

Consequences of mixed species infestation on the searching behavior and parasitism success of a larval parasitoid

Johanna Häckermann · Anja S. Rott · Silvia Dorn

Received: 21 March 2007 / Accepted: 30 August 2007 / Published online: 12 September 2007
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Abstract When two herbivore pest species are potential hosts of a single parasitoid species, two questions arise. Firstly, which host is preferable for mass rearing in terms of later parasitoid performance, and secondly, how do parasitoids perform in mixed herbivore situations after colony establishment? We tested *Hyssopus pallidus*, a gregarious parasitoid of two major pests of apple, *Cydia (Grapholita) molesta* and *Cydia pomonella*, before and after landing on apples infested by one of the two *Cydia* species. Pre-alighting host preference was tested in a Y-tube olfactometer setup, and parasitism success in a contact bioassay. To gain information on parasitoid performance throughout the growing season, different fruit growth stages were used. Irrespective of the host they had developed on, the parasitoids showed similar olfactory preferences when given a dual choice between infested and healthy fruits, and they did not discriminate between fruits infested by *C. molesta* and *C. pomonella*. Responsiveness was generally high, especially late in the season close to harvest. Both hosts are parasitized regardless of the host the parasitoid female had developed on, and no differences in parasitism rates or number of offspring were noted for the two hosts offered. Results were consistent for all apple growth stages tested. In conclusion, mass rearing of this parasitoid can be carried out on either host,

J. Häckermann · A. S. Rott · S. Dorn
Institute of Plant Sciences, Applied Entomology, ETH Zurich, Schmelzbergstrasse 9, LFO,
Zurich 8092, Switzerland

S. Dorn
e-mail: silvia.dorn@ipw.agrl.ethz.ch

J. Häckermann
Institute of Plant Sciences, Applied Entomology, SafeCrop, Center for Research and Development
of Crop Protection with Low Environmental and Consumer Health Impact, c/o ETH Zurich, Zurich,
Switzerland
e-mail: jomh@gmx.net

A. S. Rott (✉)
School of Pharmacy and Biomolecular Sciences, University of Brighton, Cockcroft Building,
Mouslecoomb, Brighton BN2 4GJ, UK
e-mail: a.s.rott@brighton.ac.uk

without limiting the future efficacy of the bio-control agent. Similarly, established colonies are expected to develop further on both hosts without any bias in host preference.

Keywords Apple · *Cydia pomonella* · *Cydia (Grapholita) molesta* · Discrimination · Host location · *Hyssopus pallidus* · Natal host · Volatiles

Introduction

The efficiency of a parasitoid depends on its ability to locate potential hosts in a given habitat and to successfully reproduce thereafter. When resources are distant, parasitoids are predicted to search for hosts in a non-random manner in order to optimize their fitness (Desouhant et al. 2005). Under these circumstances, host habitat related cues are decisive in the searching process, because cues derived from the host itself are often not strong enough to be detected over long distances. Host habitat cues are therefore considered the primary stimulus for the niche selection by parasitoids (Vet et al. 1995). Indeed, changes in the chemical composition of host plants infested with herbivores convey important information for searching parasitoids (Mattiacci et al. 2000; Meiners et al. 2005; Tentelier et al. 2005), which is then used to identify suitable habitats. Within a habitat, parasitoids generally rely on direct cues from the host to locate potential hosts (Godfray 1994) although there are exceptions (Dutton et al. 2000, 2002). Host related chemical cues, such as stimuli contained in host frass, have been shown to elicit an area restricted searching behavior in parasitoid (Mattiacci et al. 1999; Tanaka et al. 2001), because frass usually indicates host presence and serves as reliable information for searching females (Vet and Dicke 1992).

Not only can the host's environment have an important influence on the performance of a parasitoid (Bjorksten and Hoffmann 1998a; Mattiacci et al. 2000; Gandolfi et al. 2003b), but also the host species, on which the parasitoid develops, may influence the performance of the subsequent generation (Mansfield and Mills 2004). Rearing effects on chemosensory responsiveness and host preference have been demonstrated for several species. For example, *Trichogramma brassicae* showed greater preference for the grain moth *Sitotroga cerealella* when reared from this species than when reared from other host species (Bjorksten and Hoffmann 1998b). In a parasitoid that attacks *Musca domestica* and *Drosophila melanogaster* a clear influence of the natal host on the performance of the next generation has been observed (Morris and Fellowes 2002).

An example of two herbivore species as potential hosts for one single parasitoid species is the tritrophic system composed of the apple tree, the herbivore pests *Cydia (Grapholita) molesta* (Busck) (Lepidoptera: Tortricidae) and *Cydia pomonella* (L.) (Lepidoptera: Tortricidae), and their common parasitoid *Hyssopus pallidus* (Askew) (Hymenoptera: Eulophidae). While the codling moth *C. pomonella* is a notorious pest of apple trees (Barns 1991; Dorn et al. 1999) the oriental fruit moth, *C. molesta*, originally known as a key pest of peach, has been appearing in recent years to an increasing degree as a pest insect in apple orchards in various countries (Rothschild and Vickers 1991; Pollini and Bariselli 1993; Natale et al. 2004). As a consequence, apple growers are confronted with the need to control both tortricid pests in their orchards, and improved integrated pest management (IPM) strategies are required.

Hyssopus pallidus, a candidate biocontrol agent (Mattiacci et al. 1999), is a gregarious ectoparasitoid of the oriental fruit moth and the codling moth, and endemic to Europe (Askew 1964; Zaviezo and Mills 2000; Tschudi-Rein et al. 2004). Similar to other

Eulophidae, this species has a rapid preimaginal development (Häckermann et al. 2007), high lifetime fecundity, and a female biased sex ratio (Brown 1996). Furthermore it uses plant as well as host-derived cues to locate its host, and host frass from apple-fed caterpillars triggered a particularly high response. Moreover, rates of host attack and parasitism can attain 86% in the presence of apple cues (Mattiacci et al. 2000). Given its biological characteristics, *H. pallidus* could be used for inoculative or inundative release to keep *Cydia* populations below a certain threshold level. *Cydia pomonella* and *C. molesta* are the only known and documented hosts for this relatively specialized parasitoid (Askew 1964; Zaviezo and Mills 1999; Tschudi-Rein et al. 2004), which appears to be well adapted to the apple habitat (Hausmann et al. 2005). Once a female parasitoid has found a fruit infested by a *Cydia* larva, it enters the apple either through the gallery made by the caterpillar or through the calyx and parasitizes the host caterpillar inside the apple (Mattiacci et al. 1999). Upon successful parasitism the female displays brood guarding, and after 15 days (at 24°C), the next generation of parasitoids emerges from the apple (Zaviezo and Mills 1999).

This study investigates the significance of the natal host on the behavior of the subsequent *H. pallidus* generation, to ensure good quality parasitoids. This relationship holds potential to influence success of biological control in two ways: if the parasitoid is used for conservation biological control or for inoculative release, the wasps might emerge from one or both potential host species. The question arising thereupon is whether the parasitoid will subsequently control both herbivore hosts equally well, irrespective of the host the parasitoid had developed on. In case the parasitoid should be used for inundative release, the wasp will be mass reared on one single host species in the laboratory and is subsequently mass released. Will the parasitoid in this case control both herbivore species equally well even after rearing on one single potential host?

The main focus of this project was on the role of chemical cues mediating the parasitoid's behavior before and after landing of the parasitoid. We investigated the behavior of parasitoids, reared on *C. molesta* and *C. pomonella* by determining (1) response to chemical cues emitted by infested apples, (2) parasitism success and (3) host preference in mixed species infestation. Implications for the release of this parasitoid as biological control agent against *Cydia* species in apple production are discussed.

Material and methods

Parasitoid rearing

The initial colony of *Hyssopus pallidus* was provided in 1996 by T. Unruh (USDA-ARS Research Laboratory, Wapato Washington, USA) and originated from France. Following detection of this parasitoid in Switzerland (Tschudi-Rein et al. 2004) the colony was refreshed by the introduction of field-collected adult wasps and maintained as a single colony. Starting from this single colony, two strains were obtained by rearing the parasitoids on two different hosts. One strain was reared on *Cydia pomonella* hosts (CP strain), the other on *Cydia molesta* hosts (CM strain). Both strains had been reared on the respective host for more than 30 generations.

The CM parasitoid strain was maintained on last instar *C. molesta* caterpillars, the CP parasitoid strain on last instar *C. pomonella* caterpillars. Both host species had been reared on wheat-germ-based artificial diet (Huber et al. 1972). Newly hatched first instar caterpillars were placed individually in a plastic box (18 mm × 18 mm × 10 mm) filled with 3.4 g of artificial diet. Boxes containing *C. pomonella* hosts and *C. molesta* hosts

respectively were kept at $25 \pm 2^\circ\text{C}$, $60 \pm 10\%$ RH and 16L:8D. Last instar caterpillars were offered to 4–7 days old mated female parasitoids. In the permanent rearing, host caterpillars were offered to the female wasp in glass vials (10 cm of length, 2.8 cm of diameter) at a ratio of two parasitoids per host, resulting in a constant supply of parasitoids.

Since plant cues offered during the ontogenesis of the parasitoid are of crucial importance for the behavioral quality of the emerged wasps (Gandolfi et al. 2003b), a small piece of fresh apple (Gandolfi et al. 2003a) was added to the vial, and a drop of undiluted honey served as food source to the female parasitoids of the parental generation. The vials were closed with a piece of thin meshed net. The wasps were removed from the vial 1 week later. Parasitized caterpillars were kept under standardized laboratory conditions at a temperature of $24 \pm 2^\circ\text{C}$, RH of $60 \pm 10\%$ and a regime of 16L:8D until the emergence of the parasitoid's progeny 14–17 days later. Upon emergence, progeny were removed from the vial and transferred to a Plexiglas[®] cage ($25 \times 25 \times 25$ cm), where they were fed with honey and water.

Plant material

The apple variety *Malus* “Golden Delicious” (*Malus domestica* Borkh.) was used for all experiments; all apples originated from commercial orchards, treated against fungal pathogens and insect pests according to the Swiss guidelines of integrated fruit production (Höhn et al. 2005). In the period between June and September, no sulfur containing fungicides were used. Insect control was made using the insect growth regulator methoxyfenozide, which is classified as non-toxic to hymenopteran parasitoids (Höhn et al. 2005). Apple fruits were infested with one of the two *Cydia* species and thereafter kept under standardized laboratory conditions at a temperature of $24 \pm 2^\circ\text{C}$, RH of $60 \pm 10\%$ and a 16L:8D regime.

Choice experiment before landing: Y-tube olfactometer

To determine the olfactory response of the adult parasitoids to odors emitted by infested apples, dual choice experiments were conducted with volatiles from *C. molesta* and *C. pomonella* infested apples as well as from healthy apples. This bioassay set-up has been proven to be appropriate for this parasitoid to discriminate between odors, and significant olfactorial preference has been reported using this method (Rott et al. 2005, unpublished data). Apples were infested either with the penultimate instar (third) of *C. molesta* or the penultimate (fourth) of *C. pomonella*, leaving the caterpillar to feed for 48 h at $24 \pm 2^\circ\text{C}$, $60 \pm 10\%$ RH and L18:D6. This method was chosen because a long feeding period leads to the infection with post-harvest fungi. Three different apple growth stages were tested: fruits collected early in the season in June (growth stage 74, 2.5–3.5 cm of diameter), according to the BBCH coding system (Meier 2001), in mid season (growth stage 78, 3.5–4.5 cm of diameter) and late in the season in September, shortly before harvest (growth stage 81, 4.5–6.0 cm of diameter). In each experiment, one entire apple at the time was inserted into the volatile chamber.

The olfactory response was determined in a Y-tube olfactometer, which consisted of a Y-shaped glass tube, with each arm 22 cm long and 1.8 cm in diameter and two odor source chambers (9.5 cm diameter \times 11 cm height). Moistened, charcoal filtered air entered at a constant rate of 230 ± 5 ml/min through each arm of the olfactometer. The flow rate through each arm was controlled by a flow meter. To avoid any visual

influence on the choice, the walls on the right and left side of the experimental construction were covered with white paper. The whole construction was placed beneath seven equally distributed neon lamps allowing an even light intensity of 3000 ± 20 Lux. The conditions of the experimental room were set at $24 \pm 2^\circ\text{C}$, and a RH of $60 \pm 5\%$.

On the day of each experiment, female parasitoids were removed from their cage and kept in a Plexiglas[®] cylinder (5 cm of diameter, 10 cm of length) with a droplet of honey. The 4–6 day old mated and inexperienced parasitoids were brought to the experimental laboratory in a small glass vial (0.7 cm of diameter, 2 cm of length) 30 min prior to the experiment giving them time to adapt to the new environment. One parasitoid at a time was introduced into the common arm of the Y-tube, by letting them walk out of the glass vial. Its behavior was observed for 10 min. Each arm was divided into two zones, starting at the junction, with zone 1 having a length of 8 cm (Bertschy et al. 1997). If a female entered zone 2 (starting 8 cm away from the junction), it was considered having made a choice. Observations were discontinued, when the tested parasitoid entered zone 2 or after 10 min had elapsed. If it stayed in the common arm or zone 1 for the whole observation period it was classified as not having made a choice. To avoid any asymmetrical bias in the set-up, the odor sources and their position were changed after five parasitoids had been tested. Both parasitoids strains were tested in the following set-up combinations of odor source: *C. molesta* infested versus *C. pomonella* infested apples, *C. molesta* infested versus uninfested apples and *C. pomonella* infested versus uninfested apples. Each parasitoid was used only once. Overall 40 females were tested for each apple stage. Tests were carried out on different days to avoid any bias; on each day, every odor combination was tested.

Choice experiment after landing: contact bioassay

The same apple growth stages as for the Y-tube olfactometer experiment were used (74, 78 and 81). Apples were infested with a third to fourth instar larva of either *C. molesta* or *C. pomonella*, which had been reared on an artificial wheat germ based diet (Huber et al. 1972). For infestation, a third instar larva was placed onto the surface of an apple and the whole set-up, i.e. the entire fruit-herbivore complex, was covered with a Plexiglas[®] cylinder (6 cm of diameter, h = 8 cm). One end of the cylinder was closed with a thin meshed net. After 24 h the larva had drilled into the apple.

Upon successful infestation, a *C. molesta* and a *C. pomonella* infested apple were each placed onto an elevated wire mesh respectively, to ensure that parasitoids had full access to the apples. The setup was covered with a plastic box (10 × 20 × 8 cm). A 3–7 day old mated female parasitoid was added to the set-up in a ratio of one parasitoid per box, with a droplet of honey as food. The parasitoid was given 7 days to choose either of the offered hosts, to parasitize it and to leave the apple again. Upon removal of the parasitoid, apples were separated again and placed individually under a Plexiglas[®] cylinder. New adult parasitoids emerged 15–22 days later. For each apple stage, 20 replicates were tested. Choice was defined as parasitized *Cydia* larva, success as number of progeny produced on one host. All the experiments were carried out with parasitoids of the CM strain as well as the CP strain.

Data analysis

Differences in choice for odor sources (olfactometer experiments) or for host caterpillars (contact bioassays) were analyzed using the non-parametric χ^2 test, while differences in

number of offspring within apple stages were analyzed with an independent *t*-test (data were normally distributed (Kolmogorov-Smirnov Test) and equality of variance (Levene's test) was assumed).

Results

Y-tube olfactometer experiments

The parasitoid *H. pallidus* did not display any preference for volatiles of either of the host-herbivore complexes irrespective of the host caterpillar they had developed on.

Parasitoids that had been reared on *C. molesta* as hosts did not prefer the volatile bouquet of *C. molesta* infested apples over *C. pomonella* infested apples neither early in the season nor in mid summer nor late in the season (for all χ^2 , $P > 0.05$) (Fig. 1A). A

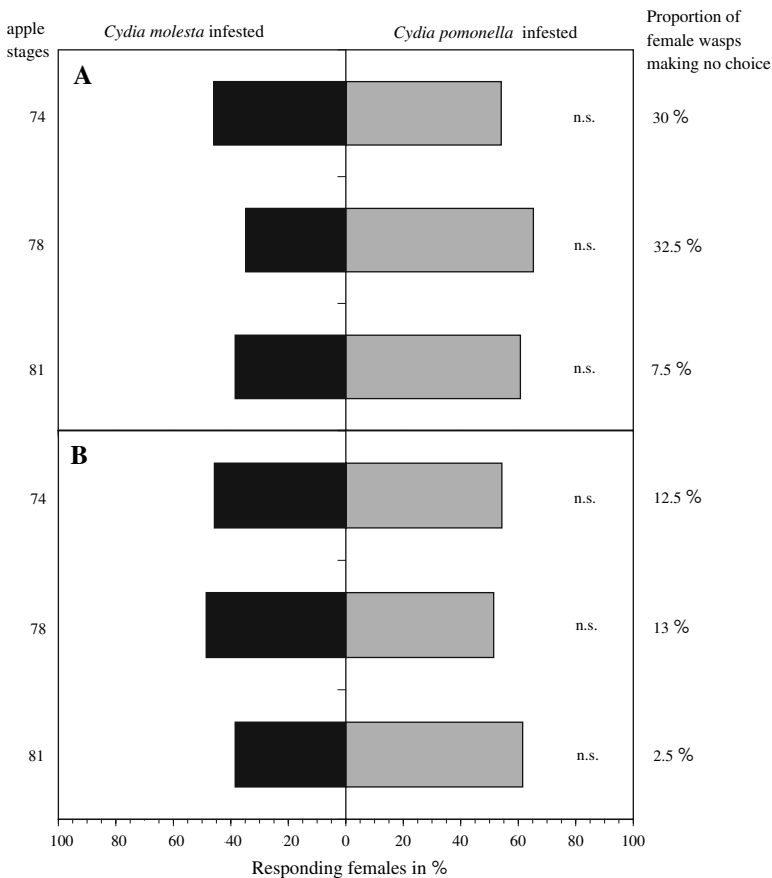


Fig. 1 Choice (in percentage of responding individuals) of *Hyssopus pallidus* parasitoids reared (A) on *Cydia molesta* or (B) *Cydia pomonella* in the Y-tube olfactometer experiment. The female wasps were offered the choice between apple fruits infested with *C. molesta* and apples infested with *C. pomonella*. Different apple growth stages represent different times during the season, with stage 74 occurring in June and stage 81 in September. $N = 40$ females were tested per treatment (n.s. indicates that χ^2 -test showed no significant differences, $P > 0.05$)

significantly higher preference for odors emitted by healthy apples was observed in the parasitoid wasp when tested against *C. molesta* infested apples ($\chi^2 = 4.8$, $df = 1$, $P < 0.05$) early in the season (Table 1A), but later on, no discrimination occurred between the two odor bouquets (χ^2 , $P > 0.05$). When given a choice between healthy and *C. pomonella* infested apples, there was no preference for either of the odor bouquets at any time in the season (for all χ^2 , $P > 0.05$). The proportion of female parasitoids not making a choice varied between 32.5% and 7.5%, being lowest late in the season (Fig. 1A).

Parasitoids reared on *C. pomonella* did not prefer volatiles from apples infested with *C. pomonella* over those infested with *C. molesta* regardless of the apple growth stage (for all χ^2 , $P > 0.05$) (Fig. 1B). *C. molesta* infested apples were not preferred over healthy apples, irrespective of the point of time in the season (for all χ^2 , $P > 0.05$). Equally, *C. pomonella* infested apples were not preferred over healthy apples when tested against each other (for all χ^2 , $P > 0.05$) (Table 1B). The proportion of females not making a choice varied between 13% and 2.5% being lowest late in the season (Fig. 1B).

Contact bioassays

Parasitoids from the *C. molesta* strain that were given the choice between a *C. molesta* and a *C. pomonella* infested apple parasitized both host species equally frequently, based on assessments of the number of apple fruits from which a new generation of parasitoids emerged. Across the growing season, no preference for either of the hosts was noted (for all χ^2 , $P > 0.05$). The overall parasitism rates varied between 24% and 57% per treatment and apple stage. The majority of females oviposited in either one of the offered host, with only 11% of parasitizing both hosts. The proportion of apples without a next generation of parasitoids emerging varied between 43.4% and 76.6%, and was lowest at the beginning and the end of the season. Focusing on the number of parasitoid offspring that emerged

Table 1 Choice (in percentage) of responding individuals ($N = 40$ tested individuals for each setup) of (A) *C. molesta* and (B) *C. pomonella* reared parasitoids in the olfactometer

Apple stage ^a	(1) <i>C. molesta</i> versus healthy			(2) <i>C. pomonella</i> versus healthy		
	Infested	Healthy	No choice	Infested	Healthy	No choice
(A) Choice of <i>C. molesta</i> reared parasitoids						
74	30	70*	26	41.9	58.1	22.5
78	50	50	30	44.0	56.0	37.5
81	44.4	55.6	10	57.9	42.1	5
(B) Choice of <i>C. pomonella</i> reared parasitoids						
74	67.7	32.4	15	55.6	44.4	10
78	48.9	51.5	17.5	63.9	36.1	10
81	51.3	48.7	2.5	36.8	63.2	5

Both strains were tested in the following dual choice situations: (1) *C. molesta* infested against healthy apples and (2) *C. pomonella* infested against healthy apples. In the fourth and the seventh column the proportion of females that did not make a choice is shown

^a Apple growth stages relate to progressing season, with the apple stage 74 occurring in June and the apple stage 81 in September

$\chi^2 = 0.028$, * $P < 0.05$

from the parasitized apple, no difference was found between the two host species (for all t -tests, $P > 0.05$). These results are consistent all over the three apple growth stages tested (Table 2). The number of offspring varied between 5 and 19 for parasitoids emerging from *C. molesta* hosts and 2 and 35 for those having developed on *C. pomonella* caterpillars.

Similarly, *C. pomonella* reared parasitoids did not discriminate between either of the host species when these were offered simultaneously. Both host caterpillars were equally well parasitized inside the apples irrespective of the time in the season (for all χ^2 , $P > 0.05$). The overall parasitism rate was 47.5% up to 77.5% per treatment. Again the parasitism incident was predominantly on either one of the offered hosts (18% parasitizing both hosts). The number of apples without a next generation of parasitoids emerging varied between 22.5% and 52.5% and was lowest in mid season. The number of offspring produced per host larva did not vary between the two host species (for all t -tests, $P > 0.05$). Early (74) as well as later on (78 and 81) in the season, the same amount of progeny was produced per host larva independent of the host species (Table 2). The number of offspring per host varied between 2 and 39 for *C. molesta* caterpillars, and in the case of *C. pomonella*, 1–30 individuals emerged per host caterpillar.

Discussion

This study focused on the role of chemical cues mediating the parasitoid's behavior before and after landing on the apple. Simultaneously offered volatiles from *C. molesta* and *C. pomonella* infested apples were equally attractive to *H. pallidus* females in a dual choice situation, irrespective of the host they had developed on. As is known from previous studies, volatiles from the host-fruit complex are pivotal to searching parasitoids (Mattiacci et al. 1999), although not all potential fruit-host complexes may elicit the same response. Our results provide empirical evidence that the parasitoid does not discriminate between the odor bouquets emitted by the two different host species on the same host plant, indicating that plant volatiles (such as apple odors) are primarily used as host finding cues when exposed to them during its preimaginal development (Gandolfi et al. 2003b). Regardless of the host the parasitoid had developed on, females exhibited a high responsiveness in the presence of fruit odors, and they did not show any preference for either of the host species complexes. After landing, as shown in the contact bioassays, the natal host neither had an effect on the searching efficiency, nor on the reproductive success of the parasitoid. Thus *H. pallidus* is able to reproduce on both *Cydia* hosts present in the apple habitat, to which the parasitoid is highly adapted (Hausmann et al. 2005). While the role of odors emanating from the plant on the host-searching behavior is well documented in this and previous studies (Gandolfi et al. 2003a, b), the role of volatiles from the host-plant complex, i.e. of the odors emitted by herbivore-infested fruit, is less clear in this system.

The current study reveals no significant preference of parasitoid females for volatiles of infested fruit when given the choice with healthy fruit. Using the same olfactometer methodology, Rott et al. (2005) reported that the parasitoid discriminated in favor of the infested fruit at four sampling dates between June and August, but showed no preference very early (end May), mid and end of season. Coincidentally, both studies found no discrimination end of the season. Contrary to expectations, infested fruit in June (measuring around 30 mm in diameter) did not elicit a preference of the females for infested fruit in contrast to the previous study (Rott et al. 2005; fruit sizes presented in Vallat and Dorn 2005). In the first study, apple trees of the same variety were under drought stress due to

Table 2 Mean number of offspring (\pm the standard deviation) produced per host larva in a dual choice contact bioassay

Apple stage ^a	<i>C. molesta</i> reared parasitoids			<i>C. pomonella</i> reared parasitoids		
	Offspring on <i>C. molesta</i>	Number parasitized	Offspring on <i>C. pomonella</i>	Number parasitized	Offspring on <i>C. molesta</i>	Number parasitized
74	8.8 \pm 4.4	5	8.08 \pm 3.6	12	13 \pm 10.1	14
78	18.5 \pm 6.7	2	9.8 \pm 7.9	5	19.7 \pm 9.6	13
81	8.8 \pm 3.7	5	16.1 \pm 8.8	10	10.7 \pm 5.7	8
					Offspring on <i>C. pomonella</i>	Number parasitized
					12.5 \pm 8.7	15
					14.2 \pm 7.8	18
					10.27 \pm 6.1	11

One *C. molesta* and one *C. pomonella* infested apple were offered to one female parasitoid. 30 individual females of the *C. molesta* reared strain and 40 of the *C. pomonella* reared strain were tested. Only those apples were included in the analysis that gave raise to a next generation of parasitoids

^a Apple growth stages relate to progressing season, with the apple stage 74 occurring in June and the apple stage 81 in September

the unusually warm and dry summer, but fruit attained a size of 72 mm shortly before harvest, while in the current study, climatic conditions were moderate but fruit attained an average size of only 52 mm, thus rendering detailed direct comparison difficult (Rott et al. 2005; Vallat and Dorn 2005; Vallat et al. 2005). Drought stress elicits changes in volatile emissions from the apple tree. It increases the activity of lipoxxygenase, resulting in increased green leaf volatile emissions (Vallat et al. 2005). Quantitative changes in the volatile profile of the apple tree are likely to influence the strength of olfactory preference of *H. pallidus*.

Microhabitat location involves mostly the detection of host-infested sites (Vet et al. 1995). It has been demonstrated that host related kairomones are used in the short-range foraging process by *H. pallidus* (Hausmann et al. 2005), and that host feces elicit intense searching behavior (Gandolfi et al. 2003a). The host-derived kairomones are host diet independent but their effect is strongly enhanced when apple cues are additionally present (Mattiacci et al. 1999; Gandolfi et al. 2003a). Such bioactive combinations are known from other tritrophic systems, where plant constituents as well as compounds derived from the host are involved in attracting parasitoids to infested patches (Agelopoulos et al. 1995; Tanaka et al. 2001). The fact that *H. pallidus* did not show any discrimination between fruit infested by either of the two *Cydia* hosts suggests that the foraging females perceive the host-derived kairomones, offered in combination with plant cues, similarly. Our findings are also consistent with the postulate by Dutton et al. (2000) that parasitoids of concealed hosts rely more on plant-based than on host-based stimuli. The two *Cydia* species are the only known hosts in Europe for this parasitoid, as first (Askew 1964) and recent (Tschudi-Rein et al. 2004) field samplings document. Further, the parasitoid failed to develop on two other tortricid species offered in no-choice laboratory trials (Zaviezo and Mills 1999), of which the genus *Pandemis* is also known in Europe.

When offered simultaneously in a contact bioassay, *H. pallidus* females parasitized both caterpillar species, independently of the host species they had developed on. The overall parasitism incidence was slightly but not significantly higher with *C. pomonella* reared parasitoids. From other systems, different patterns of relationships between natal host and preferred hosts for oviposition were reported, such as for the generalist egg parasitoids *Trichogramma* spp. (Hymenoptera: Trichogrammatidae). Regardless of its natal host, one out of two frequent field hosts was consistently preferred by *T. pretiosum* Riley (Brotodjoja and Walter 2006). Conversely, the natal host had a fundamental influence on the preference of the next generation in *T. platneri* Nagarkatti (Mansfield and Mills 2004). In our investigation, the average number of offspring produced per host larva was also comparable on both host species, irrespective of the fact that *C. molesta* caterpillars are on average much smaller than *C. pomonella* caterpillars. A previous study on the quality of the two host species has revealed that host size was not equal to host quality suggesting that *C. molesta* caterpillars offer more favorable nutrient resources (Häckermann et al. 2007). Nonetheless, this parasitoid parasitized both hosts and progeny developed successfully to the adult stage. This fact supports the hypothesis that this association of herbivores can be characterized as sharing a natural enemy (Luhring et al. 2004) and that *H. pallidus* can therefore be considered as a potential biological control agent for both *Cydia* species.

Even though associations of different herbivore hosts with a plant may produce different odor bouquets (Geervliet et al. 1998), this variation does not necessarily impede a successful host location and reproduction of the parasitoid (Silva-Torres et al. 2005). Overall, the natal host neither had an effect on the searching efficiency, nor on the reproductive success of *H. pallidus*, thus ensuring that the parasitoid is able to reproduce on both *Cydia* hosts present in the apple habitat.

In terms of biological control programs against the two *Cydia* species in apple orchards, our results provide empirical evidence that *H. pallidus* can substantially contribute to IPM programs. In inoculative or conservation biological control, parasitoids that emerged from colonies on either of the two hosts are expected to attack and suppress both hosts without any bias. In inundative biological control programs, mass rearing can be carried out on either host without limiting the future efficacy of this candidate biological control agent. Further studies should investigate the impact of host to parasitoid ratios on the efficiency of the parasitoid in reducing *Cydia* populations (Walde and Murdoch 1988; Bezemer and Mills 2001), and of the adult parasitoid's nutrition on parasitism rates (Wanner et al. 2006a, b).

Acknowledgements We are very grateful to the farmers Daniel Wegmann, Zürich and Kurt Rennhard, Leuggern, Switzerland, who provided the plant material for these experiments. We also thank two anonymous referees for helpful comments and Dr. Silke Hein for the fruitful discussion and the critical reading of earlier versions of the manuscript. This research was proposed by Silvia Dorn and supported by SafeCrop Centre, funded by Fondo per la Ricerca, Autonomous Province of Trento.

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