Host-adapted parasitoids in biological control: Does source matter?

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Abstract. It has been hypothesized that the success of a biological control introduction is, in part, dependent on the ability of the control agent to become established in its new environment or to its new population of hosts through local adaptation. Despite this, few studies have investigated the influence of the recent coevolutionary history of pest species and natural enemies on the efficacy of biological control agents, especially for agents that are mass-reared for release in agriculture. We investigate the evolutionary potential of a biological control agent Aphidius ervi to adapt to a key pest species, the foxglove aphid Aulacorthum solani, through components essential to the evolution of parasitoid virulence. We explored (1) the influence of genetic variation from natural source populations on the ability to parasitize natal and non-natal host species; (2) the heritability of key traits related to parasitoid fitness; and (3) the efficacy of parasitoid host-selection lines in a greenhouse system. Source populations maintained genetic variation in the ability to utilize natal and non-natal host species; however, only some of the traits sampled suggested local adaptation of parasitoid populations. The ability to parasitize a host was found to be genetically determined and strongly heritable, irrespective of host species. The greenhouse study demonstrated the potential of parasitoid selection lines to substantially increase performance of parasitoids for target pest species. This research provides insight into novel techniques that can be used to increase the quality of biological control agents through the development of lines of natural enemies adapted to particular pest species.

Key words: Acrithosiphon pisum; adaptive evolution; Aphidius ervi; Aulacorthum solani; biological control; foxglove aphid; heritability; parasitoid; pea aphid; reciprocal transplant; selection experiment.

INTRODUCTION

Research in population ecology has been an essential component in the practical application of natural enemies in controlling pests, but the importance of genetics and adaptive evolution in biological control remains a controversial topic (Force 1967, Remington 1968, Messenger and van den Bosch 1971, Roush 1990, Hopper et al. 1993, Holt and Hochberg 1997, Jervis 1997, Hufbauer 2002, Hufbauer and Roderick 2005, Phillips et al. 2008). Recent research has sought to better understand the genetic structure of natural enemy populations in an attempt to identify populations that are locally adapted to environmental conditions or the organisms with which they interact (Lozier et al. 2008, Phillips et al. 2008). However, few studies attempting to increase the efficacy of biological control agents have considered the recent coevolutionary history between pest species and natural enemies. Furthermore, the role of adaptive evolution in biological control has been addressed primarily from classic introductions of natural enemies to control exotic pests, with the adaptive potential of natural enemies used in greenhouses and other areas of agriculture being virtually ignored.

The value of natural enemies as an integrative method of controlling pests in greenhouses is well recognized (van Lenteren 2000). A zero-tolerance policy for pest damage in commercial vegetable and flower markets and an increasing desire to reduce pesticide applications has made the continual improvement of biological control efforts a top priority of the greenhouse industry in general (van Lenteren 1997). Difficulty establishing natural enemy populations, unpredictable control of problematic pests by natural enemies, and lag periods associated with natural enemy adjustment to novel host species are some of the major current issues in biological control. Recently a movement to improve biological control efforts has emerged in the form of breeding pest and disease resistance in plants (Cuartero et al. 1999) or breeding plants that facilitate natural enemy foraging. Examples include selected cucumber lines with fewer hairs to increase searching efficiency of parasitoids (van Lenteren et al. 1995) and the cultivation of plant lines that produce greater amounts of natural enemy-attractive volatiles to decrease the response time to infestation (Dicke 1999). This artificial selection approach has demonstrated the potential of breeding programs in pest control.
HOST-ADAPTED PARASITOIDS IN BIOCONTROL

control; however, surprisingly little to no effort has been made to actually breed the natural enemies themselves in an attempt to improve efficacy of biological control agents. (For an exception see Croft et al. 1999.)

Insect parasitoids are one of the most common natural enemies used in greenhouse pest management. Generalist parasitoids used as biological control agents are often assumed to be equally capable of effectively utilizing all recorded host species. However, generalist parasitoids, like most generalist insects that are largely polyphagous at the species level, often exhibit limited host species use at the population or community level (Fox and Morrow 1981, Smith et al. 2007). Variation in the ability to parasitize natal and non-natal host species has been recorded for several aphid parasitoids, suggesting a genetic basis for virulence and resistance across a variety of systems (Powell and Wright 1988, Pennacchio et al. 1994, Henter 1995, Pike et al. 1999, Antolin et al. 2006). Recent research by Henry et al. (2008) demonstrated the potential of *Aphidius ervi* to adapt to a key greenhouse pest species, the foxglove aphid *Aulacorthum solani*, under controlled laboratory conditions. Evidence of host adaptation in generalist parasitoids has also been revealed in several biological control introductions in natural systems, in that parasitoids were shown to have dramatically increased their reproductive potential on a novel host species following the initial introductions (van den Bosch 1964, Lemasurier and Waage 1993). These examples provide strong evidence for the capability of generalist parasitoids to adapt to key pest species. However, to the author’s knowledge, no studies have initiated the first steps toward breeding programs for pest-adapted biological control agents. (For an exception see Croft et al. 1999.)

We used a series of experiments to investigate the potential of *A. ervi* to adapt to different host species. First, we determined if natural populations of parasitoids are locally adapted to the host species most prevalent in their environment. This addresses the importance of source populations in collecting parasitoids for use in mass-rearing programs. Second, we investigated the heritability of three traits fundamental to parasitoid performance as biological control agents. Establishing trait heritability is an important first step in the implementation of artificial selection and breeding programs of pest-adapted biological control agents. Third, using a “quasi-natural” selection experiment, we established the potential of parasitoids that have been preadapted to a pest species to outperform parasitoids that have been reared on a standard rearing host in a simulated commercial greenhouse setting.

**Materials and Methods**

**Parasitoid and aphid collections and rearing**

Parasitoids and aphids used in the reciprocal transplant and heritability experiments were collected from foxglove aphids *Aulacorthum solani* (Kaltenbach) (Hemiptera: Aphididae), feeding in large organic potato (*Solanum tuberosum* L.) fields (~10 km² field) in Delta, British Columbia, Canada, and pea aphids *Acyrthosiphon pisum* (Hemiptera: Aphididae), feeding in alfalfa (*Medicago sativa* L.) fields (~3 km² field) in Agassiz, British Columbia, Canada. Several hundred parasitoids were collected by the removal of mummies from leaf material as well as by rearing aphids that harbored parasitoids. (A mummy is an aphid exoskeleton containing a parasitoid pupa. This occurs after the larval parasitoid has consumed the host aphid and is metamorphosing into an adult.) All aphids were collected using sweep nets. Upon emergence, female parasitoids were individually given access to ~30 mixed instars of their natal hosts; then the females were identified, and the offspring of each identified female were used to propagate species-specific colonies of *Aphidius ervi* Haliday (Hymenoptera: Aphidiidae). Parasitoids and aphids were identified by taxonomic keys and by comparison to identified, exemplar specimens at the Pacific Agri-Food Research Centre in Agassiz (Agriculture Canada). Pea aphids were the only aphid species collected from the alfalfa fields, but the potato fields harbored a community of aphid species...
dominated by foxglove, potato (*Macrosiphum euphorbiae*) (Thomas), and green peach aphids (*Myzus persicae*) (Sulzer), and potentially other species at lower frequencies. However, *A. ervi* from the potato fields that were used in this study were all confirmed to be from foxglove aphids by identifying and isolating the aphids (many of which were already parasitized), then collecting mummies from the isolated foxglove aphid population.

Aphids were maintained on cuttings of their host species of origin, with the petiole inserted into water in clear plastic cups covered with tissue paper. *A. ervi* were maintained using the same system, with the addition of dilute honey for sustenance. Twenty replicate cups were maintained for each aphid host species, with 10 cups per host species maintaining the parasitoid populations.

**Reciprocal transplant experiment**

*A. ervi* collected from *A. solani* on potato and *A. pisum* on alfalfa were experimentally assayed on the host species from which they were originally collected (natal host), and the novel (non-natal) host species using a reciprocal transplant design. Natal and non-natal will be used as terms to describe the host species from which the parasitoids were collected; however, this does not reflect the history of host use, as individuals from both populations may have previously utilized alternate host species. Individual females (*N* = 40) were given access to a patch of 20 second-instar pea or foxglove aphids feeding on a leaf cutting. Each female was allowed to forage on a single aphid patch for two hours, at which time the parasitoid was removed, and the aphids were left on the leaf to develop. Each parasitoid was used only once and then preserved in 75% ethanol after each trial to confirm the parasitoid species if necessary. Total parasitism (number of mummies formed per 20 aphids), the proportion of offspring emerging from the mummies, and the sex ratio of the offspring (proportion female) served as proxies for parasitoid fitness. Natal host species of the parasitoid, the host species the parasitoid was assayed on (exposure host), and the host species maintaining the parasitoid populations.

**Heritability experiment**

A mother × daughter regression was used to determine the narrow-sense heritability (*h*²) of three traits integral to parasitoid fitness: total parasitism, proportion of offspring emerging from mummies, and offspring sex ratio. Only *A. ervi* from the population collected on pea aphids, feeding on alfalfa, were used for this experiment; however, heritability estimates were determined for performance on both pea and foxglove aphids. Female parasitoids (mothers) were assayed on their natal host species (*N* = 42) using the same protocol as in the previous experiment (i.e., 20 second-instar aphids in a petri dish for two hours). Upon emergence, each mother’s offspring were allowed to inbreed to reduce genetic variability, and then four female offspring were randomly selected and assayed on pea and foxglove aphids (two daughters assayed on pea and two daughters assayed on foxglove). Zero trait values of daughters were removed from the analyses, as we could not determine if a value of zero was due to genetic components or other biological reasons (e.g., zero sex ratio could be due to not mating, or zero parasitism may be due to an unresponsive female). Heritability was determined using mothers and daughters assayed on the same host species (i.e., genetic component only, controlling for environment). A comparison of inbred sisters from the same family assayed on the two different host species was used to determine if the expression of a phenotype is influenced by the species of the host (i.e., environmental effects). This design allowed us to determine trait heritability using a mother × daughter regression while controlling for potential environmental effects caused by developing in different host species.

Narrow-sense heritability of the aforementioned traits was estimated using a one-parent × mid-offspring (mean trait value of daughters) regression, with the coefficient of the slope of the linear regression line approximating heritability (*Falconer and Mackay 1989*). As only female phenotypes could be measured, the estimate of heritability (*h*²) is double the coefficient of the slope (single-parent heritability). Each trait was analyzed using a linear regression comparing mothers and daughters reared on pea aphids and foxglove aphids separately, blocking for mother (six linear regressions in total). The relationship between sisters reared on separate host species was assessed using a linear regression, blocking for mother, by plotting the trait value of pea aphid-reared sisters against the trait of foxglove aphid-reared sisters for each fitness proxy. The relationship between sister traits was analyzed separately for families that had emerged from pea and foxglove aphids, in order to control for potential maternal effects caused by developing in different host species.

**Host-adapted parasitoid greenhouse experiment**

Parasitoids used in the greenhouse experiment were from selection lines that had been isolated and maintained in replication on either pea or foxglove aphids at Simon Fraser University for two years (~50 parasitoid generations), as described in Henry et al. (2008). *A. ervi* selection lines were assayed for their performance on foxglove aphids in a controlled greenhouse experiment at the Pacific Agri-Food Research Centre in Agassiz. Mature pepper plants (~two months old), isolated in screened individual enclosures, in a 6.4 × 15 m greenhouse, were each heavily infested with several thousand foxglove aphids and left for a week for...
the aphids to become established. Plants were infested to the point where parasitoids would not be limited by host abundance. Parasitoid mummies were randomly chosen from the replicate populations of host-selection-line parasitoids. Parasitoids were isolated by host species and allowed to mate; then 10 females were released in each enclosure by leaning an unsealed test tube containing the parasitoids against the basal stem of the pepper plant (N = 10 replicates for each selection line). The parasitoids were left to forage on the infested plants within the enclosures for a 12-d period. This time frame was long enough that the parasitoids from the initial release had died, and no new parasitoids had emerged to additionally parasitize the aphids. Plants were supplied with water using a drip irrigation system but were otherwise not tended for the course of the experiment.

After the plants were removed from the enclosures and dissected, all mummies were removed and counted. The dissected plants were then individually placed in Plexiglas containers with fresh pepper plants to allow the aphids still harboring parasitoid larvae access to fresh plant material, where larvae developed into mummies. This methodology resulted in a precise value for total parasitism per plant (total mummies). Total parasitism was compared by parasitoid selection line (ANOVA).

All statistical analyses were performed using JMP 7.0 statistical software (SAS Institute 2007).

RESULTS

Reciprocal transplant

The total number of mummies formed differed when comparing parasitoids from the two host species populations (F3, 154 = 39.3, P < 0.0001). Parasitoids collected from the pea aphid population produced more mummies (12.6 ± 0.45) in general than parasitoids from the foxglove population (10.4 ± 0.49) (natal host: F1, 154 = 10.2, P = 0.0017), and parasitoids generally produced more mummies when exposed to foxglove aphids (14.6 ± 0.46) compared to pea aphids (8.5 ± 0.48) (exposure host: F1, 154 = 87.9, P < 0.0001). All values are mean ± SE. Parasitoids produced significantly more mummies on their natal host (natal × exposure: F1, 154 = 25.4, P < 0.0001), as indicated by the strong interaction between natal and exposure host species, which suggests parasitoids are locally adapted to their natal host species (Fig. 1A). The proportion of emergence from mummies (GLM: χ2, 140 = 93.65, P < 0.0001) differed between the two parasitoid populations. The proportion of emergence was greater from foxglove aphids at 0.90 ± 0.03 compared to pea aphids at 0.81 ± 0.03 (exposure host: χ2, 140 = 22.90, P < 0.0001). Parasitoids from the pea aphid population generally had higher emergence on both host species (0.91 ± 0.03) compared to parasitoids from the foxglove population (0.80 ± 0.03) (natal host: χ2, 140 = 68.62, P < 0.0001; Fig. 1B). Parasitoids from the foxglove population had a substantially lower proportion of offspring emerging from pea aphids (0.69 ± 0.04) compared to emergence from their natal host species (0.88 ± 0.04) (natal × exposure: χ2, 140 = 9.15, P = 0.0025). No variation was detected in the sex ratio of emerging offspring (χ2, 108 = 2.71, P = 0.44; Fig. 1C).
Estimates of heritability

Significant heritable variation in the ability to parasitize foxglove aphids was demonstrated by the mother × daughter regression ($h^2 = 0.95 \pm 0.16$) (linear regression: $F_{1,59} = 35.2, P < 0.0001$; Fig. 2A). The proportion of offspring emergence from mummies did not display heritable variation ($h^2 = 0.18 \pm 0.26$) ($F_{1,46} = 0.49, P = 0.49$). The sex ratio of offspring from pea aphid-assayed parasitoids did not show heritable variation ($h^2 = 1.72 \pm 0.85$) ($F_{1,20} = 4.11, P = 0.07$; Table 1).

The comparison of the parasitism of sisters assayed on pea and foxglove aphids had a significant negative relationship when the families had emerged from pea aphids ($F_{1,47} = 8.79, r^2 = 0.16, P = 0.0048$; Fig. 3B). However, no relationship was detected in the parasitism of sisters assayed on the two host species when families had emerged from foxglove aphids ($F_{1,57} = 0.99, r^2 = 0.02, P = 0.32$; Fig. 3A). The proportion of offspring emergence of sisters assayed on different hosts did not show a relationship when the families had emerged from foxglove ($F_{1,52} = 0.89, r^2 = 0.02, P = 0.35$) or pea aphids ($F_{1,20} = 0.79, r^2 = 0.02, P = 0.38$). No relationship was detected in the sex ratio of the offspring from families reared on foxglove ($F_{1,20} = 0.22, r^2 = 0.01, P = 0.64$) or pea aphids ($F_{1,15} = 0.001, r^2 = 9.7 \times 10^{-5}, P = 0.97$).

**Host-adapted parasitoid greenhouse experiment**

Parasitoids from the foxglove and pea aphid selection lines differed in their ability to parasitize foxglove aphids in a greenhouse setting ($F_{1,16} = 5.58, P = 0.03$). Parasitoids from the foxglove aphid selection line produced an average of 233.8 ± 51.7 mummies, whereas parasitoids from the pea aphid selection line produced an average of 86.5 ± 31.4 mummies.

**Discussion**

It has been suggested that the success of biological control is primarily based on the quality of the natural enemies produced by commercial suppliers (van Lenteren 1997). Developments in the mass production, quality control, storage, and shipment of natural enemies have decreased production costs and led to better product quality (van Lenteren 2000). However, the importance of genetic variation of natural enemies, biotypes for mass rearing, and recent coevolutionary history of parasitoids with host species has not been addressed for biological control agents used in agriculture. This is surprising, given that the closed nature of greenhouses in particular make them ideal for releasing preadapted biological control agents, and commercial biocontrol-rearing facilities are an ideal arrangement for the establishment of natural enemy breeding programs.

**Patterns of parasitism and evidence of local host adaptation**

The reciprocal transplant experiment provides evidence that wild host-associated parasitoid populations maintain genetic differences that influence their ability to utilize natal and non-natal host species. However, only some of the traits sampled indicate patterns of local adaptation. The patterns of parasitism from the reciprocal transplant experiment suggest that parasitoids are locally adapted to their natal host populations, given...
that parasitoids from both populations maintained a higher level of parasitism on their natal host (Fig. 1A). Parasitoids from the pea aphid population maintained a relatively high level of parasitism on both natal and non-natal hosts, whereas the foxglove population only performed well on its natal host, with low levels of parasitism on pea aphids. Although this pattern suggests a genetic basis for parasitism, the large difference in the two parasitoids’ ability to parasitize pea aphids, and the levels of parasitism in general, may also be influenced by nongenetic components. For instance, parasitism is most likely influenced by the extent of phenotypic plasticity exhibited by parasitoids developing in different host species. This includes host fidelity or morphological variables such as adult body size that are primarily environmentally determined (i.e., induced by developing in a host species), which can have a strong influence on the willingness to utilize a host species or the ability to overcome host defenses (Henry et al. 2008). Parasitoids from the foxglove population are, on average, half the size of parasitoids that have developed in pea aphids due to growth restrictions imposed by the size of the host species, which can influence oviposition success when attacking large aggressive host species such as the pea aphid (Henry et al. 2006). Although this may partially account for the low levels of pea aphid parasitism from foxglove aphid parasitoids, it does not account for the foxglove parasitoids outperforming pea aphid parasitoids on their natal host species, which supports the hypothesis of local adaptation.

Offspring emergence showed significant variation between the two parasitoid populations, which supports the theory of genetic differentiation in the ability to successfully develop in a host. However, this pattern does not support local host species adaptation, in that parasitoids from the pea aphid population had higher offspring emergence on both host species (Fig. 1B). The host populations these parasitoids were collected from may account for this deviation in that they differed in the composition and availability of host species in their local environment. Parasitoids from the alfalfa field most likely did not have access to alternate host species, as the pea aphid was the only host species found in the field, whereas parasitoids from the potato field had several different host species to choose from. In an environment with the option of utilizing alternate host species, parasitoids may be practicing host switching, which is thought to inherently destabilize specialization through the obliteration of locally adapted gene pools (Kawecki and Ebert 2004). The aphids themselves may have also experienced different degrees of selective pressures from parasitism. Foxglove aphids may have experienced a refuge from parasitism due to the presence

<table>
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<tr>
<th>Species/phenotypic trait</th>
<th>F</th>
<th>p</th>
<th>r²</th>
<th>h², mean ± SE</th>
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<tr>
<td>Pea aphid (Acyrthosiphon pisum)</td>
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<tr>
<td>Parasitism</td>
<td>35.2</td>
<td>&lt;0.0001</td>
<td>0.38</td>
<td>0.95 ± 0.16</td>
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<td>Proportion of offspring emerging</td>
<td>0.41</td>
<td>0.52</td>
<td>0.01</td>
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<tr>
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<td>0.27</td>
<td>0.06</td>
<td>0.64 ± 0.56</td>
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<td>Foxglove aphid (Aulacorthum solani)</td>
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<tr>
<td>Parasitism</td>
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<td>Proportion of offspring emerging</td>
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<td>Sex ratio</td>
<td>4.11</td>
<td>0.07</td>
<td>0.31</td>
<td>1.72 ± 0.85</td>
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Note: Mothers and daughters were always assayed on the same host species.
of alternate hosts, where as pea aphids are more likely to have been exposed to greater selective pressures from *Aphidius ervi*, resulting in a more highly evolved defensive system (such as an increase in the frequency of endosymbionts that confer resistance to parasitism [Oliver et al. 2005]), which may partially explain the lower levels of parasitism and emergence from pea aphids in general. Further research is required to determine the effects of alternate host species on parasitoid specialization and local host adaptation.

Local host adaptation in natural populations of parasitoids utilizing different host species is not uncommon (e.g., Vaughn and Antolin 1998, Althoff and Thompson 2001, Morehead et al. 2001, Hayward and Stone 2006, Stireman et al. 2006). Antolin et al. (2006) found that *Diaeretiella rapae* from two adjacent fields containing Russian wheat aphids (*Diaphis noxia*) and cabbage aphids (*Brevicoryne brassicae*) were genetically differentiated and locally adapted by host species. Similarly, changes in *Microtus hyperdactyloides* biotype frequencies introduced to New Zealand for control of the weevil *Listronotus bonariensis* were consistent with strong directional selection, providing one of the first clear demonstrations of adaptive evolution improving success rates of biological control introductions (Winder et al. 2003, Philips et al. 2008). These studies highlight the importance of source populations and natural genetic variation in natural enemy populations that are used in biological control of pests. Although sampling methods for detecting locally adapted populations have primarily focused on parasitoids for classical biological control introductions (Lozier et al. 2008), the techniques have clear applications for selecting the highest-quality source populations for the mass rearing of parasitoids to be released in agriculture.

**Heritability of fitness-related traits**

Knowing the heritability of life history traits is necessary for a mechanistic understanding of evolutionary processes. Results of the parent × offspring regression suggest there is significant heritable genetic variation in the capacity to parasitize a patch of aphids when assayed on both foxglove and pea aphids independently (Fig. 2A, B), indicating that this trait has a strong genetic component and that the genetic basis of parasitism is universally expressed, irrespective of host species. Heritability of parasitism on pea aphids \( h^2 = 0.75 \) was lower than on foxglove aphids \( h^2 = 0.95 \), which is not surprising, as the original population of parasitoids was collected from pea aphids, and selection should act to reduce additive genetic variation within our sample population for performance on pea aphids (Fisher 1930, Mousseau and Roff 1987). However, both of these values are still considered to be moderately high, as heritability for life history traits generally averages around 0.25 (Roff 1992). This suggests that genes involved in pea aphid parasitism have not reached fixation from our sample populations, which is interesting given that the pea aphid was the only aphid species collected from this study site. This could result from interspecific, frequency-dependent selection or migrant individuals from alternate host species or alternate host patches with differing genotypes for resistance (Henter 1995, Henter and Via 1995). Perhaps even more interesting is the high heritability of parasitism on foxglove aphids from individuals collected from the pea aphid population (Fig. 2B), which suggests that a significant amount of standing genetic variation exists within this population for the ability to parasitize foxglove aphids. No trait heritability was detected in the emergence of offspring from mummies or in the sex ratio of offspring, indicating that these traits may be primarily determined by environmental conditions, have reached allele fixation, or may be solely influenced by maternal effects.

The relationship between sisters assayed on the two different host species allowed us to investigate the influence of the environment (i.e., host species) on trait expression, using closely related individuals, with little maternal influence, as families emerged from the same host species. Results indicate that developing in different host species influences gene expression in that sister’s traits were either negatively correlated or had no detectable correlation. A strong negative relationship was detected in parasitism between sisters assayed on the two host species (Fig. 3B), when the families emerged from pea aphids. This negative fitness correlation indicates that a trade-off exists in the ability to successfully parasitize both host species, which suggests an antagonistic interaction between one or more genes. However, when parasitoids were reared on foxglove aphids, no significant relationship was detected in parasitism between sisters (Fig. 3A). One possible explanation for this deviation in the relationship between sisters when reared on different hosts is that parasitoids emerging from foxglove aphids are relatively small; previous research has shown that foxglove-reared parasitoids are limited in their ability to handle and successfully ovisposit in large, well-defended hosts such as the pea aphids (Henry et al. 2006). Thus the morphological limitations from developing in foxglove aphids may have masked the actual relationship between sisters. Additionally, no relationship between sisters was detected in the emergence or sex ratio of offspring, supporting the earlier claims that these traits may be determined by a combination of factors.

Our results support the research by Henry et al. (2008), in that the ability to parasitize a host appears to be genetically determined and strongly heritable, irrespective of the host species in which the parasitoids are developing. Identification of heritable traits in natural enemies used in biological control is an essential first step in the initiation of breeding programs. Although selectively breeding natural enemies is not a common practice by commercial producers of biological control agents, our results demonstrate the potential of artifi-
cially breeding for specific traits to increase the efficacy of parasitoids on key pest species. Furthermore, our results suggest a negative relationship between genotypes that indicates an inability of parasitoids to simultaneously maximize fitness on more than one host, which coincides with results of Henry et al. (2008). Previous research has demonstrated that there can be a physiological mechanism involved in overcoming host defenses and that this process may be under directional selection in certain host–parasitoid systems (Carton et al. 1989, Kraaijeveld et al. 2001). Our result calls into question the oversimplification of using generalist parasitoids to control multiple aphid species in greenhouses, as well as the common practice of rearing parasitoids on a host species that it is not implicitly used to control, such as the pea aphid. If success of biological control is partly based on the quality of the natural enemies (van Lenteren 2000), improving the performance of parasitoids by selective breeding has great potential to improve parasitoid efficacy, which in turn increases economical viability of biological control agents.

**Greenhouse performance of host-adapted parasitoids**

Previous research by Henry et al. (2008) demonstrated that a foxglove selection line dramatically increased their capacity to parasitize foxglove aphids in a controlled laboratory experiment. Although compelling, these results do not confirm the effectiveness of these parasitoids as a biological control agent of foxglove aphids in commercial greenhouses, as there are many unpredictable factors in greenhouses that may hamper parasitoid performance. Parasitoids from the foxglove selection line produced an average of 63% more mummies than the pea aphid selection line when assayed on foxglove aphids in the greenhouse experiment. This clearly demonstrates the potential of using host selection lines to increase the efficacy and consistency of parasitoids for problematic aphid pests in greenhouses. Increased performance of selected parasitoids occurs not only through a greater physiological virulence for overcoming host defenses but also by an increase in host fidelity (Henry et al. 2008). Host fidelity and host location are highly plastic traits in many parasitoid systems (Villagra et al. 2007). The predictive nature of these plastic responses has great potential in biological control by establishing fidelity for a host species prior to release, which increases the probability that the natural enemy population will become established through a reduction in emigration and an increased capacity to locate hosts (Dickie 1999).

These results provide insight into a novel technique to increase the quality of biological control agents through selection designs. Artificial selection designs can also be extended to nonprey resources, such as preadapting a natural enemy to the spatial structure or temperature of the intended foraging environment. Ideally, reduction in the cost of biological control to growers makes it easier and more economical to apply. The importance of increasing natural enemy efficiency is evident in the recent movement to breed plant varieties that facilitate the movement and response of natural enemies (van Lenteren 2000). Thus it seems a logical progression to develop the biological control agents themselves through discerning collections from source populations and careful breeding designs. However, the caveat of such an approach is that it not only requires greater communication and extensive collaboration of researchers with growers but also with the commercial suppliers of natural enemies themselves.

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