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Searching behavior of an aphid parasitoid and its hyperparasitoid with and without floral nectar

Salah-Eddin Araj^{a,*}, Steve Wratten^a, Alison Lister^a, Hannah Buckley^a, Ihab Ghabeish^b

^a Bio-Protection Research Centre, PO Box 84, Lincoln University, Canterbury 7647, New Zealand

^b Al-Salt University College, Department of Applied Sciences, PO Box 19117, Al-Balqa Applied University, Al-Salt, Jordan

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ABSTRACT

While enhancing the searching ability of a natural enemy can give a major improvement in host population suppression, it is important to demonstrate selectivity in favor of the third trophic level when changes, such as added floral resources, are made to agro-ecosystems to enhance biological control efficacy. To explore this question, a pea-aphid endoparasitoid, *Aphidius ervi*, and its hyperparasitoid, *Dendrocerus aphidum*, were used to test the effects of prior feeding with buckwheat nectar on searching behavior of both the parasitoid and hyperparasitoid. Digital video was used to record behavior and data were scored and analyzed using Observer Video-Pro software. *A. ervi* females in nectar treatments spent a higher proportion of their time actively searching than those with access to water only. Fed parasitoids antennated, stung and groomed significantly more than unfed female parasitoids, and spent almost twice as much time attacking and carried out nearly twice as many attacks as unfed parasitoids. *D. aphidum* spent the greatest proportion of time attacking potential hosts in both 'fed' and 'unfed' treatments. However, although fed females spent a significantly longer time antennating, there was no significant difference in walking or grooming between treatments. Unfed female hyperparasitoids spent significantly more time stationary than fed females. The results demonstrate that the searching efficiency of both third and fourth trophic level parasitoids is enhanced by access to floral nectar. Nectar provision can therefore potentially have positive or negative effects on biological control, depending on the relative proportion of each species.

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1. Introduction

Understanding the behavior of natural enemies and their parasitoids is important for determining how they influence the population dynamics of their hosts and the role they play in the structure and function of the insect communities. However, the fourth trophic level has generally been ignored in studies of parasitoid behavior, particularly in the context of conservation biological control, which is an application of food web dynamics (Polis and Winemiller, 1996) to improve natural-enemy efficacy. Modeling suggests that a large reduction in pest populations arises from enhancing the efficiency of natural enemies (e.g., Hassell, 2000; Kean et al., 2003). For example, resource subsidies, such as nectar, may enhance natural enemy searching ability, which in turn can be manipulated particularly if the provision of these subsidies leads to natural enemies spending a greater proportion of their available time actively searching (Kean et al., 2003). The relative influence of floral nectar on hyperparasitoids and their parasitoid hosts has

been explored using *Aphidius ervi* (Haliday) (Hymenoptera: Ichneumonidae), a solitary parasitoid of various macrosiphine aphid species of economic importance; these aphids attack many vegetables, legumes, cereals and weeds. Furthermore, they can transmit serious viral diseases (Farrell and Stufkens, 1988). The hosts of *A. ervi* include the pea aphid *Acyrtosiphon pisum* (Harris) (Homoptera: Aphididae) (Mackauer and Starý, 1967), and it can be easily reared on all nymphal stages of this aphid in the laboratory (Sequeira and Mackauer, 1992). *A. ervi* has been extensively studied and, with its pea aphid host, has provided a valuable model system for studies on aphid-parasitoid behavior and physiology (Guerrieri et al., 1993; Battaglia et al., 1995; Digilio et al., 1998). *Dendrocerus aphidum* (Rondani) (Hymenoptera: Megaspilidae) is an ectophagous hyperparasitoid which is an idiobiont – 'a parasitoid which prevents further development of its host' (Gauld and Bolton, 1988) – that attacks the pre-pupa or the pupa of the primary parasitoid after the latter has killed and mummified the aphid (Chow and Mackauer, 1996). Rates of hyperparasitism in the field vary during the season from 5% early on to as much as 60–80% later (Wilson and Swincer, 1984; Ayal and Green, 1993; Müller and Godfray, 1998; Hullé et al., 2010).

* Corresponding author. Fax: +64 3 325 3864.

E-mail address: Salah.Araj@lincolnuni.ac.nz (S.-E. Araj).

In the research described here, the effect of buckwheat *Fagopyrum esculentum* Moench cv. Katowase (Polygonaceae) on the searching behavior of *A. ervi* and *D. aphidum* females was investigated. Buckwheat is 'an annual Asian plant having clusters of small whitish or pinkish flowers and small, seedlike, triangular fruits, used either whole or ground into flour' (Mazza, 1992). It was used here because its nectar leads to enhanced 'fitness' of a wide range of beneficial insects (Jervis et al., 1993; Landis et al., 2000; Berndt et al., 2002; Irvin et al., 2006; Zehnder et al., 2007; Scarratt et al., 2008; Jonsson et al., 2009).

2. Materials and Methods

2.1. Insect rearing

Video techniques are useful in the investigation of the foraging, reproductive, feeding, dispersal and searching behavior of vertebrates and invertebrates (Wratten, 1994; Merfield et al., 2004; Frank et al., 2007). Pea aphids were reared on potted plants of broad bean (*Vicia faba* L. cv. Cole's Prolific) in a controlled temperature room at 20 °C with a 4 °C range and RH 60–70% with a photoperiod of 16:8 h light:dark. Light intensity was 122 $\mu\text{mol}/\text{m}^2/\text{s}$.

Aphid mummies were collected from fields of lucerne (*Medicago sativa* L. cv. 'Kaituna'), then put singly into 600 μl gelatin capsules and kept in a transparent polystyrene box (20 \times 10 \times 5 cm) under the above conditions. When parasitoids or hyperparasitoids emerged, they were identified using the keys of Mertins (1985). An *A. ervi* colony was then reared on pea aphids under the above conditions. A colony of *D. aphidum* was established from individuals (*A. ervi* or *A. eadyi* (Stary) (Hymenoptera: Braconidae)) emerging from parasitized pea aphids collected as above. The hyperparasitoids were reared on newly-formed laboratory mummies containing of *A. ervi* pupae, which form approximately 9 days after oviposition by this parasitoid (Walker and Cameron, 1981) and were maintained as above.

2.2. Experimental Procedure

A behavioral catalogue was developed from preliminary observations of searching behavior of the parasitoid and hyperparasitoid. Some behaviors were pooled for simplicity (see Wang and Keller (2002)), so that in the main experiments, five groupings were used: antennate, attack, groom, walk and stationary (see Table 1 for complete descriptions).

All parasitoid experiments were conducted with newly-emerged *A. ervi* females, which were put singly into a transparent polycarbonate jar (120 mm in length and 85 mm in diameter) and provided with four males to ensure fertilization. Each cage was allocated to one of four treatments: either water or buckwheat for either 24 h or 48 h (preliminary investigations showed 'water-only' parasitoids would not survive beyond 2 days). Buckwheat flowers were provided as a single shoot with newly-opened flowers from a potted plant. There were six replicates per treatment.

For *D. aphidum*, similar protocols were used, although water or buckwheat flowers were provided for 24, 48, 72 and 96 h, since preliminary investigations showed that many female hyperparasitoids would not survive beyond 4 days with only water provided.

After exposure to water or flowers, individual *A. ervi* females were placed in 8.5 cm Petri dishes with a broad bean leaflet on which 80–100 (3–5 days old) pea aphids were feeding. Each parasitoid's behavior was then continuously recorded for 20 min using a digital video recorder (JVC Digital Video Camera, optical 16x zoom, 520 lines of resolution) with Marumi lenses added, which magnified the area by an additional 7x. Data were then scored and analyzed using The Observer Video-Pro (Noldus et al., 2000).

For *D. aphidum*, individual females were placed in Petri dishes as above, but the leaflet had 6–8 newly formed mummies. Hyperparasitoid behavior was then recorded, scored and analyzed as for parasitoids. All experiments were carried out at room temperature with 7.3 $\mu\text{mol}/\text{m}^2/\text{s}$ light intensity.

2.3. Statistical analysis

Data from the elementary statistics table generated by The Observer Video-Pro were exported to Excel. For *A. ervi*, each behavior was analyzed using analysis of variance (ANOVA). The effect of buckwheat and length of exposure on both the number of events and on the time spent in the behavior were analyzed. The number of events was square-root-transformed before analysis. For *D. aphidum*, data for the time spent in each activity were \log_{10} transformed. The number of events was square root transformed. No attacking and antennating occurred in hyperparasitoid females that were exposed to water for 4 days, so they were omitted from the analysis. All data transformations were conducted to satisfy the ANOVA assumptions of normality and equal variances. Normality was assessed by inspecting the residual plots generated by the ANOVA procedure. All analyses were carried out using GenStat 7.

3. Results

3.1. Parasitoid behavior

The time spent in each behavioral class and the number of events recorded for each class over a 20-min period differed significantly between fed and unfed treatments. The female parasitoids were mainly stationary, with unfed ones spending significantly more time in this condition than those fed on buckwheat ($F_{1,20} = 12.35$, $P = 0.002$). Fed females spent significantly more time antennating ($F_{1,20} = 13.45$, $P = 0.002$), attacking ($F_{1,20} = 7.83$, $P = 0.01$) and grooming ($F_{1,20} = 12.47$, $P = 0.002$) than did unfed females (Fig. 1).

For time spent walking there was a significant interaction between feeding and time treatments ($F_{1,20} = 8.48$, $P = 0.009$). Parasitoids fed for 24 h did not differ in this respect from unfed ones. However, after 48 h, fed parasitoids spent significantly more time walking than did those in the unfed treatment.

Table 1
Behavioral catalogue for *Aphidius ervi* and its hyperparasitoid, *Dendrocerus aphidum*, females.

Behavior	Description
Antennate	The parasitoid (hyperparasitoid) touches substrate with antennal tips while moving slowly and in varying directions. Associated with intensive searching activity.
Sting/attack	The parasitoid inserts its ovipositor into the aphid by curving its abdomen under its body. (the hyperparasitoid female extends the ovipositor and drills a hole through the mummy exoskeleton).
Groom	The parasitoid (hyperparasitoid) cleans its body by brushing antennae, head, thorax, wings, abdomen or ovipositor with its legs.
Walk	The parasitoid (hyperparasitoid) moves over the surface.
Stationary	The parasitoid (hyperparasitoid) is immobile.

Modified from Wang and Keller (2002).

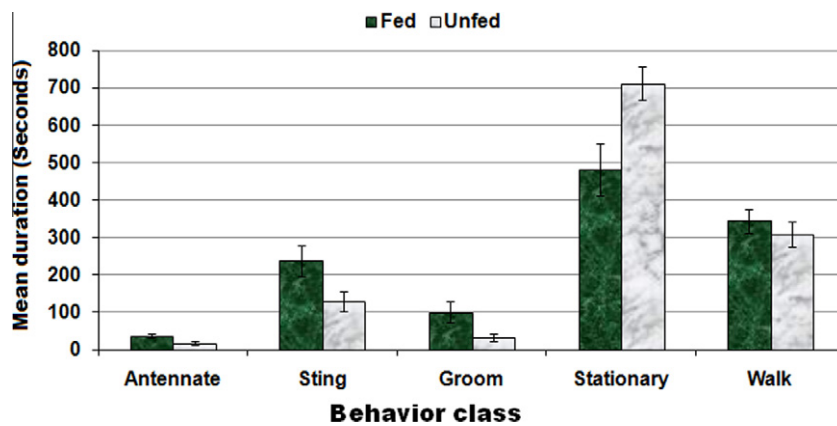


Fig. 1. Mean duration (sec) of activities by *Aphidius ervi* in fed and unfed treatments when attacking *Acyrtosiphon pisum* during a 20-min observation period. Values are the mean for observations at 24 and 48 h with six replicates.

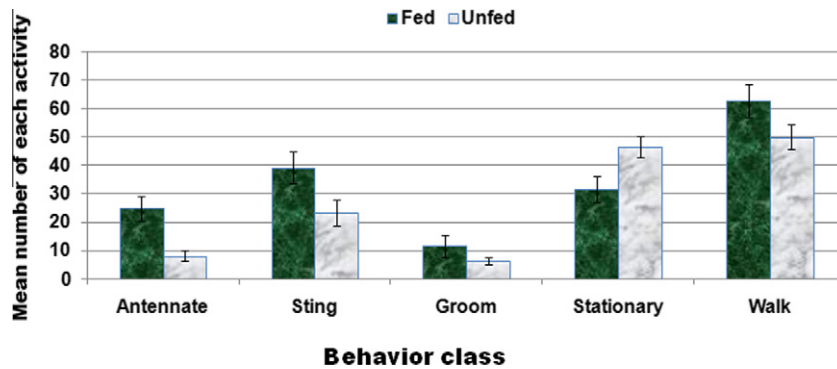


Fig. 2. Mean number of behavioral events for *Aphidius ervi* that had been supplied with floral nectar or left unfed and then exposed to *Acyrtosiphon pisum*, during one 20-min observation period. Values are the mean for observations at 24 and 48 h with six replicates.

Fed female parasitoids carried out significantly more antennating ($F_{1,20} = 36.55, P < 0.001$), attacking ($F_{1,20} = 9.57, P = 0.006$), grooming ($F_{1,20} = 4.47, P < 0.05$) and walking ($F_{1,20} = 5.15, P = 0.034$) events than did those in the unfed treatment. The unfed female parasitoids were stationary significantly more often than were fed female parasitoids ($F_{1,20} = 19.60, P < 0.001$) (Fig. 2). There were no significant interactions between feeding and time treatments in the amount of time spent on each behavior and the number of occurrences of each of the five behaviors; i. e., time has no effect on the behavior class. Instead, feeding on nectar was the main cause of the behavioral differences found.

3.2. Hyperparasitoid behavior

The female hyperparasitoids spent most of the time attacking, with no significant difference between the unfed and fed treatments ($F_{1,35} = 4.5, P = 0.98$). On the other hand, fed females spent a significantly longer time in antennating behavior than did unfed ($F_{1,35} = 16.88, P < 0.001$), but there was no significant difference between the treatments in time spent walking ($F_{1,40} = 0.04, P = 0.85$) (Fig. 3).

For time spent grooming or stationary, there was a significant interaction between feeding and time ($F_{3,40} = 6.05, P = 0.002$ and

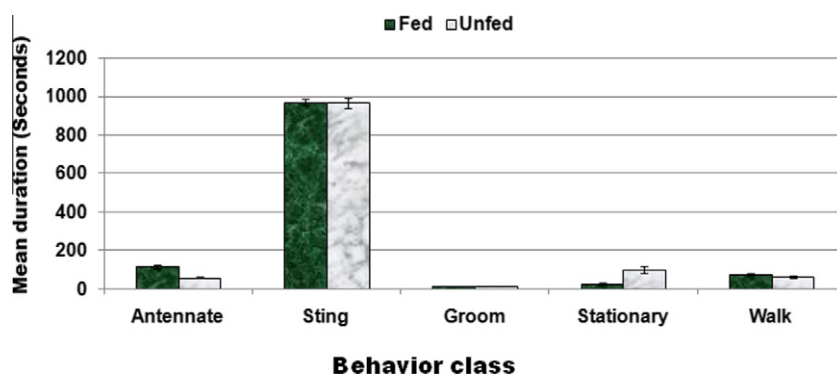


Fig. 3. Mean duration (sec) of activities by *Dendrocerus aphidum* in fed and unfed treatments when presented with *Acyrtosiphon pisum* mummies and observed for one 20-min period.

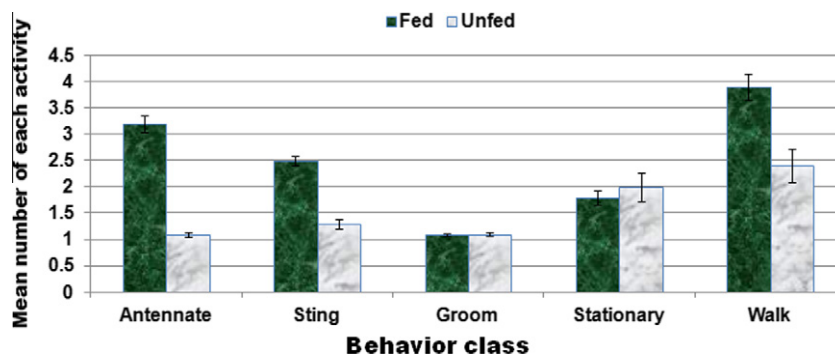


Fig. 4. Mean number of each activity by *Dendrocerus aphidum* in fed and unfed treatments when presented with *Acyrtosiphon pisum* mummies and observed for one 20-min period.

Table 2

Mean duration (sec) and number of attacks by *Aphidius ervi* and its hyperparasitoid, *Dendrocerus aphidum*, after exposure for 24 or 48 h (data combined here) in fed and unfed treatments. Behavior was recorded for a 20-min period.

Treatment	<i>A. ervi</i>		<i>D. aphidum</i>	
	Duration	Number	Duration	Number
Fed	238.0 ± 41.0	38.3 ± 5.6	1016.0 ± 12.5	2.3 ± 0.09
Unfed	130.0 ± 26.2	22.0 ± 4.5	951.4 ± 26.4	1.3 ± 0.08

$F_{3,40} = 3.15$, $P = 0.04$, respectively). Providing hyperparasitoids with buckwheat for up to 72 h had little or no effect on the time spent grooming or stationary when compared to unfed hyperparasitoids. However, where exposure was for 96 h, the unfed females spent significantly more time grooming and stationary than fed females.

Fed female hyperparasitoids stung more frequently ($F_{1,35} = 40.50$, $P < 0.001$) than did those in the unfed treatment, but there was no significant difference in the frequency of grooming ($F_{1,40} = 1.45$, $P = 0.24$) (Fig. 4). Stationary behavior of female hyperparasitoids was significantly more frequent in the unfed than fed treatment ($F_{3,40} = 7.91$, $P < 0.001$), with the difference being greatest among hyperparasitoids exposed to the treatments for 96 h. The number of antennation events was significantly higher for fed than unfed hyperparasitoids, with the difference being greatest after 72 h ($F_{2,35} = 3.67$, $P = 0.04$) (Fig. 4). After 72 h, fed hyperparasitoids had significantly more walking events than the unfed hyperparasitoids, but the trend was reversed after 96 h, with fewer walking events for fed than for unfed hyperparasitoids (Fig. 4). There was however a significant interaction between feeding and time in the number of walking events ($F_{3,40} = 5.27$, $P = 0.004$).

3.3. Comparison of parasitoid and hyperparasitoid behavior

Since parasitoids were exposed to water or buckwheat for just 24 or 48 h, comparison of parasitoid and hyperparasitoid data is based only on these periods. *A. ervi* females needed shorter periods of time to attack their hosts compared with *D. aphidum*, either in fed or unfed treatments (Table 2). Overall, the parasitoids attacked more hosts than did the hyperparasitoids, even in the unfed treatment. Fed parasitoids spent almost twice as much time attacking and also carried out almost twice as many attacks as did unfed ones. However, fed hyperparasitoids attacked twice as many hosts within the same period of time as did unfed (Table 2). Also, the response to buckwheat feeding differed between the parasitoids and hyperparasitoids, with fed parasitoids having a greater attack rate (number of attacks per minute) than did unfed (two hosts per min for fed and one host per min for unfed), while the attack rate for hyperparasitoids was 0.1 host per min for fed and 0.05 host per min for unfed treatments.

4. Discussion

Plant diversity can influence the aphid-parasitoid-hyperparasitoid interaction through trophic interactions. The ability of parasitoids to find and attack hosts has always been considered an important feature when evaluating their efficiency at suppressing pests in biological control programs (Vinson, 1977; Powell, 1986; Bigler, 1994; Le Ralec et al., 2005). In fact, parameters describing parasitoid searching efficiency have long been components of difference-equations and other models of parasitoid-host dynamics (Zhu and Zhao, 2007). Those models focus on inter-generational parasitoid/host population stability through density-dependent negative feedback processes in relatively stable ecosystems (e.g., forests). However, in agroecosystems, short-term changes in parasitoid 'fitness' can potentially have a significant impact on pest population suppression. In many annual cropping systems, pests and their natural enemies may pass through only one or a few generations, and inter-generational population stability is not likely under these conditions, especially with a rapidly-maturing host plant (Landis et al., 2000). The work presented here illustrates how floral nectar can affect such changes in parasitoid 'fitness' in short-lived agro-ecosystems.

This study showed that both *A. ervi* and *D. aphidum* females differed substantially in their host-searching behavior, depending on whether or not they had previous access to floral nectar. Chippendale (1978) reported that sugar deprivation affects not only the mobility of insects but also the functioning of the neural network important for information processing. In the present experiments, fed and unfed *A. ervi* parasitoids allocated most of their time to being stationary or walking, a similar pattern to that seen from the data of Wang and Keller (2002). Fed *A. ervi* females spent longer in antennation, attacking, grooming and walking but less time being stationary than did unfed parasitoids. Previous work had shown that parasitoids with access to floral nectar matured more eggs and parasitized more aphids (Araj et al., 2006, 2008, 2009) than did unfed parasitoids. Aphid honeydew has also been shown to improve parasitoid searching efficiency. For example, *Aphidius nigripes* Ashmead (Hymenoptera: Aphididae) had longer searching times, visited more leaves and spent more time

per leaf in response to honeydew than it did without access to honeydew (Cloutier and Bauduin, 1990). Also, Mehrnejad and Copland (2006) found that searching time, walking, antennal drumming and ovipositor probing of *Psyllaephagus pistaciae* Ferrière (Hymenoptera: Encyrtidae), which is a parasitoid of the pistachio psylla, *Agonoscaena pistaciae* Burckhardt and Lauterer (Hemiptera: Psylloidea: Rhinocolinae), were all increased in rate when the parasitoid encountered honeydew-contaminated areas on pistachio leaves.

In the present study, aphid mummies were provided as hosts for *D. aphidum* females without the presence of live aphids or adult parasitoids at the same time. Other studies have shown however, that aphids respond to the presence of hyperparasitoids with an increased reproductive rate (Boenisch et al., 1997) and some aphid hyperparasitoids produce kairomones to disperse parasitoids (Holler et al., 1994), which could lead to reduced aphid parasitism.

It is obvious in this study that buckwheat nectar altered the behavior of *A. ervi* as well as that of *D. Aphidum*. Furthermore, Vattala et al. (2006) suggested that nectar quality, specifically the sucrose/(glucose + fructose) ratio of the nectar, had a strong effect on *Microctonus hyperodae* Loan longevity. Laboratory bioassays to test the effect of different types of artificial nectars on insects, ideally constructed initially based on the four main nectar categories of Baker and Baker (1983) could be useful. This classification had four ratio classes: hexose-rich (<0.1), hexose-dominant (0.1–0.49), sucrose-rich (0.5–0.99) and sucrose-dominant (>0.99). However, recent work by Tompkins et al. (2010) indicated that such ratios do not influence parasitoid longevity. This implies that factors such as diurnal patterns of nectar availability and flower morphology may have a more important role.

Access to floral nectar resources from buckwheat significantly changed the behavior of *A. ervi* as well as that of *D. aphidum*, compared with unfed treatments. This suggests that knowledge of the factors that enhance the searching behavior of parasitoids and hyperparasitoids has important practical implications when attempts are made to increase functional biodiversity in agriculture to improve biological control success (Jonsson et al., 2008; Wade et al., 2008).

To understand more fully the relative effects of floral nectar on more than one trophic level, a combination of field and laboratory work would ideally be needed, supported by appropriate modeling (e.g., Kean et al. (2003)) combined with selective biodiversity which favors the targeted natural enemy trophic level or guild (Baggen et al., 1999; Lavandero et al., 2006).

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