1970), mass rearing *S. frugiperda* is time consuming due to high cannibalism rates of the larvae and activity of the moths (Chapman et al. 1999; personal experience rearing *S. frugiperda*).

Reproductive potential is one of 8 criteria that needs to be evaluated when selecting parasitoids as potential biocontrol agents (van Lenteren 1986). An efficient parasitoid should have a potential maximum rate of population increase ($r_m$) equal to, or larger than, that of the host (van Lenteren and Manzaroli 1999). If a parasitoid causes additional substantial mortality (through host feeding or mortality of parasitised host before parasitoid development), then the overall host killing rate should be larger than the rate of population increase of the host, in the absence of the natural enemy, to be considered an efficient parasitoid. In the current study, the intrinsic rate of natural increase for fertility and realised fecundity of *C. sonorensis* were larger than those obtained for *T. ni* by Zote et al. (2006) (0.24 and 0.27, respectively). Thus, *C. sonorensis* passes the first criteria as a potential biological control of *T. ni*. However, the other 7 criteria compiled by van Lenteren (1986) have still to be evaluated.

## References

Andrewartha HG, Birch LG (1954) The distribution and abundance of animals. University of Chicago Press. Chicago, Illinois.

Ashley TR (1986) Geographical distribution and parasitization levels for parasitoids of the fall armyworm, *Spodoptera frugiperda*. Florida Entomologist 69: 516-524.

Awadalla SS (1996) Biological studies on *Monorthochaeta nigra* Blood & Kryger (Hym.: Trichogrammatidae) as egg parasitoid on the tortoise beetle, *Cassida vittata* Vill. (Col., Chrysomelidae). Journal of Applied Entomology 120: 353-355.

Babendreier D (2000) Life history of *Aptesis nigrocincta* (Hymenoptera: Ichneumonidae) a cocoon parasitoid of the apple sawfly, *Hoplocampa testudinea* (Hymenoptera: Tenthredinidae). Bulletin of Entomological Research 90: 291–297.

Bezemer TM, Harvey JA, Mills NJ (2005) Influence of adult nutrition on the relationship between body size and reproductive parameters in a parasitoid wasp. Ecological Entomology 30: 571–580.

Bigornia AE (1956) Studies on the biology and morphology of *Campoletis perdistinctus* (Viereck), a parasite of the Tobacco Budworm, *Heliothis virescens* (F.). MSc thesis. North Carolina State College, Raleigh.

Birch LC (1948) The intrinsic rate of natural increase of an insect population. The Journal of Animal Ecology 17: 15-26.

CAB International (2005) Crop Protection Compendium. CABI Publishing. Wallingford, Oxfordshire. UK.

Carlson RW (1972) Suppression of the name *Campoletis persdistincta* (Hymenoptera: Ichneumonidae) and the identity of species to which the name has been applied. Entomological News 83: 75-82.

Chapman JW, Williams T, Escribano A, Caballero P, Cave RD, Goulson D (1999) Fitness consequences of cannibalism in the fall armyworm, *Spodoptera frugiperda*. Behavioral Ecology 10: 298-303

Charnov EL, Los-den Hartogh RL, Jones WT, van Den Assem J (1981) Sex ratio evolution in a variable environment. Nature 289: 28–33.

Cruz I, Figueiredo MLC, Gonçalves EP, Lima DAN, Diniz EE (1997) Efeito da Idade de Lagartas de *Spodoptera frugiperda* (Smith) (Lepidoptera: Noctuidae) no Desempenho do Parasitóide *Campoletis flavicincta* (Ashmead) (Hymenoptera: Ichneumonidae) e Consumo Foliar por Lagartas Parasitadas e Não-Parasitadas Anais de Sociedade Entomologica do Brasil 26: 229-234.

Cui L, Soldevila AI, Webb BA (2000) Relationships between polydnavirus gene expression and host range of the parasitoid wasp *Campoletis sonorensis*. Journal of Insect Physiology 46: 1397-1407

de Moraes RR, Loeck AE, Belarmino LC (1991) Natural enemies of *Rachiplusia nu* (Guenée, 1852) and *Pseudoplusia includens* (Walker, 1857) (Lepidoptera: Noctuidae) on soybean in Rio Grande do Sul. [In Portuguese.] Pesquisa Agropecuária Brasileira 26: 57-64.

Dover BA, Vinson SB (1990) Stage-specific effects of *Campoletis sonorensis* parasitism on *Heliothis virescens* development and prothoracic glands. Physiological Entomology 15: 405-414.

Ellers J, van Alphen JJM, Sevenster JG (1998) A field study of size fitness relationships in the parasitoid *Asobara tabida*. Journal of Animal Ecology 67: 318 324.

Fellowes MDE, van Alphen JJM, Jervis MA (2005) Foraging behavior. In: Jervis MA (ed) Insects as natural enemies: A practical perspective. Springer. Dordrecht, Netherlands. pp. 1-72.

Fox LRT, Letourneau DK, Eisenbaeh J, van Nouhuys S (1990) Parasitism rates and sex ratios of a parasitoid wasp: effects of herbivore and plant quality. Oecologia 83: 414-419

Gillespie DR, Raworth DA, Shipp JL (2002) *Trichoplusia ni* Hübner, Cabbage Looper (Lepidoptera: Noctuidae). In Mason PG, Huber JT (Eds) Biological control programmes in Canada. CABI Publishing. Wallinford, UK. Pp. 269-271.

Godfray HCJ (1994) Parasitoids: behavioral and evolutionary ecology. Princeton University Press, Princeton, New Jersey, USA.

Gunasena GH, Vinson SB, Williams HJ (1989) Interrelationships between growth of *Heliothis virescens* (Lepidoptera: Noctuidae) and that of its parasitoid *Campoletis sonorensis* (Hymenoptera: Ichneumonidae). Annals of the Entomological Society of America 82: 187-191.

Gupta RK, Raj D, Nirmala D (2004) Biological and impact assessment studies on *Campoletis chlorideae* Uchida: a promising solitary larval endoparasitoid of *Helicoverpa armigera* (Hübner). Journal of Asia-Pacific Entomology 7:239-247.

Harvey JA, Harvey IF, Thompson DJ (2001) Lifetime reproductive success in the solitary endoparasitoid, *Venturia canescens*. Journal of Insect Behavior 14: 573-592.

Hoelscher CE, Vinson SB (1971) The sex ratio of a hymenopterous parasitoid, *Campoletis perdistinctus,* as affected by photoperiod, mating and temperature. Annals of the Entomological Society of America 64: 1373-76.

Hogg DB, Anderson RE, Pitre HN (1982) Early-season parasitization of fall armyworm (Lepidoptera: Noctuidae) larvae in Mississippi. Florida Entomologist 65: 584-585.

Hu JS, Vinson SB (2000) Interaction between the larval endoparasitoid *Campoletis sonorensis* (Hymenoptera: Ichneumonidae) and its host the tobacco budworm (Lepidoptera: Noctuidae). Annals of the Entomological Society of America 93: 220-224.

Isenhour DJ (1985) *Campoletis sonorensis* (Hym.: Ichneumonidae) as a parasitoid of *Spodoptera frugiperda* (Lep.: Noctuidae): host stage preference and functional response. Entomophaga 30: 31-36.

Isenhour DJ (1986) Developmental time, adult reproductive capability, and longevity of *Campoletis sonorensis* (Hymenoptera: Ichneumonidae) as a parasitoid of fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae). Annals of the Entomological Society of America 79: 893-897.

Iwasa Y, Suzuki Y, Matsuda H (1984) Theory of oviposition strategy of parasitoids. I. Effect of mortality and limited egg number. Theoretical Population Biology 26: 205-227.

James DG (1993) Biology of *Anastatus biproruli* (Hym.: Eupelmidae) a parasitoid of *Biprorulus bibax* (Hem.: Pentatomidae). Entomophaga 38: 155-161.

Janmaat AF, Myers J (2003) Rapid evolution and the cost of resistance to *Bacillus thuringiensis* in greenhouse populations of cabbage loopers, *Trichoplusia ni*. Proceding of Biological Science Royal Society *B* 270: 2263-2270.

Janmaat AF, Wang P, Kain W, Zhao JZ, Myers J (2004) Inheritance of Resistance to *Bacillus thuringiensis* subsp. *kurstaki* in *Trichoplusia ni*. Applied and Environmental Microbiology 70: 5859-5867.

Jansson J (2003) The influence of plant fertilization regime on plant-aphid-parasitoid interactions. Doctoral thesis. Department of Entomology, Swedish University of Agricultural Sciences. Uppsala.

Jervis MA, Kidd NAC, Almey HE (1994) Post-reproductive life in the parasitoid *Bracon hebetor* (Say) (Hym., Braconidae). Journal of Applied Entomology 117: 72-77.

Jervis MA, Heimpel GE, Ferns PN, Harvey JA, Kidd NA (2001) Life-history strategies in parasitoid wasps: a comparative analysis of 'ovigeny'. Journal of Animal Ecology 70: 442-458.

Jervis MA, Copland MJW, Harvey JA (2005) The life-cycle. In: Jervis MA (Ed) Insects as natural enemies: A practical perspective. Springer, Dordrecht, Netherlands, pp. 73-165.

Kivan M, Kilic N (2005) Effects of temperature on reproductive capacity and longevity of *Trissolcus simoni*, an egg parasitoid of *Eurygaster integriceps*. Journal of Pest Science 78: 105-108.

Kopelman AH, Chabora PC (1992) Resource variability and life history parameters of *Leptopilina boulardi* (Hymenoptera: Eucoilidae). Annals of Entomological Society of America 85: 195-199.

Kumar A, Tripathi CPM (1987) Parasitoid host relationship between *Trioxys (Binodoxys) indicus* Subba Rao and Sharma (Hym., Aphidiidae) and *Aphis craccivora* Koch, (Hem., Aphididae). IV. Effect of host plants on the sex ratio of the parasitoid. Entomon 12: 96-97.

Lafontaine JD, Poole RW (1991) Noctuoidea, Noctuidae, Plusiinae. In Dominick RB, Dominick T, Ferguson DC, Franclemont JG, Hodges RW, Munroe EG (eds) The Moths of America North of Mexico, fascicle 25.1: 1-182, The Wedge Entomological Research Foundation, Washington, D.C.

Laughlin R (1965) Capacity for increase: a useful population statistic. Journal of Animal Ecology 34: 77-91.

Lentz AJ, Kester KM (2008) Post-emergence experience affects sex ratio allocation in a gregarious insect parasitoid. Journal of Insect Behavoir 21: 34-45.

Lingren PD, Guerra RF, Nickelsen JW, White C, 1970. Hosts and host-age preference of *Campoletis perdistinctus*. Journal of Economic Entomology 63: 518–522.

Lingren PD, Noble LW (1972) Preference of *Campoletis perdistinctus* for certain Noctuidae larvae. Journal of Economic Entomology 65: 104-107.

Loomans AJM (2003) Parasitoids as biological control of Thrips pests. PhD Thesis, Wageningen University. Netherlands.

Machuca Jr, Arretz P, Araya J (1989) Presencia de *Campoletis sonorensis* (Cameron, 1886) (Hymenoptera: Ichneumonidae) en Chile. Acta Entomologica Chilena 15: 269-270.

Matos NFC, Zanuncio JC, Cruz I, Guedes RNC, Picanco MC (2005) Progeny production and parasitism by *Campoletis flavicincta* (Hym.: Ichneumonidae) as affected by female ageing. Biological Agriculture and Horticulture 22: 369-378.

May RM (1976) Estimating r: a pedagogical note. American Naturalist 110: 496-499.

Messenger, P.S. (1964) Use of life tables in a bioclimatic study of an experimental aphid-braconid wasp host-parasite system. Ecology 45: 119-131.

Minitab for Windows, Rel. 15.1.1.0. (2006) State College, PA: Minitab Inc.

Molina-Ochoa J, Hamm JJ, Lezama-Gutierrez RM, Lopez-Edwards M, Gonzalez-Ramirez M, Pescador-Rubio A (2001) A survey of fall armyworm (Lepidoptera: Noctuidae) parasitoids in the Mexican states of Michoacán, Colima, Jalisco, and Tamaulipas. Florida Entomologist 84: 31-36.

Noble and Graham (1966) Behavior of *Campoletis perdistinctus* (Viereck) as a parasite of the Tobacco budworm. Journal of Economic Entomology 59: 1118-1120.

Onagbola EO, Fadamiro HY, Mbata GN (2007) Longevity, fecundity, and progeny sex ratio of *Pteromalus cerealellae* in relation to diet, host provision, and mating. Biological Control 40: 222-229.

Pandey P, Kumar N, Tripathi CPM (2004) Impact of males on the progeny sex ratio of *Campoletis chlorideae* (Hym., Ichneumonidae), a parasitoid of *Helicoverpa armigera* (Hübner) (Lep., Noctuidae). Journal of Applied Entomology 128: 254-257.

Pandey AK, Tripathi CPM (2007) Effect of temperature on the development, fecundity, progeny sex ratio and life-table of *Campoletis chlorideae*, an endolarval parasitoid of the pod borer, *Helicoverpa armigera*. Biocontrol. DOI 10.1007/s10526-007-9083-3

Patel PN, Habib MEM (1987) Biological studies on *Campoletis flavicincta* (Ashmead, 1890) (Hym., Ichneumonidae), an endoparasite of the fall armyworm, *Spodoptera frugiperda* (Abbot & Smith, 1797) (Lepid., Noctuidae). Zeitschrift für Angewandte Entomologie 104: 28-35

Quicke DLG (1997) Parasitic wasps. Chapman and Hall, London.

Roitberg BD, Boivin G, Vet L (2001) Fitness, parasitoids, and biological control: an opinion. The Canadian Entomologist 133: 429-438.

Sahragard A, Jervis MA, Kidd NAC (1991) Influence of host availability on rates of oviposition and host-feeding, and on longevity in *Dicondylus indianus* Olmi (Hymenoptera: Dryinidae), a parasitoid of rice brown planthopper *Nilaparvata lugens* Stal (Hemiptera: Delphacidae). Journal of Applied Entomology 112: 153-162.

Sétamou M, Jiang N, Schulthess F (2005) Effect of the host plant on the survivorship of parasitized *Chilo partellus* Swinhoe (Lepidoptera: Crambidae) larvae and performance of its larval parasitoid *Cotesia favipes* Cameron (Hymenoptera: Braconidae). Biological Control 32: 183-190.

Shorey HH, Hale RL (1965) Mass-rearing of the larvae of nine noctuid species on a simple artificial medium. Journal of Economic Entomology 58: 522-524.

Southwood TRE (1978) Ecological Methods, With Particular Reference to the Study of Insect Populations. Second edition. Chapman and Hall, London. 524 pp.

SPSS for Windows, Rel. 15.0.0. (2006) Chicago, IL: SPSS Inc.

Summers MD, Dib-Hajj SD (1995) Polydnavirus-facilitated endoparasite protection against host immune defenses. Procedings of the National Academy of Science 92: 29-36.

Tauber MJ, Tauber CA, Masaki S (1986). Seasonal Adaptations of Insects. Oxford University Press, USA.

Townes H, Townes M (1951) Family Ichneumonidae. In: Muesebeck CFW, Krombein KV, Townes HK (eds.) Hymenoptera of America north of Mexico - synoptic catalog. United States Department of Agriculture Agricultural Monograph 2: 1-1420.

van Den Assem J, van Lersel JJA, Los-Den Hartogh RL (1989) Is being large more important for female than for male parasitic wasps? Behaviour 108: 160-195.

VanLaerhoven, SL; Stephen, FM (2003) Host species influences body size and egg load of the bark beetle (Coleoptera: Scolytidae) parasitoid, *Roptrocerus xylophagorum* Ratzeburg (Hymenoptera: Pteromalidae). The Canadian Entomologist 135: 737-740.

van Lenteren JC (1986) Parasitoid in the greenhouse: successes with seasonal inoculative release systems. In: Waage J, Greathead D (Eds) Insect Parasitoids. Academic Press, London. pp. 341-374

van Lenteren JC, Manzaroli G (1999) Evaluation and use of predators and parasitoids for biological control of pests in greenhouses. In: Albajes RM, Gullino L, van Lenteren JC, Elad Y (eds) Integrated pest and disease management in

greenhouse crops. Kluwer Academic Publishers – CIHEAM, Dordrecht, pp. 183-201.

Vinson SB, Stoltz DB (1986) Cross-protection experiments with two parasitoid (Hymenoptera: Ichneumonidae) viruses. Annals of the Entomological Society of America 79: 216-218.

Visser ME (1994) The importance of being large: the relationship between size and fitness in females of the parasitoid *Aphaereta minuta* (Hymenoptera: Braconidae). Journal of Animal Ecology 63:963-978.

Webb BA, Summers MD (1990) Venom and viral expression products of the endoparasitic wasp *Campoletis sonorensis* share epitopes and related sequences. Proc. Natl. Acad. Sci. Microbiology 87: 4961-4965.

WanXue L, FangHao W, ShiTao Y. (2004) Mass-rearing and bionomics of *Campoletis chlorideae*. Chinese Journal of Biological Control 20: 17-20.

Waterhouse DF (1998) Biological Control of Insect Pests: Southeast Asian Prospects Australian Centre for International Agricultural Research. Canberra.

Weathersbee III AA, Mckenzie CL, Tang YQ (2004) Host plant and temperature effects on *Lysiphlebus testaceipes* (Hymenoptera: Aphidiidae), a native parasitoid of the exotic Brown Citrus Aphid (Homoptera: Aphididae). Annals of the Entomological Society of America 97: 476-480.

Yan Z, Yan Y, Wang C (2005) Attractiveness of tobacco volatiles induced by *Helicoverpa armigera* and *Helicoverpa assulta* to *Campoletis chlorideae*. Chinese Science Bulletin 50: 1334-1341.

Zote VK, Bilapate GG, Jadhav (2006) Life-fecundity tables of *Trichoplusia ni* (Hübner) on different host plants. Journal of Maharashtra Agricultural Universities 31: 314-317.

Table 4.1: Mean (± SE) values for age-specific fertility parameters of *Campoletis sonorensis* with *Trichoplusia ni* as a host. Means followed by the same letter are not significantly different (Dunn's multiple comparison test, P>0.05).

| Age (days) | Realised fecundity (# parasitised larvae*) | Fertility (# parasitised larvae**) | No emergence from cocoon (#) | # Males | # females | Sex ratio |
|---|---|---|---|---|---|---|
| | Mean±SE | Mean±SE | Mean±SE | Mean±SE | Mean±SE | Mean±SE |
| 4 | 3.4 ± 0.9 | 3.1± **0.9abc** | 0.3±0.2 | 1.3±0.9 | 1.8±0.5 | 0.20±0.11 |
| 5 | 3.9± 1.0 | 3.8±**1.0abc** | 0.2±0.1 | 0.9±0.4 | 2.8±0.6 | 0.16±0.06 |
| 6 | 3.3± 0.7 | 2.8±0.6**abc** | 0.5±0.2 | 0.6±0.3 | 2.3±0.5 | 0.25±0.10 |
| 7 | 4.8± 0.8 | 4.0±0.8**abc** | 0.8±0.3 | 0.8±0.4 | 3.3±0.7 | 0.19±0.10 |
| 8 | 8.1± 1.5 | 7.6±1.5**a** | 0.5±0.3 | 0.8±0.2 | 6.8±1.4 | 0.10±0.02 |
| 9 | 7.2± 1.8 | 6.8±1.7**a** | 0.4±0.2 | 1.0±0.3 | 5.8±1.6 | 0.18±0.06 |
| 10 | 5.4± 1.1 | 4.9±1.1**a** | 0.5±0.2 | 0.8±0.4 | 4.1±0.9 | 0.20±0.10 |
| 11 | 3.3± 0.7 | 3.0±0.6**abc** | 0.3±0.2 | 0.5±0.2 | 2.5±0.5 | 0.16±0.06 |
| 12 | 5.2± 0.7 | 4.4±0.6**a** | 0.8±0.4 | 0.7±0.2 | 3.8±0.6 | 0.18±0.08 |
| 13 | 3.9± 1.1 | 3.6±**1.1abc** | 0.3±0.2 | 0.8±0.3 | 3.1±0.9 | 0.21±0.07 |
| 14 | 2.9± 1.0 | 2.7±**0.9abc** | 0.3±0.1 | 0.4±0.3 | 2.3±0.8 | 0.17±0.12 |
| 15 | 2.2±0.8 | 1.8±**0.8abc** | 0.3±0.2 | 0.1±0.1 | 1.8±0.7 | 0.02±0.02 |
| 16 | 3.3±1.2 | 2.8±**1.0abc** | 0.4±0.3 | 0.3±0.1 | 2.6±0.9 | 0.06±0.03 |
| 17 | 3.0±0.9 | 2.8±**0.8abc** | 0.3±0.1 | 0.5±0.5 | 2.3±0.7 | 0.12±0.11 |
| 18 | 2.9±1.3 | 2.7±**1.2abc** | 0.3±0.1 | 0.4±0.3 | 2.3±1.0 | 0.12±0.08 |
| 19 | 0.9±0.5 | 0.8±**0.4b** | 0.2±0.2 | 0.1±0.1 | 0.7±0.4 | 0.11±0.11 |
| 20 | 0.8±0.8 | 0.7±**0.7b** | 0.1±0.1 | 0.0±0.0 | 0.7±0.7 | 0.00 |
| 21 | 0.6±0.5 | 0.6±**0.5b** | 0.0±0.0 | 0.2±0.2 | 0.4±0.3 | 0.17±0.17 |
| 22 | 0.5±0.4 | 0.5±**0.4c** | 0.0±0.0 | 0.0±0.0 | 0.5±0.4 | 0.00±0.00 |
| 23 | 0.4±0.2 | 0.4±**0.2b** | 0.0±0.0 | 0.1±0.1 | 0.4±0.2 | 0.00±0.00 |
| 24 | 0.1±0.1 | 0.1±0.1 | 0.0±0.0 | 0.0±0.0 | 0.1±0.1 | 0.00 |
| 25 | 0.0±0.0 | 0.0±0.0 | 0.0±0.0 | 0.0±0.0 | 0.0±0.0 | - |
| 26 | 0.0±0.0 | 0.0±0.0 | 0.0±0.0 | 0.0±0.0 | 0.0±0.0 | - |
| 27 | 0.1±0.1 | 0.1±0.1 | 0.0±0.0 | 0.0±0.0 | 0.1±0.1 | 0.00 |
| 28 | 0.1±0.1 | 0.1±0.1 | 0.0±0.0 | 0.0±0.0 | 0.1±0.1 | 0.00 |
| 29 | 0.0±0.0 | 0.0±0.0 | 0.0±0.0 | 0.0±0.0 | 0.0±0.0 | - |
| 30 | 0.1±0.1 | 0.1±0.1 | 0.0±0.0 | 0.0±0.0 | 0.1±0.1 | 0.00 |
| 31 | 0.0±0.0 | 0.0±0.0 | 0.0±0.0 | 0.0±0.0 | 0.0±0.0 | - |
| 32 | 0.0±0.0 | 0.0±0.0 | 0.0±0.0 | 0.0±0.0 | 0.0±0.0 | - |
| 33 | 0.3±0.3 | 0.3±0.3 | 0.0±0.0 | 0.3±0.3 | 0.0±0.0 | 1.00 |
| 34 | 0.2±0.2 | 0.2±0.2 | 0.0±0.0 | 0.2±0.2 | 0.0±0.0 | 1.00 |
| 35 | 0.3±0.3 | 0.3±0.3 | 0.0±0.0 | 0.0±0.0 | 0.3±0.3 | 0.00 |

*Developed or not as adult parasitoids **Developed as adult parasitoids

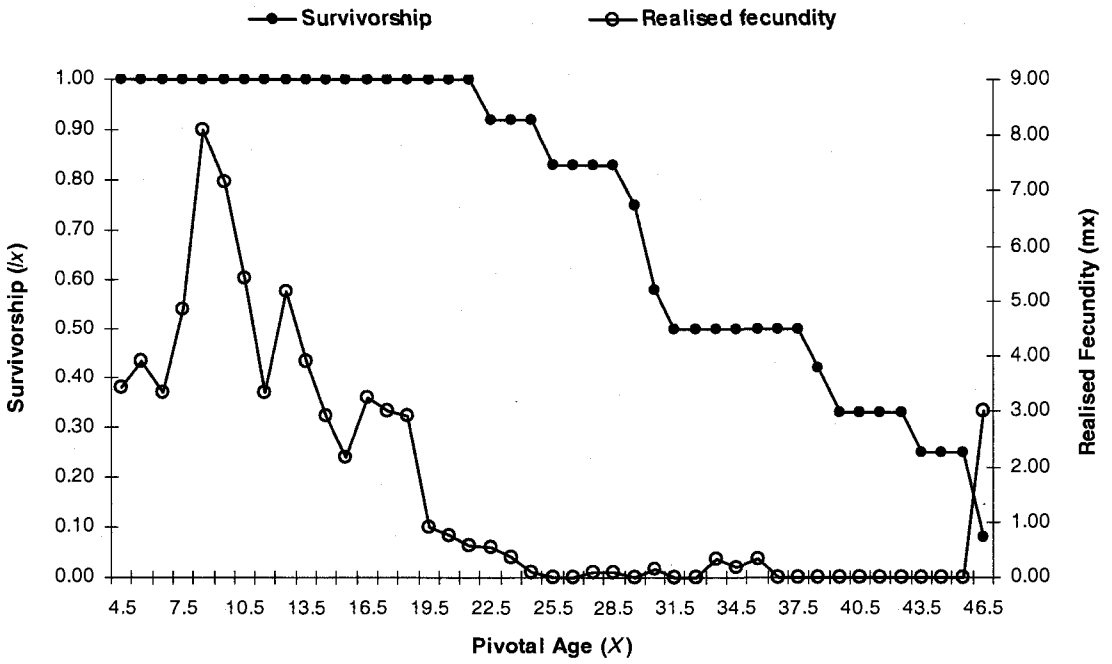
Table 4.2: Life-table for *Campoletis sonorensis* female cohort. ***x*** is the mid-point of age intervals (pivotal age) in days, ***lx*** is the fraction of the females surviving to age ***x***, and $m_x$ is the mean number of female 'births' during age interval ***x*** per female aged ***x***.

| Pivotal Ages (Days) *X* | Survival rate $l_x$ | Realised fecundity rate $m_{xt}$ | $l_x m_{xt}$ | $x * l_x * m_{xt}$ | Effective fertility rate $m_{xe}$ | $l_x m_{xe}$ | $x * le * m_{xe}$ |
|---|---|---|---|---|---|---|---|
| 4.5 | 1.00 | 3.42 | 3.42 | 15.38 | 3.08 | 3.08 | 13.88 |
| 5.5 | 1.00 | 3.92 | 3.92 | 21.54 | 3.75 | 3.75 | 20.63 |
| 6.5 | 1.00 | 3.33 | 3.33 | 21.67 | 2.83 | 2.83 | 18.42 |
| 7.5 | 1.00 | 4.83 | 4.83 | 36.25 | 4.00 | 4.00 | 30.00 |
| 8.5 | 1.00 | 8.08 | 8.08 | 68.71 | 7.58 | 7.58 | 64.46 |
| 9.5 | 1.00 | 7.17 | 7.17 | 68.08 | 6.75 | 6.75 | 64.13 |
| 10.5 | 1.00 | 5.42 | 5.42 | 56.88 | 4.92 | 4.92 | 51.63 |
| 11.5 | 1.00 | 3.33 | 3.33 | 38.33 | 3.00 | 3.00 | 34.50 |
| 12.5 | 1.00 | 5.17 | 5.17 | 64.58 | 4.42 | 4.42 | 55.21 |
| 13.5 | 1.00 | 3.92 | 3.92 | 52.88 | 3.58 | 3.58 | 48.38 |
| 14.5 | 1.00 | 2.92 | 2.92 | 42.29 | 2.67 | 2.67 | 38.67 |
| 15.5 | 1.00 | 2.17 | 2.17 | 33.58 | 1.83 | 1.83 | 28.42 |
| 16.5 | 1.00 | 3.25 | 3.25 | 53.63 | 2.83 | 2.83 | 46.75 |
| 17.5 | 1.00 | 3.00 | 3.00 | 52.50 | 2.75 | 2.75 | 48.13 |
| 18.5 | 1.00 | 2.92 | 2.92 | 53.96 | 2.67 | 2.67 | 49.33 |
| 19.5 | 1.00 | 0.92 | 0.92 | 17.88 | 0.75 | 0.75 | 14.63 |
| 20.5 | 1.00 | 0.75 | 0.75 | 15.38 | 0.67 | 0.67 | 13.67 |
| 21.5 | 1.00 | 0.58 | 0.58 | 12.54 | 0.58 | 0.58 | 12.54 |
| 22.5 | 0.92 | 0.55 | 0.50 | 11.29 | 0.55 | 0.50 | 11.29 |
| 23.5 | 0.92 | 0.36 | 0.33 | 7.86 | 0.36 | 0.33 | 7.86 |
| 24.5 | 0.92 | 0.09 | 0.08 | 2.05 | 0.09 | 0.08 | 2.05 |
| 25.5 | 0.83 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 26.5 | 0.83 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 27.5 | 0.83 | 0.10 | 0.08 | 2.28 | 0.10 | 0.08 | 2.28 |
| 28.5 | 0.83 | 0.10 | 0.08 | 2.37 | 0.10 | 0.08 | 2.37 |
| 29.5 | 0.75 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 30.5 | 0.58 | 0.14 | 0.08 | 2.53 | 0.14 | 0.08 | 2.53 |
| 31.5 | 0.50 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 32.5 | 0.50 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 33.5 | 0.50 | 0.33 | 0.17 | 5.58 | 0.33 | 0.17 | 5.58 |
| 34.5 | 0.50 | 0.17 | 0.08 | 2.88 | 0.17 | 0.08 | 2.88 |
| 35.5 | 0.50 | 0.33 | 0.17 | 5.92 | 0.33 | 0.17 | 5.92 |
| 36.5 | 0.50 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 37.5 | 0.50 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 38.5 | 0.42 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 39.5 | 0.33 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 40.5 | 0.33 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 41.5 | 0.33 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 42.5 | 0.33 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 43.5 | 0.25 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 44.5 | 0.25 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 45.5 | 0.25 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 46.5 | 0.08 | 3.00 | 0.24 | 11.16 | 2.00 | 0.16 | 7.44 |

Table 4.3: Life table parameters of *Campoletis sonorensis*

| Parameter | Realised Fecundity | Fertility |
|---|---|---|
| Intrinsic rate of natural increase | 0.27 | 0.24 |
| Gross reproductive rate | 70.26 | 62.84 |
| Net reproductive rate | 66.91 | 60.41 |
| Finite capacity for increase | 1.31 | 1.27 |
| Mean generation time | 15.57 | 17.09 |
| Doubling time | 2.57 | 2.89 |
| Capacity for increase | 0.36 | 0.35 |
| Cohort generation time | 11.66 | 11.65 |

Figure 4.1: Survivorship (*lx*) and fecundity ($m_x$) curves of *Campoletis sonorensis*



## Chapter 5

## General discussion and conclusions

Although a specific set of criteria for selecting parasitoids was not followed by Noble and Graham 1966; Lingren et al. 1970; Lingren and Noble 1972; Lingren 1977 and Isenhour 1985, 1986, they provide considerable evidence supporting the potential of *C. sonorensis* as a biocontrol agent for control of *Helicoverpa* spp and *S. frugiperda*. A more detailed procedure has been done for the evaluation of *C. chlorideae* as a potential biocontrol agent of *Helicoverpa armigera* in India and China and its commercialization for augmentative biocontrol programs started a few year ago (Dai 1989, 1990; Kumar et al. 1994; WanXue et al. 2004, Pandey and Tripathi 2007; Ballal C, personal communication). Until the current study, no research had been done specifically to evaluate the potential of *C. sonorensis* as a biocontrol agent of *T. ni.* Using van Lenteren's (1986) compilation of criteria for selecting parasitoid biocontrol agents, I will discuss why I conclude that *C. sonorensis* demonstrates potential as a biocontrol agent in an augmentative biological control program against *T. ni,* which is one of the main insect pest problems in greenhouse vegetables crops in Southwestern Ontario, Canada. I will also discuss the possibilities of using this parasitoid as a model for conservation biological control for *T. ni* and other Lepidoptera pests in field crops as a way of assisting in the regulation of insect pests before they migrate into greenhouses.

The eight criteria for selecting parasitoids compiled by van Lenteren (1986) are discussed as follows:

1) Seasonal synchronization with host

In biological control, seasonal synchronization occurs when the parasitoid is present when the pest occurs (van Lenteren and Manzaroli 1999). For an augmentative approach in vegetable greenhouses, this criteria is not important because the grower could artificially synchronize the parasitoid and host by

introducing the parasitoid when most of the *T. ni* larvae are in the early second instar, the preferred stage of parasitisation by *C. sonorensis*. The presence of host larvae (density) must be regularly monitored or predicted by developing a population model in order to determine the timing and frequency of the parasitoid releases. On the other hand, for a conservation approach in field crops, synchronization will be important because the degree of host–parasitoid synchrony influences the subsequent parasitoid population size, as well as the persistence and the rate of colonization of previously uninhabited host populations (Münster-Swendson and Nachman 1978; Godfray et al. 1994, van Nouhuys and Lei 2004). As reported in the survey of parasitoids of *T. ni* in Chapter 2, in Southwestern Ontario the populations of *C. sonorensis* and *T. ni* are well synchronized but strategies of conservation should be developed in order to strength the interaction because the temperature at the time when this interaction begins may be deleterious to the parasitoid populations (Godfray et al. 1994; van Nouhuys and Lei 2004). In addition, other factors such as chemical pesticide sprays could be reducing the overwintering parasitoid population and therefore, the parasitoid population available for synchronization with the *T. ni* immigration in spring. As evidenced in Chapter 2 as well, *C. sonorensis* populations are also well synchronized with *S. frugiperda*, and probably with *Helicoverpa* species which migrate to Southwestern Ontario by mid-summer in order to feed mostly in corn fields when the parasitoid populations are well established on *T. ni* and probably on other pests and wild hosts.

2) Internal synchronization with host

As per Pak (1991), this criterion should be termed "host suitability" to describe the ability of a parasitoid to complete development in a host. As reported in Chapter 3, *C. sonorensis* development is synchronous with that of *T. ni* so that adult parasitoids will be available when suitable host stages are present. To use an augmentation approach in greenhouse and field crops, the internal synchronization will be especially important at the end of spring and early summer when *T. ni* generations are still discrete, although poor synchronization

could be corrected in part through repeated introductions (inundative releases). The results of the current evaluation demonstrated that at laboratory conditions, 24°C, 60% HR and 12:12 L:D, *C. sonorensis* females complete their development to adult in about 19.4 days (ranging 15 to 25 days) and have an oviposition period of 22.7 days (ranging 15 to 35 days), whereas *T. ni* development time is about 33 days (ranging 30 to 37 days) and has an oviposition period of about 5 days. Therefore, the parasitoid has about 1.7 generations compared to one generation of the host. The long parasitisation and emergence periods ensure that emergence of the parasitoid overlaps with suitable larval instars of the host. For conservation biocontrol using *C. sonorensis* against *T. ni*, the internal synchronization criteria is perfectly met as well, as explained above, but conservation practices should still be developed to strengthen this interaction.

3) Climatic adaptation

Climatic adaptation describes the ability of natural enemies to tolerate the extreme abiotic conditions of their environment compared to their host. Climatic tolerance is a determining factor for the survival and/or the reproduction of a natural enemy (Pak 1991). Because *C. sonorensis* is a native parasitoid of the area where it is intended to be used and because it is very well adapted to the pest population dynamics it will be used against, there are no indications that this criterion will be a problem for the implementation of any biological control program. However, the one exception is that inside greenhouses in the summer, the temperature can reach up to 40°C. Hoelscher and Vinson (1971) reported that 27°C was the most suitable temperature for production of the greatest numbers of *C. sonorensis*. At 36°C, Noble and Graham (1966) reported a mean offspring number of 27.2 per female, whereas in the current studies at 24°C, I reported a mean value of 60.4, thus it is possible that high temperatures may affect the number of offspring per female. However, the two studies also differed in the host species, the experimental conditions, the number of adults that did not emerge, and the number of parasitised hosts that died prior to the parasitoid developing into cocoons. I expect that the number of parasitised larvae that die

before parasitoid development reaches the cocoon stage is higher at higher temperatures, and if so, the overall mortality of hosts caused by *C. sonorensis* could be similar to the actual mortality caused by the successful parasitism and emergence of a new parasitoid adult.

4) No negative effects

The augmentation or conservation of *C. sonorensis* populations in greenhouses or field crops should not have any negative effects on other beneficial organisms or non-pest hosts. In greenhouses, *C. sonorensis* will be intended for the regulation of *T. ni* and probably other potential Lepidoptera pest problems that could enter the greenhouse such as Alfalfa Looper (*Autographa californica* Speyer, Lepidoptera: Noctuidae), Tomato Fruitworm (*H. virescens*) and Tomato Looper (*Chrysodeixis chalcites* Esper, Lepidoptera: Noctuidae). The only beneficial organism that is heavily used against these pests is the bacterium *Bacillus thuringiensis* (*Bt*). I predict that the parasitoid will synergize the effect of *Bt* because the regulation of *T. ni* will be improved since *C. sonorensis* could parasitise a portion of the *T. ni* larvae that is usually not controlled by the bacteria due to difficulties in reaching all of the larvae with the *Bt* spray. However, the potential effects of the bacterium on *C. sonorensis* have to be evaluated. The use of *C. sonorensis* could be a good alternative in order to reduce the probability of a *T. ni* population developing resistance to *Bt* but this potential positive interaction also needs to be evaluated. For non-pest hosts, *C. sonorensis* does not represent any risk as it is a native species of America.

5) Good culture methods

I agree with Waage (1990) and Pack (1991) that this criterion should not be in this compilation. They concluded that the ability to culture a given natural enemy is a conditional necessity of concern to the producer, rather than a useful selection criterion for a researcher conducting an evaluation program of potential biocontrol agents. Instead, it is expected that after a potential biocontrol agent passes the selection criteria, that culture and application methods will need to be

developed and implemented. However, if a culture method already exists or is easy to develop, it is ideal.

For *C. sonorensis*, a laboratory culture method exists but it needs to be improved in order to produce commercial quantities of the parasitoid as is the case with *C. chlorideae* in India (Ballal C, personal communications) although for a greenhouse grower or a group of them who afford the cost of the parasitoid production with the current method, it could be worth it if the parasitoid is highly effective at regulating *T. ni* populations below economic injury levels in vegetables greenhouses.

6) Host specificity or potential for development of host preference

Since *C. sonorensis* has a broad host range including the entire Lepidoptera Noctuidae family, the wide range of host species within the family reported by Lingren et al. (1970) will not be important if the parasitoid is going to be released in greenhouse crops because the only available host will be *T. ni* or other Noctuidae pests such as *H. virescens*. In contrast, *C. sonorensis* does not satisfy this criterion, which states that a narrow host range is desirable, if the parasitoid would be intended in field crops such as tomato and corn. To solve this controversy, I agree with the conclusion of Chang and Kareiva (1996) regarding selection of generalist and specialist natural enemies. They reported that in many cases, a generalist parasitoid (wide host range) will be a better biocontrol agent candidate than a specialist parasitoid (narrow host range). Generalist natural enemies may not be as effective *per capita* as specialists, but they can compensate for this deficiency in host regulation by being present earlier in the season (Nyffeler et al. 1994; Settle et al. 1996) and survive in the system on alternative hosts so that they are present when pest populations re-enter the system. As I will illustrate with *C. sonorensis,* this is beneficial for a species within an augmentation / conservation biocontrol program in field crops. I believe that *C. sonorensis* overwinters in Southwestern Ontario, probably diapausing; if so, by early May, *C. sonorensis* could begin coming out of this overwintering period as

*Hydraecia micacea* and other Lepidoptera overwintering species, which could be the first hosts, do (Howard et al. 1994; Kullik et al. 2005; West et al. 1983; Chaput 2000). At this time, *T ni* that had overwintered in greenhouses due to a bad clean up could be another of the first possible hosts (OMAFRA 2005). By Late May, when the migrating population of *T. ni* and probably other Lepidoptera Noctuidae species arrive in this area, *C. sonorensis* may still be coming out of the overwintering period and probably emerging from the parasitised overwintering hosts. On these hosts, the parasitoid population will increase its size until the next wave of migrating hosts as *S. frugiperda, Helicoverpa* species, *and Peridroma saucia* start arriving by mid-summer (Lingren et al. 1970; Hudon et al. 1985; Howard et al. 1994, Marino et al. 2006). Thus, the ability of *C. sonorensis* to parasitise multiple hosts allows it to persist, but also to affect the population dynamics of multiple pest species, not just *T. ni.*

7) Great reproductive potential

This criterion states that an efficient parasitoid should have a potential maximum rate of population increase ($r_m$) equal to, or larger than that of the host, as is the case in the current evaluation. The intrinsic rate of natural increase for fertility (0.24) and realised fecundity (0.27) of *C. sonorensis* were larger than those obtained for *T. ni* by Zote et al (2006), 0.12 to 0.19. Since *C. sonorensis* causes a considerable rate of mortality of parasitised hosts before parasitoid development and a portion of the parasitoid adults did not emerged from the cocoons, the overall host killing rate should be contrasted against the rate of population increase of the host instead of the parasitoid $r_m$ (van Lenteren and Manzaroli 1999). In this criterion, also the net reproductive rate of *C. sonorensis* should be considered as an important factor of the great reproductive potential of this parasitoid which was 66.91 offspring per female per generation.

For inundative biological control the reproductive potential does not appear to be a useful selection criterion, because a limited parasitoid fecundity can, in theory, be adjusted by releasing more parasitoids (Pak 1991). However, it would be

important to calculate whether releasing more parasitoids is economically feasible, given their individual fecundity.

8) Good density responsiveness

This criterion is often said to be an invaluable characteristic of an efficient natural enemy. Although there is a controversy about what the best method for determining a parasitoid's response to host density is (van Lenteren 1986), using the most common methods, regression analysis and correlations, in this study *C. sonorensis* exhibits a positively density dependent relationship with *T. ni* populations. Thus, the parasitoid is able to locate and reduce the host populations. However, we have not yet evaluated whether *C. sonorensis* is capable of reducing *T. ni* populations below economic injury levels and this is a very important factor which must be determined before any augmentative biological control program is started.

Pak (1991) found the coexistence of pest and natural enemy at a low density to be an essential feature of augmentative approaches by inoculation of the natural enemy, but not of augmentative approaches by inundation of the agent. Inoculation approaches to conservation biocontrol, where natural enemies that do not go extinct at low host/prey populations, should be considered as important priorities in selection of a biocontrol agent, as the cost of inundation (repeated releases) depending on cost of the agent and effectiveness of the agent, is likely to be too expensive.

In addition to these criteria, there is one criterion regarding the selection *C. sonorensis as* a biocontrol agent for *T. ni* that I consider very important that I have not found in my review of the papers. This criterion is the reduction in the feeding by parasitised hosts. It has been documented that in parasitised larval hosts, the reduction of their feeding rate has a direct effect on the damage they inflict (Guillot and Vinson 1973; Mani et al. 1982; van Loon et al. 2000; Fritzsche-Hoballah and Turlings 2001). This is very important in this specific case, and

probably in many more cases similar to this one, because the regulation of the *T. ni* population by *C. sonorensis* occurs mostly during the early 2nd instar of the host, a time when the feeding rate is low and not detrimental to the crop yield as bigger and more voracious host instar stages are. This factor may become more important because as Lingren et al. (1970) and I have found, these early 2nd instar parasitised hosts stop feeding within 3 to 4 days of being parasitised and they never reach a size that could represent a real economic risk to the crop. Lingren et al. (1970) concluded that this fact would be an asset if an augmentation approach by inundative releases of *C. sonorensis* proves to be a feasible method for control of pests as *H. zea* and *H. virescens* in cotton.

Now that I have demonstrated that *C. sonorensis* fits the criteria for a potential biological control agent *T. ni*, further research is required to finish the development of a biological control programme. For the development of an augmentation approach I propose two major steps. The first would be the evaluation of the biological and economic effectiveness (control capacity) of inundative releases of the parasitoid into the vegetable greenhouses, with a comparison of the cost of production and release using the current method of laboratory parasitoid mass rearing available, with the economic benefit provided by *T. ni* control, and including the cost of *T. ni* control using Btk or other measures, risk of Btk resistance, etc in the analysis. This requires evaluation of the timing of release, number of parasitoids released, distribution of release, interaction with other biocontrol agents and Btk and effect on population dynamics of *T. ni*. The second step requires improvement of the mass rearing system in order to allow a scale-up of the system and to be able to produce commercial amounts of the parasitoid at a lower cost.

For the development of a conservation approach using *C. sonorensis* as a model, I also propose two major steps. The first is the evaluation of the population dynamics of *C. sonorensis* and other parasitoids of Noctuidae in the representative field crops of Southwestern Ontario. This should include crop

species that contain Lepidoptera species that migrate or have the potential to migrate into greenhouses, as well as crops that also are critical to maintaining species of natural enemies during vulnerable points in their seasonal dynamics. The second step is the evaluation of the main factors (e.g., chemical pesticide sprays, alternative refugees, food supplies, etc.) affecting the growth of the natural enemies' populations.

## References

Chang GC, Kareiva P (1996) The case for indigenous generalist in biological control. In Hawkins BA, Cornell HV (eds) Theoretical approach to biological control. Cambridge University Press, Cambridge, pp. 103-115.

Chaput J (2000) Managing Cutworms in vegetable crops. Ontario Ministry of Agriculture, Fact Sheet 00-055.

Dai XF (1989). Observations on *Campoletis chlorideae* (Hym.: Ichneumonidae), an important native parasitoid of cotton bollworm, *Helicoverpa armigera*. Chinese Journal of Biological Control 5: 183.

Dai XF (1990). Biology of *Campoletis chlorideae* (Hym.: Ichneumonidae) and its control of cotton bollworm in the field. Chinese Journal of Biological Control 6: 153-156.

Fritzsche-Hoballah ME, Turlings TCJ (2001) Experimental evidence that plants under caterpillar attack may benefit from attracting parasitoids. Evolutionary Ecology Research 3: 1-13.

Godfray HCJ, Hassell MP, Holt RD (1994) The population dynamic consequences of phenological asynchrony between parasitoids and their hosts. Journal of Animal Ecology 63: 1-10.

Guillot FS, Vinson SB (1973) Effect of parasitism by *Cardiochiles nigriceps* on food consumption and utilisation by *Heliothis virescens*. Journal Insect Physiology 19: 2073-2082.

Hoelscher CE, Vinson SB (1971) The sex ratio of a Hymenopterous parasitoid, *Campoletis perdistinctus*, as affected by photoperiod, mating, and temperature. Annals of the Entomological Society of America 64: 1373-1376.

Howard RJ, Garland JA, Seaman WL (1994) Diseases and pests of vegetables crops in Canada. Canadian Phytopathology Society and Entomological Society of Canada, Ottawa. Ontario.

Hudon M, Foott WH, Martel P (1985) Insects damaging corn in Eastern Canada. Agriculture Canada. Publication 1788/E.

Isenhour DJ (1985) *Campoletis sonorensis* (Hym.: Ichneumonidae) as a parasitoid of *Spodoptera frugiperda* (Lep.: Noctuidae): host stage preference and functional response. Entomophaga 30: 31-36.

Isenhour DJ (1986) Developmental time, adult reproductive capability, and longevity of *Campoletis sonorensis* (Hymenoptera: Ichneumonidae) as a parasitoid of fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae). Annals of the Entomological Society of America 79: 893-897.

Kullik SA, Sears MK, McLeod DGR, Gualtieri LL, Schaafsma AW (2005) Phenology and field biology of Black Cutworm (Lepidoptera: Noctuidae) in Ontario no-till corn. Journal of Economic Entomology 98: 1594-1602.

Kumar N, Kumar A, Tripathi CPM (1994). Functional response of *Campoletis chloridae* Uchida (Hymenoptera: Ichneumonidae), a parasitoid of *Heliothis armigera* (Hübner) (Lepidoptera: Noctuidae) in an enclosed experimental system. Biological Agriculture and Horticulture 10: 287-295.

Lingren PD, Guerra RF, Nickelsen JW, White C (1970) Hosts and host-age preference of *Campoletis perdistinctus*. Journal of Economic Entomology 63: 518-522.

Lingren PD, Noble LW (1972) Preference of *Campoletis perdistinctus* for certain Noctuidae larvae. Journal of Economic Entomology 65: 104-107.

Lingren PD (1977) *Campoletis sonorensis*: maintenance of a population on tobacco budworm in a field cage. Environmental Entomology 6:72-76.

Mani M, Nagarkatti S, Narayanan K (1982) Influence of parasitism by *Eucelatoria bryani* (Dip.: Tachinidae) on the consumption and utilization of chickpea flour diet by *Heliothis armigera* (Lep.: Noctuidea). Biocontrol 27: 399-404.

Marino PC, Landis DA, Bradford AH (2006) Conserving parasitoid assemblages of North American pest Lepidoptera: Does biological control by native parasitoids depend on landscape complexity? Biological Control 37: 173-185.

Münster-Swendson M, Nachman G (1978) Asynchrony in host–parasite interaction and its effect on stability studied by a simulation model. Journal of Animal Ecology 47: 159-171.

Nyffeler M, Sterling WL, Dean DA (1994) How spiders make a living. Environmental Entomology 23: 1357-1367.

Noble and Graham (1966) Behavior of *Campoletis perdistinctus* (Viereck) as a parasite of the Tobacco budworm. Journal of Economic Entomology 59: 1118-1120.

OMAFRA (2005) Growing greenhouses vegetables. Publication 371. Ontario Ministry of Agriculture, Food and Rural Affairs.

Pandey AK, Tripathi CPM (2007) Effect of temperature on the development, fecundity, progeny sex ratio and life-table of *Campoletis chlorideae*, an endolarval parasitoid of the pod borer, *Helicoverpa armigera.* Biocontrol. DOI 10.1007/s10526-007-9083-3

Pak GA (1991) Inundative Release of *Trichogramma* for the control of cruciferous Lepidoptera: Pre-introductory selection of an effective parasitoid. In: Talekar NS (ed.) Diamondback moth management: Proceedings of the Second International Workshop. AVRDC. Taiwan. Pp 297-308.

Settle WH, Ariawan H, Astuti ET, Cahyana W, Hakim AL, Hindayana D, Lestari AS, Pajarningsih, Sartano (1996) Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. Ecology 77: 1975-1988.

van Lenteren JC (1986) Parasitoid in the greenhouse: successes with seasonal inoculative release systems. In: Waage J, Greathead D (eds) Insect Parasitoids. Academic Press, London. pp. 341-374.

van Lenteren JC, Manzaroli G (1999) Evaluation and use of predators and parasitoids for biological control of pests in greenhouses. In: Albajes RM, Gullino L, Lenteren JC van, Elad Y (eds) Integrated pest and disease management in greenhouse crops. Kluwer Academic Publishers – CIHEAM, Dordrecht, pp. 183-201.

van Loon JA, De Boer JG, Dicke M (2000) Parasitoid-plant mutualism: parasitoid attack of herbivore increases plant reproduction. Entomologia Experimentalis et Applicata 97: 219-227.

van Nouhuys S, Lei G (2004) Parasitoid–host metapopulation dynamics: the causes and consequences of phenological asynchrony. Journal of Animal Ecology 73: 526-535.

Waage JK (1990) Ecological theory and the selection of biological control agents. In Mackauer M, Ehler LE, Roland J (eds) Critical issues in biological control. Intercept. Andover, pp. 135-157.

WanXue L, FangHao W, ShiTao Y. (2004) Mass-rearing and bionomics of *Campoletis chlorideae*. Chinese Journal of Biological Control 20: 17-20.

West RJ, Laing JE, Marshall SA (1983) Parasites of the potato stem borer *Hydraecia micacea* (Lepidoptera: Noctuidae). Proceeding of the Entomological Society of Ontario 114: 69-82.

Zote VK, Bilapate GG, Jadhav (2006) Life-fecundity tables of *Trichoplusia ni* (Hübner) on different host plants. Journal of the Maharashtra Agricultural Universities 31: 314-317.

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Henry Murillo was born in 1967 in Villavicencio, Meta, Colombia. He graduated from High School in 1986. From there he went on to the University of the Eastern Plains of Colombia where he obtained a B.Sc. in Agronomy in 1993. He is currently a candidate for the Master's degree in Biology Sciences at the University of Windsor and hopes to graduate in Fall 2008.