

Optimal foraging by an aphid parasitoid affects the outcome of apparent competition

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Abstract. 1. Apparent competition is an indirect, negative interaction occurring between two or more host species, mediated by a shared parasitoid. Host species' population growth rates, parasitoid attack rates, and parasitoid population size can mediate the outcomes of apparent competition. It has also been suggested that optimal foraging by a natural enemy can influence the outcome of apparent competition, resulting in increased suppression of the optimal host.

2. While this has been shown in theory, to date no studies have empirically tested the link between parasitoid optimal foraging behaviour and the outcome of apparent competition.

3. The present study examined how optimal foraging behaviour influences the outcome of apparent competition in an aphid banker plant system. First, *Aphidius colemani* Viereck's preference for *Myzus persicae* Sulzer or *Rhopalosiphum padi* L., the non-pest host on the banker plant, was examined, and then the difference in *M. persicae* suppression in the presence and absence of *R. padi* was assessed.

4. It was found that optimal foraging behaviour led female *A. colemani* to prefer *M. persicae* over *R. padi*, due to increased offspring survival and female size. Consequently, optimally foraging *A. colemani* parasitised significantly more *M. persicae* in the presence of both aphid hosts than in the presence of *M. persicae* alone.

5. Understanding the interaction between optimal foraging and apparent competition has important implications for biological control of arthropod pests and could help to predict the outcome of biological control programmes.

Key words. *Aphidius colemani*, banker plant, biological control, fitness, *Myzus persicae*, *Rhopalosiphum padi*.

Introduction

Apparent competition is an important mechanism structuring herbivore communities in natural and managed ecosystems (Holt & Lawton, 1994; Morris *et al.*, 2005). Apparent competition is the indirect negative interaction between two hosts mediated by a shared parasitoid. The host species in a two-host system can support more parasitoids than one host species in a one-host system. Consequently, the parasitoid population in a two-host system can grow larger and parasitise more of each host species than would be the case in a one-host system

(Bonsall & Hassell, 1997). In some cases, higher parasitism will be evenly distributed across host populations, resulting in equally reduced host species populations (Holt, 1977). More often apparent competition is asymmetrical, with one host parasitised more than the other. In either case, the host species able to support the highest parasitoid population will become more abundant than the other, which may be excluded from the system (e.g. Settle & Wilson, 1990; Holt & Lawton, 1994; Bonsall & Hassell, 1998).

Over two decades ago, Holt and Kotler (1987) predicted that apparent competition should be affected by natural enemy foraging behaviour. More specifically, they suggested that natural enemies forage in accordance with optimal foraging theory (Holt & Kotler, 1987), which predicts that female parasitoids should selectively oviposit into hosts that result in

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the greatest reproductive success (Charnov & Skinner, 1985). This suggests that in a one-parasitoid, two-host system, fitness of parasitoid offspring should play a role in host selection and consequently may determine which host will be excluded from the system. While much theoretical information is available on apparent competition (Holt, 1977; Holt & Lawton, 1994) and optimal foraging (Hughes, 1979; Charnov & Stephens, 2012), to our knowledge, no studies other than Veech (2001) have investigated the link between natural enemy optimal foraging behaviour and the outcome of apparent competition.

Apparent competition is a particularly important concept to understand when developing banker plant systems for conservation biological control (Frank, 2010; Huang *et al.*, 2011). Banker plants are non-crop plants used to support natural enemy abundance and reproduction by providing them with an alternative host or food source (Frank, 2010). Typically, aphid banker plant systems consist of grain plants infested with bird cherry oat aphids, *Rhopalosiphum padi* L. (Hemiptera: Aphididae), which only feed on monocots and therefore are not a pest in most greenhouses (Frank, 2010). *Rhopalosiphum padi* share the parasitoid *Aphidius colemani* Viereck (Hymenoptera: Braconidae) with important pests such as the green peach aphid, *Myzus persicae* Sulzer (Hemiptera: Aphididae). By providing *A. colemani* with two hosts, the parasitoid population can grow larger than it would in a one-host system (e.g. augmentative biological control), and will not become extinct if the pests become extinct (Holt & Lawton, 1994). Asymmetric apparent competition, which increases parasitism of pest aphids, should increase biological control. This would occur if parasitoids prefer the pest (Bonsall & Hassell, 1998). However, the availability of the alternative non-pest hosts can also reduce parasitism of the pest host if the parasitoid prefers the non-pest or parasitises both hosts equally (Holt & Lawton, 1994; Bonsall & Hassell, 1998).

In this paper, we examine how parasitoid optimal foraging behaviour affects parasitoid preference and the outcome of apparent competition by comparing *M. persicae* suppression in a two-host banker plant system with that of a one-host augmentative biological control system. Ode *et al.* (2005) found that parasitoid offspring survival and female sex ratio were significantly lower on *R. padi* than on *M. persicae*, suggesting that it is an inferior host for *A. colemani*. Similarly, Bilu *et al.* (2006) found that *A. colemani* preferred *M. persicae* to *R. padi*, and suggested that *R. padi* was the least suitable host for *A. colemani* as determined by offspring body size. Therefore, we hypothesise that optimally foraging *A. colemani* will prefer *M. persicae* to *R. padi*, resulting in greater *M. persicae* suppression in the two-host banker plant system than in the one-host augmentative biological control system. In addition, although it has also been suggested that parasitoids prefer their natal host (Messing, 1995; Storeck *et al.*, 2000; Bilu *et al.*, 2006), this is not the case for parasitoids reared on *R. padi* (Bilu *et al.*, 2006). To test optimal foraging by *A. colemani*, we first determined how natal host and offspring fitness influence *A. colemani* host preference in Petri dish and caged choice experiments. To determine how optimal foraging affects the outcome of apparent competition, we compared *M. persicae* suppression in our two-host banker plant system

with that in a one-host augmentative biological control system with *M. persicae* and *A. colemani*.

Materials and methods

Effect of offspring fitness on Aphidius colemani host preference

Study system. All *Aphidius colemani* used in this experiment originally came from Koppert Biological (Aphipar) (Howell, Michigan). Three *A. colemani* sources were used: Koppert Biological; *A. colemani* reared on *R. padi* on barley (*Hordeum vulgare* 'Price'); and *A. colemani* reared on *M. persicae* on ornamental Black Pearl pepper plants (*Capsicum annuum* 'Black Pearl'). These three sources will be referred to as 'store', 'barley' and 'pepper', respectively. After receiving the parasitoids from Koppert Biological, we reared pepper and barley parasitoids on their respective host aphid and plant for at least 1 month (around two to three generations) prior to the initiation of the experiments. Store parasitoids purchased from Koppert Biological were reared on unknown host plants and aphids and were used within 48 h of receipt. Separate parasitoid-free aphid colonies were also started: *M. persicae* and *R. padi* were started from field-collected aphids and maintained in the laboratory on pepper and barley plants, respectively. Aphid and parasitoid colonies were maintained in separate incubators at 25 °C and 70–80% RH with LD 16:8.

Black Pearl pepper plants were obtained from C. Raker and Sons, Inc (Litchfield, Michigan) as plugs (128 plugs < 7 cm in height). They were repotted into 15.2-cm-diameter pots filled with Fafard 2P soil mix (Agawam, Massachusetts) and 8.86 g of Scotts Osmocote (N-P-K, 14-14-14) fertiliser (Marysville, Ohio) per pot. All pepper plants were 3–4 months old. Barley plants were started by planting 14 g of barley seeds into 15.2-cm-diameter pots filled with the same Fafard 2P soil mixed with Scotts Osmocote as used for the pepper plants, and left to grow for 3 weeks before the start of the experiment.

Effect of natal host on parasitoid host preference. To determine if the *A. colemani* natal host affects host preference, we conducted a choice assay by presenting *A. colemani* with *M. persicae* on pepper and *R. padi* on barley, and monitoring parasitoid probing behaviour. Before the experiment began, mummies were removed from barley and pepper plants and placed into separate 61 × 61 cm cages containing a 25% sucrose-water solution. The same procedure was taken upon receipt of store mummies from Koppert Biological. Parasitoids were left in the cages in the laboratory at 24 °C, to emerge, eat, and mate for 48 h.

We began by placing 1.5-cm-long segments of Black Pearl pepper and barley leaves 12 cm apart in a 14.5-cm-diameter Petri dish. Two *M. persicae* and two *R. padi* were then transferred onto the pepper and barley leaves, respectively. We left the aphids in the Petri dish in the laboratory for 1 h before starting the experiment. During that hour, female *A. colemani* were randomly aspirated from their respective cages.

After 1 h, one of either pepper, barley or store parasitoids was placed in the centre of the Petri dish and observed for 30 min to record which species of aphid was first probed ('*R. padi*' or '*M. persicae*'). This experiment was replicated 30 times for each parasitoid source, resulting in the use of 90 female *A. colemani*. Thirteen store, 20 pepper and 16 barley parasitoids did not probe an aphid within 30 min, and were removed from the preference analysis, leaving 17, 10, and 14 replicates, respectively. However, all 30 replicates were used to determine the percentage of probing *A. colemani* from each source.

A Pearson's χ^2 test was then used to compare the frequency that parasitoids reared on store, barley and pepper probed *M. persicae* or *R. padi*. A second χ^2 test was used to determine the frequency that parasitoids reared on store, barley and pepper probed at *M. persicae* or *R. padi* once during the experiment.

Effect of offspring fitness on parasitoid host preference. To determine the effect of offspring fitness on *A. colemani* host choice, we presented *A. colemani* from all three sources (store, barley and pepper) with *M. persicae* on pepper and *R. padi* on barley plants. We allowed parasitism to occur and then measured life-history traits of the emerging offspring. Before the experiment began, mummies were removed from barley and pepper plants and placed into separate 61 × 61 cm cages, at 24 °C, which contained a 25% sucrose-water solution. The same procedure was followed upon receipt of mummies from Koppert Biological. Parasitoids were left in the cages to emerge, eat and mate for < 72 h.

Our experimental arena consisted of 24 cages (61 × 61 cm each) built using PVC pipes and organdi fabric. We placed one barley and one pepper plant 34 cm apart in each cage. One day before the start of the experiment, 20 *M. persicae* and 20 *R. padi* were placed on the pepper and barley plants, respectively. The next day, female *A. colemani* were aspirated from their respective cages and transported in their individual, labelled, aspirator vials to the greenhouse. Each aspirator vial containing one female parasitoid was placed in between the two plants in the cage and opened so that the parasitoid could fly out. Parasitoids were allowed to move around the cage for 4 h, after which they were removed to end the experiment.

The plants were left in their cages for 7 days, at which time we removed them, counted all mummies, and determined their life-history traits (see the following section for a description of how this was done). This experiment was replicated 40 times for barley and store sourced parasitoids, and 51 times for pepper sourced parasitoids. Thirty-five of the pepper-, 15 of the barley-, and eight of the store-sourced parasitoids did not parasitise any aphids and therefore were removed from the preference analysis. However, all replicates were used to determine the percentage of *A. colemani* that parasitised aphids from each source.

A Pearson's χ^2 test was then used to compare the frequency that parasitoids reared on store, barley or pepper parasitised *M. persicae* or *R. padi*. A second χ^2 test was used to determine

the frequency that *A. colemani* reared on store, barley or pepper parasitised any aphid within the allotted time. A two-way ANOVA was used to determine the effect of parasitoid source and chosen host on the mean number of emerging females per host species. The mean number of emerging females was log + 1-transformed to obtain normality. χ^2 tests were performed to determine if sex ratio and percentage emergence were affected by parasitoid source and host choice. A three-way ANOVA was used to determine the effect of source, chosen host, and sex on parasitoid size.

Determining parasitoid life-history traits

We first removed the mummies by gently lifting them off the leaves of their host plant using a small paintbrush. We then placed them into labelled vials, which were stopped with a cotton ball to prevent parasitoids from flying out upon emergence. Parasitoids were reared out of the mummies in the laboratory, and preserved in 90% alcohol upon emergence. To assess offspring fitness, we measured parasitoids' size and sex ratio and adult parasitoid percentage emergence. We examined each parasitoid under a dissecting microscope with an ocular micrometer to determine its gender and measure the length of the left hind tibia. Parasitoid percentage emergence was determined by dividing the total number of emerged parasitoids by the total number of mummies.

Effect of parasitoid optimal foraging on the outcome of apparent competition

Study system. As in the previous experiment, all *A. colemani* used in this experiment originally came from Koppert Biological. *Aphidius colemani* were used either directly from Koppert Biological or from a laboratory colony of *A. colemani* reared on *R. padi* on barley (*H. vulgare* 'Price'). These two sources will be referred to as 'store' and 'barley', respectively. The barley parasitoids had been reared on *R. padi* for over 4 months (around nine generations) before the experiment began. Store parasitoids, which were reared on unknown aphid and plant hosts, were used within 24 h of receipt of the parasitoids. We used *M. persicae* and *R. padi* from laboratory colonies that were started from field-collected aphids. All insects were reared on their respective plant/aphid in incubators at 25 °C and 70–80% RH with LD 16:8. Under such conditions, *M. persicae* generation time is, on average, 13.8 days (Satar *et al.*, 2008). *Aphidius colemani* take, on average, 12–13 days to develop into adults, which can live between 5 and 7.4 days (Kalule & Wright, 2005).

All Black Pearl pepper plants (*Capsicum annum* 'Black Pearl') were obtained from cuttings. Source plants were cut 5–10 cm below the bud. The cut tips were then dipped into 'Rhizopon AA Dry Powder Rooting Hormone #1' (active ingredient: 0.1% 3-indolebuteric acid; Earth City, Missouri) and potted into a sifted Fafard 2P mix for germination. All cuttings were planted in 48 pot trays (56 cm × 25.5 cm tray). The cuttings were left to root for 6 weeks before they were transplanted into 6-inch (15.2 cm) pots containing

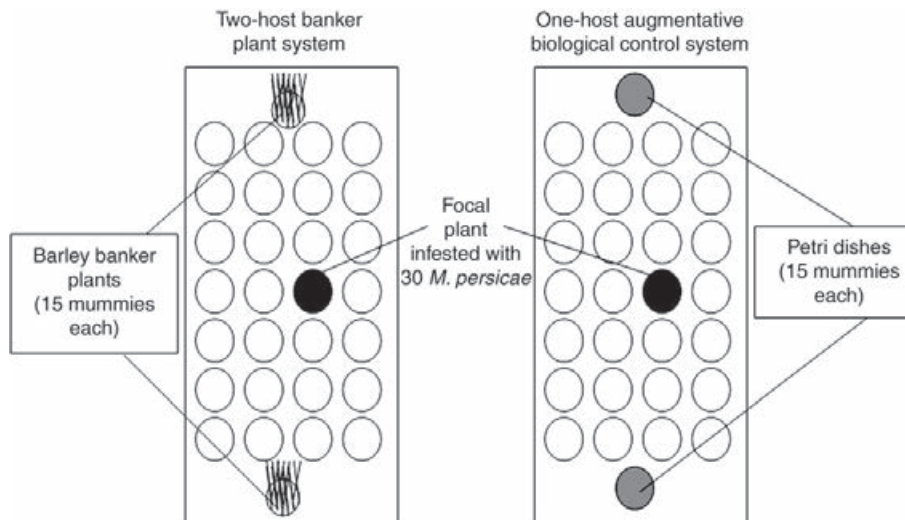


Fig. 1. Greenhouse design for both bays: two-host banker plant system and one-host augmentative biological control system. Empty circles represent pepper plants that were uninfested at the beginning of the experiment. Black circles represent infested ‘focal’ plants, which had 30 *Myzus persicae* mummies. A parasitoid source is located on either end of the greenhouse bench: barley banker plant and Petri dish with mummies from Koppert Biological.

Farfard 2P soil mix and 8.86 g of Scotts Osmocote (N-P-K: 14-14-14) fertiliser per pot. All pepper plants were between 2 and 3 months old. Barley plants were started by planting 14 g of barley seeds into 15.2-cm-diameter pots filled with the same Farfard 2P soil mixed with Scotts Osmocote. One week after seeding, barley plants were moved into the incubator containing the *R. padi* and *A. colemani* colonies. This allowed the barley plants to become infested with both aphids and parasitoids. All barley plants were 2 weeks old at the start of the experiments.

Experimental design. Two greenhouses were arranged in the same way as Vásquez *et al.* (2006). Part of each greenhouse was partitioned into two bays (2.08 × 6.1 m) using Pro19 grade AgroFabric (Alpharetta, Georgia), which allowed air circulation between the bays but no movement of aphids or parasitoids. Within each greenhouse, we used one bay for the two-host (*M. persicae*, *R. padi*) banker plant system and the other for the one-host (*M. persicae*) augmentative biological control system, such that one greenhouse was used for one replication. Two days before the start of this experiment, two pepper plants were infested with 30 *M. persicae*. These infested plants (‘focal plants’) were kept in an incubator at 25 °C and 70–80% RH with LD 16:8 until the experiment began. On the first day of the experiment, 27 pepper plants and one focal pepper plant were placed in each bay (Fig. 1). The focal plants were used to simulate an aphid outbreak on the pepper plants in the greenhouse. In the two-host banker plant bay, we placed two barley plants containing 11–42 *R. padi* and 15 *A. colemani* mummies per plant at each end of the greenhouse bench. In the one-host augmentative biological control bay, two Petri dishes containing 15 store mummies were placed at each end of the greenhouse bench. The barley banker plants and Petri

dishes with *A. colemani* mummies acted as sources for the parasitoids. Each of the 28 pepper plants were numbered in order to facilitate counting of aphids and monitoring of their movement within each bay.

In addition to monitoring aphid populations, we collected data on parasitoid life-history traits before and after the experiment in order to confirm our findings from the first two experiments. On the first day of the experiment, we placed 30 barley mummies and 30 store mummies in separate vials with cotton balls as stoppers. Mummies were removed from barley plants and barley and store parasitoid life-history traits were determined as described earlier.

On the seventh, 14th, 21st and 28th days of the experiment, all aphids and mummies were counted on all the pepper and barley plants in each bay. At the end of the experiment (day 28), we removed all mummies and determined the parasitoid life-history traits. This allowed us to determine what the parasitoids’ life-history traits were after parasitism of *M. persicae* on pepper. Using pre- and post-parasitism life-history traits allowed us to understand what drives parasitoid preference for one host over the other. For example, comparing life-history traits of parasitoids emerging from *R. padi* on barley with those emerging from *M. persicae* on pepper in the two-host banker plant system allowed us to understand what drove barley parasitoids to parasitise *M. persicae* instead of *R. padi*, their natal host.

This experiment was conducted four times: on 17 February and 30 March in one greenhouse and on 16 March and 27 April in the second greenhouse (four replicates per treatment). However, one replicate of each treatment had zero parasitism throughout the experiment, and was therefore removed from the analysis. As such, we had three replicates for each of the two treatments (two-host banker plant system and one-host augmentative biological control system).

To determine if apparent competition increased suppression of the pest aphid, *M. persicae*, we compared aphid and mummy abundance and percentage parasitism in the two-host banker plant system with those in the one-host augmentative biological control system. We used three mixed-effects ANOVAs to determine how time and treatment interacted to affect aphid abundance, mummy abundance, and percentage parasitism. Percentage parasitism was calculated by dividing the total number of parasitised *M. persicae* (mummies) by the total number of parasitised and unparasitised *M. persicae*. To obtain normality, aphid abundance was log-transformed, and mummy abundance was log + 1-transformed. To determine if optimal foraging behaviour was taking place in the two-host banker plant system, we used a two-way ANOVA to determine if barley, store and pepper (both one-host and two-host) parasitoid size varied with sex and source (barley, store). Due to the small sample size, a Mann–Whitney *U*-test was used to determine if parasitoid percentage emergence was affected by treatment and source. Lastly, a second Mann–Whitney *U*-test was used to determine if parasitoid female sex ratio was affected by treatment and source.

Results

Effect of offspring fitness on *Aphidius colemani* host preference

Effect of natal host on parasitoid host preference. When given the choice between *M. persicae* on pepper or *R. padi* on barley, pepper parasitoids probed *M. persicae* at a significantly higher frequency than did barley and store parasitoids ($\chi_2^2 = 7.1238$, $P = 0.0284$) (Fig. 2a). Not all 30 parasitoids used from each source probed aphids. Store parasitoids probed aphids at a significantly higher frequency than did pepper parasitoids ($\chi_1^2 = 5.4$, $P = 0.0201$), but no significant difference in probing frequency was found between store and barley parasitoids, or between barley and pepper parasitoids ($\chi_1^2 = 0.625$, $P = 0.4292$ and $\chi_1^2 = 1.6968$, $P = 0.1927$, respectively) (Fig. 2b).

Effect of offspring fitness on parasitoid host preference. As in the previous experiment, when given the choice between *M. persicae* on pepper or *R. padi* on barley, pepper parasitoids parasitised *M. persicae* at a significantly higher frequency than did barley and store parasitoids ($\chi_2^2 = 38.85$, $P < 0.0001$) (Fig. 3a). Barley and store parasitoids showed no preference for either host ($\chi_1^2 = 0.0068$, $P = 0.9343$). Of the 40 barley and store parasitoids and the 51 pepper parasitoids used in the experiment, store parasitoids parasitised aphids at a higher frequency than barley and pepper parasitoids ($\chi_1^2 = 7.5839$, $P = 0.0059$ and $\chi_1^2 = 7.0286$, $P = 0.0080$, respectively) (Fig. 3b). Barley and pepper parasitoids parasitised aphids at the same frequency ($\chi_1^2 = 0.0068$, $P = 0.9343$).

The frequency of emerging store and barley parasitoids did not differ when emerging from *M. persicae* (on pepper) and *R. padi* (on barley) ($\chi_1^2 = 0.0336$, $P = 0.85$ and

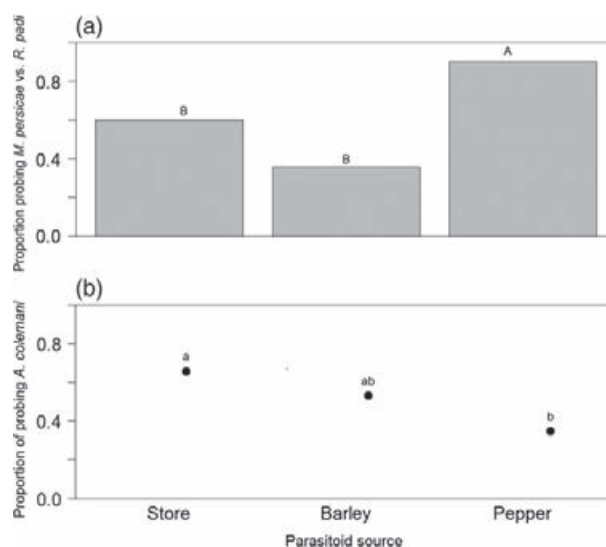


Fig. 2. (a) The effect of parasitoid source on the proportion of parasitoids probing *Myzus persicae* on Black Pearl pepper plants instead of *Rhopalosiphum padi* on barley, over a 30-min period. Bars with different letters are significantly different at the $P < 0.05$ level. (b) The effect of parasitoid source on the proportion of *Aphidius colemani* that probed an aphid out of the 30 replicates for each treatment. Dots with different letters are significantly different at the $P < 0.05$ level. Frequency data were analysed with χ^2 tests, but as replication varied per source, data are shown as proportions.

$\chi_1^2 = 0.0005$, $P = 0.9822$, respectively). On the other hand, a significantly higher frequency (31% greater) of pepper parasitoids emerged from *M. persicae* than from *R. padi* ($\chi_1^2 = 10.1446$, $P = 0.0015$), indicating that *R. padi* is a less suitable aphid host for pepper parasitoids than *M. persicae* (Table 1). The mean number of females emerging did not differ among parasitoids reared on either host ($F_{2,59} = 2.24$, $P = 0.12$ and $F_{1,59} = 0.15$, $P = 0.70$, respectively) (Table 1). There was also no significant interaction between host and source on the mean number of emerged female parasitoids ($F_{2,59} = 0.79$, $P = 0.46$). The frequency of female and male emergence did not differ significantly across sources for each host (*R. padi*: $\chi_2^2 = 1.9225$, $P = 0.3824$; *M. persicae*: $\chi_2^2 = 1.1842$, $P = 0.5532$) (Table 1).

Parasitoid size was significantly affected by parasitoid sex and chosen host ($F_{1,375} = 8.94$, $P = 0.003$ and $F_{1,375} = 91.47$, $P < 0.0001$, respectively); however, there was no significant main effect of source ($F_{2,375} = 2.69$, $P = 0.07$). There was a significant interaction between parasitoid source and sex on parasitoid size ($F_{2,375} = 3.02$, $P = 0.05$), wherein pepper parasitoids were significantly larger than barley parasitoids, but only female pepper parasitoids were larger than store parasitoids. The interaction among sex, host, and source was not significant ($F_{2,375} = 0.27$, $P = 0.76$) (Table 1), nor were the interactions between sex and host or host and source ($F_{1,375} = 0.88$, $P = 0.35$ and $F_{2,375} = 0.87$, $P = 0.42$, respectively).

Table 1. *Aphidius colemani* life-history traits after parasitism of *Myzus persicae* on pepper and *Rhopalosiphum padi* on barley. The three parasitoid sources were as follows: Koppert biological (store); reared on *R. padi* on barley (barley); and reared on *M. persicae* on pepper (pepper). Pepper parasitoids experienced reduced offspring survival on *R. padi*.

| Source | Store parasitoids | | Barley parasitoids | | Pepper parasitoids | |
|------------------------|------------------------------|----------------|--------------------|----------------|--------------------|----------------|
| | <i>M. persicae</i> | <i>R. padi</i> | <i>M. persicae</i> | <i>R. padi</i> | <i>M. persicae</i> | <i>R. padi</i> |
| Chosen host | <i>M. persicae</i> | <i>R. padi</i> | <i>M. persicae</i> | <i>R. padi</i> | <i>M. persicae</i> | <i>R. padi</i> |
| Percentage emergence | 71% a | 69.8% a | 71.6% a | 73.6% a | 69.5% a | 21% b |
| Female:total emerged | 32:78 a | 29:67 a | 58:101 a | 35:81 a | 36:66 a | 2:3 a |
| Mean females per plant | 3.2 ± 1.4 a | 1.45 ± 0.4 a | 3.63 ± 0.8 a | 2.5 ± 0.5 a | 1 ± 1 a | 2.6 ± 0.6 a |
| Size (mm) | No host × source interaction | | | | | |

Means with different letters next to them are significantly different at the $P \leq 0.05$ level.

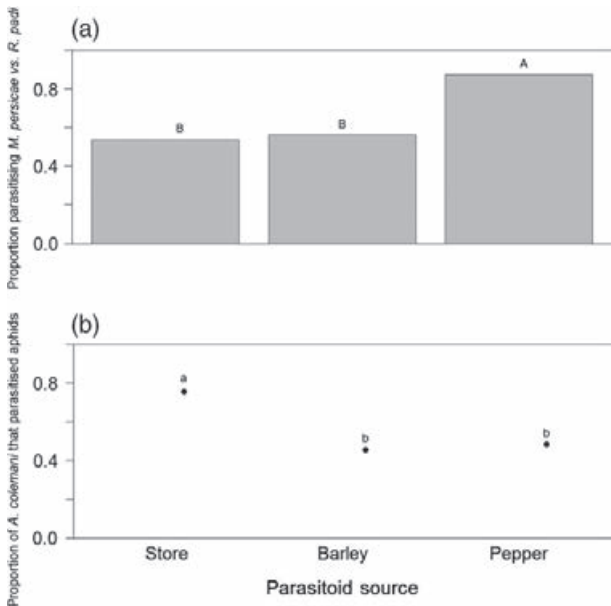


Fig. 3. (a) The effect of parasitoid source on the proportion of *Aphidius colemani* that parasitised *Myzus persicae* on pepper instead of *Rhopalosiphum padi* on barley. Bars with different letters are significantly different at the $P < 0.05$ level. (b) The effect of parasitoid source on the proportion of *A. colemani* (out of the 40 replicates for store and barley parasitoids and the 52 replicates for pepper parasitoids) that parasitised an aphid. Dots with different letters are significantly different at the $P < 0.05$ level. Frequency data were analysed with χ^2 tests, but as replication varied per source, data are shown as proportions.

Effect of parasitoid optimal foraging on the outcome of apparent competition

There were no significant main effects of time or treatment on aphid abundance ($F_{1,18} = 2.77$, $P = 0.11$, $F_{1,18} = 3.21$, $P = 0.09$, respectively). There was a significant interaction between time and treatment on aphid abundance on the pepper plants ($F_{1,18} = 4.31$, $P = 0.05$), wherein aphid abundance in the one-host augmentative biological control system ('one host') was at least double the aphid abundance in the two-host banker plant system ('two-host') from days 14 to 28 (Fig. 4a). Mummy abundance on the pepper plants was also significantly affected by time, ($F_{1,18} = 11.92$, $P = 0.003$) (Fig. 4b),

but was not significantly affected by treatment or the interaction between treatment and time ($F_{1,18} = 0.33$, $P = 0.57$ and $F_{1,18} = 0.48$, $P = 0.50$, respectively). Percentage parasitism was significantly affected by treatment ($F_{1,18} = 4.22$, $P = 0.05$), wherein a significantly higher percentage parasitism was found in the two-host treatment than in the one-host treatment. The main effect of time also significantly affected percentage parasitism ($F_{1,18} = 8.66$, $P = 0.009$), but no significant interaction between time and percentage parasitism was found ($F_{1,18} = 2.70$, $P = 0.11$) (Fig. 4c).

There were significant main effects of parasitoid sex and source on parasitoid size ($F_{1,365} = 8.425$, $P = 0.004$ and $F_{3,365} = 108.896$, $P < 0.0001$, respectively). There was also a significant interaction between parasitoid sex and source on parasitoid size ($F_{3,365} = 4.471$, $P = 0.004$) (Fig. 5), wherein female store and barley parasitoids were significantly smaller than those emerging post-parasitism of *M. persicae* on pepper. This suggests that pepper-reared female parasitoids have higher fitness than store and barley female parasitoids. Pepper-reared male parasitoids collected from pepper plants in the one-host augmentative biological control system did not differ in size from the store and the barley parasitoids. Pepper-reared male parasitoids collected from pepper plants in the two-host banker plant system were larger than store and barley parasitoids.

Mann–Whitney U -tests showed no significant difference between the percentage emergence of parasitoids from mummies collected from barley and pepper plants (two-host) ($W = 5$, $P = 0.86$) (Fig. 6). There was also no difference in percentage emergence between mummies collected from barley and pepper (one-host) plants ($W = 2.5$, $P = 0.48$) (Fig. 6). No significant difference in percentage emergence was found between mummies collected from pepper in the two-host system and those from pepper in the one-host system ($W = 4$, $P = 0.80$), nor was there one between mummies collected from store and pepper (two-host) ($W = 8$, $P = 0.48$). There was a significantly higher parasitoid percentage emergence from pepper (one-host) mummies than from store mummies ($W = 8$, $P = 0.03$). There was also a significantly higher parasitoid percentage emergence from barley mummies than from store mummies ($W = 16$, $P = 0.02016$).

Parasitoid female sex ratio differed significantly between the barley (0.68 ± 0.17) and store (0.46 ± 0.05) parasitoids ($W = 0$, $P = 0.05$) and between the barley and pepper (one-host) (0.34 ± 0.18) parasitoids ($W = 9$, $P = 0.05$). Parasitoid female

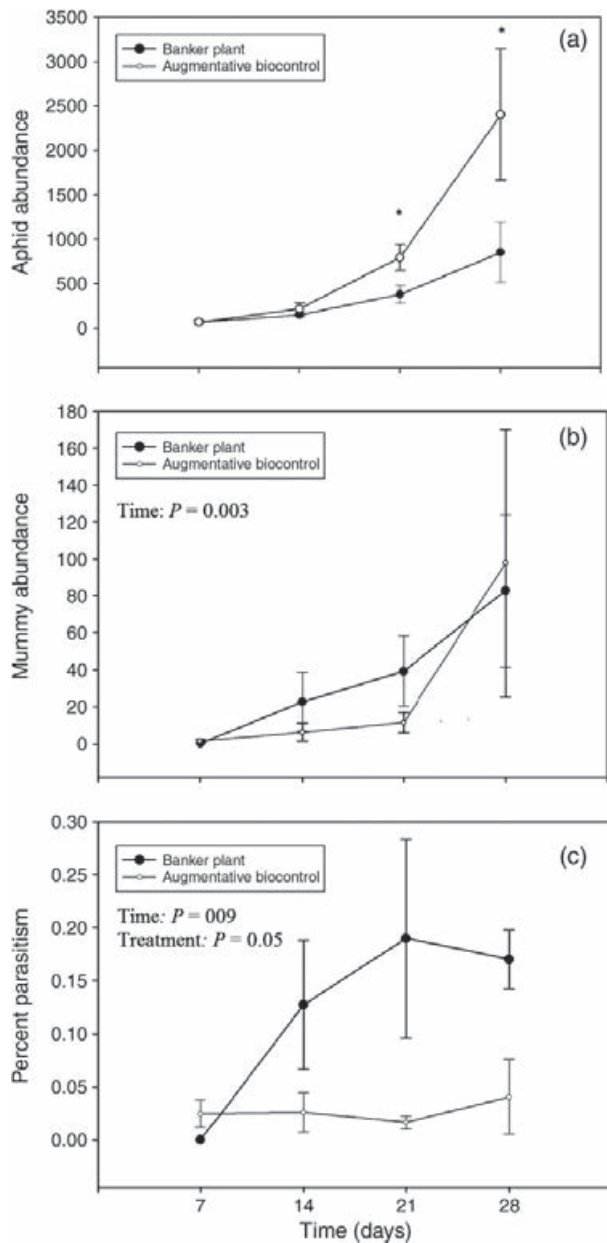


Fig. 4. (a) Mean (\pm SE) number of *Myzus persicae* present over the course of 28 days in a one-host (*M. persicae*), one-parasitoid treatment and a two-host (*Rhopalosiphum padi* and *M. persicae*, one-parasitoid treatment). A significant treatment \times time interaction was found to affect *M. persicae* abundance. Means with asterisk are significantly different at the $P < 0.05$ level. (b) Mean (\pm SE) number of *M. persicae* mummies over the course of 28 days, in a one-host (*M. persicae*), one-parasitoid treatment and a two-host (*R. padi* and *M. persicae*, one-parasitoid treatment). There was no significant difference between mummy abundance in each treatment. (c) Mean (\pm SE) percentage parasitism of *M. persicae* (mummies/mummies + aphids) over 28 days in a one-host (*M. persicae*), one-parasitoid treatment and a two-host (*R. padi* and *M. persicae*, one-parasitoid treatment). There was a significant difference between percentage parasitism in the one-host and two-host treatments.

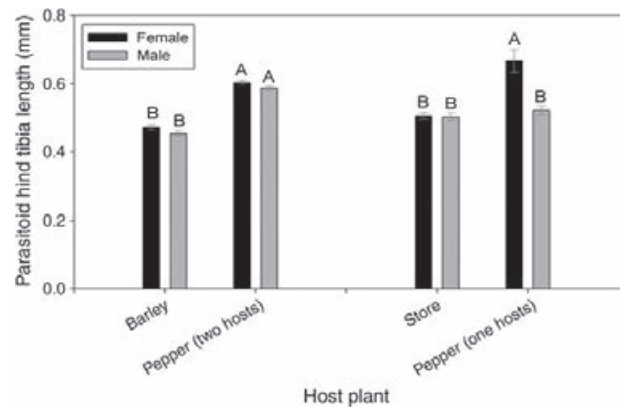


Fig. 5. Initial (barley and store) and final (pepper one-host, pepper two-host) parasitoid sizes were measured to determine host effects. Means with different letters are significantly different at the $P < 0.05$ level.

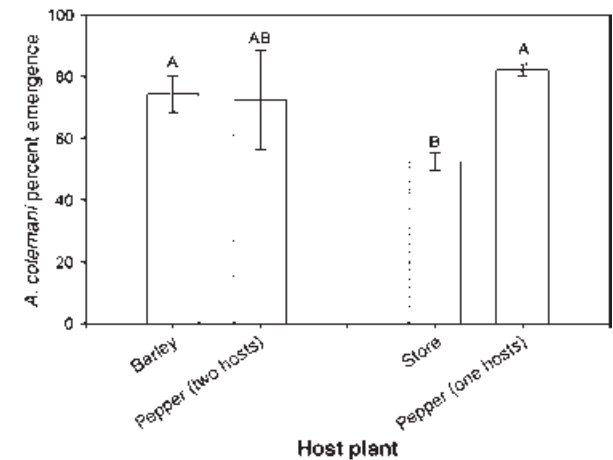


Fig. 6. Initial (barley and store) and final (pepper one-host, pepper two-host) parasitoid percentage emergences were determined. Means with different letters are significantly different at the $P < 0.05$ level.

sex ratio (female:total) did not differ significantly between pepper parasitoids in the one-host system (0.34 ± 0.18) and pepper parasitoids in the two-host system (0.59 ± 0.11) ($W = 9$, $P = 0.1$), or between barley and pepper (two-host) parasitoids ($W = 6$, $P = 0.8$). No significant differences were found between female sex ratio of store and pepper (two-host) ($W = 4$, $P = 0.5$) or between store and pepper (one host) parasitoids ($W = 8$, $P = 0.95$).

Discussion

In the presence of two aphid hosts, a parasitoid population can grow larger and parasitise more aphids than it would in the presence of one host alone (Holt & Lawton, 1994; Bonsall *et al.*, 1997). In the short term, the presence of two hosts can relax parasitism experienced by either host (Holt & Lawton, 1994). However, on a longer-term basis, apparent

competition may arise between the two hosts, resulting in greater suppression of one host species than the other (Holt & Lawton, 1994). Holt and Kotler (1987) suggested that this interaction between the two host species could be influenced by their natural enemy's optimal foraging behaviour. More specifically, using a mathematical model, they demonstrated that optimal foraging by a natural enemy can result in apparent competition favouring the survival of the least ideal host (Holt & Kotler, 1987). In our system, optimal foraging behaviour led female *A. colemani* to prefer *M. persicae* over *R. padi*. Thus, in the presence of both hosts, apparent competition resulted in *A. colemani* suppressing significantly more *M. persicae* than in the presence of one host alone.

Optimal foraging theory predicts that female parasitoids should preferentially oviposit in hosts that would produce offspring with the highest fitness (Cook & Hubbard, 1977; Charnov & Skinner, 1985). We found that offspring survival influences *A. colemani* oviposition behaviour. Specifically, our results indicate that when *A. colemani* experiences reduced offspring survival on one host, as was the case for pepper parasitoids (reared on *M. persicae* on pepper) ovipositing in *R. padi*, it prefers the other host, *M. persicae*. On the other hand, when no negative effects are experienced by offspring reared on either host, as was the case for store (from Koppert Biological – unknown host) and barley parasitoids (reared on *R. padi* on barley), *A. colemani* has no preference for either host.

Optimal foraging by a natural enemy can influence the outcome of apparent competition (Holt & Kotler, 1987). To determine how *A. colemani* foraging behaviour affects the outcome of apparent competition between *M. persicae* and *R. padi*, we compared *M. persicae* suppression in a banker plant system with two hosts with that in an augmentative biological control system with one host. We found that percentage parasitism of *M. persicae* was over 10 times greater in the banker plant system than in the augmentative biological control system. The low parasitism in the augmentative biological control system resulted in over twice as many *M. persicae* infesting the pepper plants during the second half of our experiment. Our findings suggest that, in the presence of both *M. persicae* and *R. padi*, optimal foraging behaviour led *A. colemani* to selectively parasitise *M. persicae*, its preferred host. As such, we believe that apparent competition between *R. padi* and *M. persicae* is what caused the increased suppression of *M. persicae*.

To ensure that parasitoids were optimally foraging in our banker plant and augmentative biological control system, we compared parasitoid life-history traits before and after *M. persicae* parasitism. Our analysis showed that store parasitoid emergence was significantly lower than pepper parasitoid emergence, and that female store and barley parasitoids were smaller than pepper parasitoids. In the augmentative biological control system, we found fewer store parasitoids emerging as adults than was the case for pepper parasitoids. As such, by parasitising *M. persicae* on pepper, store parasitoids were increasing their fitness by increasing their offspring survival. Unlike store parasitoids, barley parasitoid emergence did not differ after parasitism of *M. persicae*. In the banker plant

system, we found that female barley and store parasitoids were smaller than female pepper parasitoids. Size is often positively correlated with parasitoid fitness, as with host searching efficiency (Visser, 1994), flight distance (Eijs & Van Alphen, 1999), and egg number (Sampaio *et al.*, 2008). Therefore we believe larger parasitoids have higher fitness than smaller ones, and that this behaviour is consistent with optimal foraging. We suggest that store and barley parasitoids were optimally foraging on *M. persicae*, as their offspring increased in size and the offspring survival of store parasitoids improved.

As only female parasitoids can parasitise aphids, the sex ratio of the emerged parasitoids can greatly affect aphid suppression (Hagen & Van den Bosch, 1968). Female sex ratio did not differ after parasitism of *M. persicae* in both the two-host banker plant system and the one-host augmentative biological control system. Despite this, we observed greater *M. persicae* suppression in the banker plant system, suggesting that either parasitoid preference for *M. persicae* or the greater parasitoid abundance compensated for lower female sex ratio.

While there is strong evidence that the difference in aphid suppression in both systems was caused by optimal foraging and apparent competition in the banker plant system, we cannot eliminate the possibility that reduced store parasitoid emergence and female sex ratio could have influenced our results. We believe these initial differences had minimal, if any, effect on the outcome of the experiment. Although the percentage emergence of store parasitoids was 22% less than that of barley parasitoids, we found no effect of treatment on *M. persicae* mummy abundance, indicating that the same numbers of aphids were being parasitised in both treatments. This is likely because the life span fecundity of female *A. colemani* is, on average, 388 eggs per female at 25 °C and thus many aphids can be parasitised by a single parasitoid (van Steenis, 1993). Furthermore, the percentage of adult parasitoids emerging from *M. persicae* was the same in both treatments, suggesting that the same number of adult pepper parasitoids would be present in each treatment after the initial parasitism. In fact, we suspect that the store parasitoids were at a starting advantage due to their close to equal sex ratio, and their early, synchronised emergence (S. G. Prado, pers. obs.; Fernández & Nentwig, 1997), which probably allowed for easy mate-finding and mating within the first days of the experiment. Lastly, based on our observations in the caged preference experiment, a greater percentage of store (80%) than barley (65%) parasitoids parasitised aphids. Therefore, we do not believe that the low adult percentage emergence and female sex ratio of store parasitoids influenced the outcome of our experiment.

We also acknowledge that in more complex situations, dominance in apparent competition may not simply reflect a change in average parasitoid and host abundance. For instance, fluctuations in the external environment may lead to population fluctuations not directly caused by apparent competition (Holt & Lawton, 1993). Similarly, host-parasitoid populations may be so unstable that populations of both species are driven to extinction (Holt & Lawton, 1993). Although these are distinct possibilities, we feel confident that our conclusions are sound, as both our parasitoid and host populations persisted throughout the experiment (Holt &

Lawton, 1993). Additionally, we do not believe that direct, density-dependent interactions took place among hosts, as *A. colemani* effectively depressed *M. persicae* to population levels too low for such an occurrence (Holt & Lawton, 1993).

This study demonstrates the relationship among parasitoid preference, offspring fitness and apparent competition. The results provide an insight into how apparent competition structures herbivore communities and why it is so often asymmetrical (Holt, 1977; Holt & Lawton, 1994). As demonstrated here, understanding these ecological theories has important implications for biological control of arthropod pests and could help to predict when biological control will succeed or fail.

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