Covariance of phenotypically plastic traits induces an adaptive shift in host selection behaviour

Lee M. Henry^{1,*}, Bernard D. Roitberg¹ and David R. Gillespie²

¹Department of Biological Sciences, Simon Fraser University, Burnaby, BC, V5A 1S6 Canada

²Pacific Agri-Food Research Centre, Agriculture and Agri-Food Canada, PO Box 1000 Agassiz, BC V0M 1A0, Canada

Flexibility in adult body size allows generalist parasitoids to use many host species at a cost of producing a range of adult sizes. Consequently, host selection behaviour must also maintain a level of flexibility as adult size is related to capture efficiency. In the present study, we investigated covariance of two plastic traits—size at pupation and host size selection behaviour—using *Aphidius ervi* reared on either *Acyrthosiphon pisum* or *Aulacorthum solani*, generating females of disparate sizes. Natal host was shown to change the ranking of perceived host quality with relation to host size. Parasitoids preferentially attacked hosts that corresponded to the size of the second instar of their natal host species. This resulted in optimal host selection behaviour when parasitoids were exposed to the same host species from which they emerged. Parasitoid size was positively correlated with host size preference, indicating that females use relative measurements when selecting suitable hosts. These coadapted gene complexes allow generalist parasitoids to effectively use multiple host species over several generations. However, the fixed nature of the behavioural response, within a parasitoid's lifetime, suggests that these traits may have evolved in a patchy host species environment.

Keywords: host size preference; body size; adaptive behaviour; linked traits; capture efficiency; evolution

1. INTRODUCTION

Phenotypic plasticity is defined as the ability of an organism to change its phenotype in response to varying biotic and abiotic conditions (Agrawal 2001). Although phenotypic plasticity refers to changes in chemistry, physiology, development, morphology or behaviour, the main focus of studies involving phenotypic plasticity have tended to concentrate on changes in morphology, physiology and life-history traits (DeWitt & Scheiner 2004). Conceptually, plasticity in behaviour is very different from other attributes, in that behaviour is a labile trait that can change in expression from several to many times within an organism's lifetime. By contrast, developmental plasticity is much more rigid, in that once a form has been adopted it can be irreversible or, at least, slow to revert (Tufto 2000). However, variation in behaviour owing to adaptive differences between populations may restrict behavioural flexibility, within a given environment, resulting in a mosaic of fixed policies across ecosystems (Foster 1999). Plastic traits often react in conjunction, forming a correlated response to environmental change. When the performance of a trait is conditional on the response of another, phenotypic linkages may form which connect trait responses through adaptive evolution.

The adaptive plasticity hypothesis refers to the evolution of plastic phenotypes that maximize fitness in a variable environment (Dudley & Schmitt 1996). Maintenance of fitness upon entering into a novel environment is almost always a result of purely phenotypic change, reflecting a species' plasticity, which translates into genetic differences later by natural selection (Price *et al.* 2003). High levels of plasticity often coincide with generalism, given that

generalist species are thought to have evolved to tolerate a greater breadth of environmental heterogeneity (reviewed in Kassen 2002). When a single species occurs over a range of ecosystems, diverged populations may exhibit very different phenotypes that are adapted to a discrete set of environmental conditions. This is a phenomenon that has been well documented in generalist herbivores locally adapted to different host plants (Funk *et al.* 2002; Simon *et al.* 2003). Diverged populations have also been shown to exhibit biases in host, habitat or prey preference, which are factors that contribute to reduced gene flow between populations (Funk & Bernays 2001; Vos & Vet 2004).

Host-seeking generalist parasitoids function within a complex environment where they may encounter a diverse number of host species varying in size, defensive capabilities and quality for offspring development. Furthermore, parasitoids also have to choose a suitable developmental stage within each host species as instars provide another level of resource and defensive variability (Gerling *et al.* 1990). When parasitoid species occur over a wide geographical range, divergent populations can form that are adapted to survive on the sympatric host species which are most prevalent in their region (Vaughn & Antolin 1996). Studies have demonstrated that the same species of parasitoid from different populations can vary in morphology (Biron *et al.* 2002) and behaviour (Kraaijeveld *et al.* 1995), which has been attributed to a combination of selective pressures on physiological and behavioural traits that, over time, result in local adaptation (Thompson 1994). Although several studies have demonstrated the variability in traits expressed by parasitoids across populations, few studies have investigated whether plasticity in these traits function in an adaptive manner.

* Author for correspondence (lmhenry@sfu.ca).

Aphidius ervi (Haliday) (Hymenoptera: Aphidiidae) is a generalist aphid parasitoid that inhabits a large continuous range throughout Europe and Asia, where it has been reported using over 15 host species (Mackauer & Stary 1967). Studies have shown that *A. ervi* expresses plasticity in several traits, including developmental time and adult size (Sequeira & Mackauer 1992a). Adult size is a highly flexible trait in many generalist parasitoids that is conferred by host size (Nicol & Mackauer 1999). This allows aphid parasitoids to use many host species and often all instars within a particular host, at a cost of producing a range of adult sizes (Daza-Bustamante *et al.* 2003). The four aphid instars, or developmental stages, offer discrete levels of resources to developing parasitoid larvae. Young aphid instars have fewer available resources, which often results in female parasitoids allocating proportionately more sons to the lower quality first instar hosts (Charnov 1982). In contrast, adult aphids are large enough for parasitoid development; however, the larvae must compete with the host's embryos for resources, and adult aphids are thought to possess greater physiological resistance to parasitism (Walker & Hoy 2003; Colinet *et al.* 2005). This can result in high larval or pupae mortality when parasitoid larvae develop in older aphids (Chau & Mackauer 2001; Walker & Hoy 2003; Colinet *et al.* 2005; Henry *et al.* 2005). For koinobiotic aphid parasitoids (i.e. hosts continue to grow after being parasitized), second and third instar hosts typically represent the most suitable developmental stage for harbouring larvae until pupation (ranking: second > third > first > fourth; Colinet *et al.* 2005). When attacking sympatric host species, parasitoids can distinguish between high- and low-quality host instars and preferentially oviposit in higher quality hosts (Godfray 1994; Mackauer *et al.* 1996). However, when confronted with novel host species, females may make incorrect decisions by preferring lower quality host instars (Henry *et al.* 2005). To the authors' knowledge, it has never been demonstrated how koinobiotic parasitoids determine which instars are most suitable for oviposition. Furthermore, when confronted with multiple host species of dissimilar sizes, it is unclear how parasitoids modify host selection behaviour (i.e. phenotypic plasticity) to accommodate the differences in the size of the optimal instar that occur between host species.

In the present study, we investigated covariance of plastic morphology (size at pupation) and host selection behaviour using parasitoids reared on two aphid species of dissimilar sizes, resulting in morphologically disparate parasitoid adults. Our objectives were to determine if natal host influenced the oviposition success rate and host size preference of females when choosing between instars of each host species, given that there is an approximate twofold difference in the optimal-sized host instar between the two aphid species. Results are discussed in the context of coadapted plastic traits that are closely associated with reproductive fitness and the evolution of phenotypic linkage in variable environments.

2. MATERIAL AND METHODS

(a) Study system and general procedures

All insect colonies were maintained at $20 \pm 2.0^\circ\text{C}$, 50–60% relative humidity and a 16L:8D photoperiod for approximately four months prior to experimentation. Parasitoids

were reared on *Acyrtosiphon pisum* (Harris) (Hemiptera: Aphididae) on broad beans *Vicia faba* L. (cv. 'Broad Windsor') from stock *A. ervi* colonies at the Southern Crop Protection and Food Research Centre, Agriculture Canada (London). Parasitoids reared on foxglove aphids, *Aulacorthum solani* (Kaltenbach; Hemiptera: Aphididae), were exposed to aphids under the same rearing conditions and host plant as *A. pisum*. Parasitoids reared on *A. solani* were only allowed one generation on this host, whereupon mummified first generation offspring were removed. Mummies were clipped from plant material and left to develop in separate containers. Test parasitoids, reared on *A. pisum* or *A. solani*, were always 2–3-day-old females that had been given continuous access to dilute honey (for sustenance), water and males (for fertilization). Parasitoid females were naive, in that they had no contact with any hosts, except for the mummy casings from which they emerged. Each parasitoid was used only once and then discarded.

(b) Host preference experimental design

Individual parasitoids from the two rearing host environments were exposed to a patch of *A. solani* or *A. pisum*. A patch consisted of 40 aphids, 10 of each of the four instars. Aphid instars were determined by age which corresponded to: 24–36 h first instar, 48–60 h second instar, 72–84 h third instar and 96–108 h fourth instar.

Parasitoids were allowed to forage for 10 min in a Petri dish on either *A. solani* or *A. pisum*. During the foraging bout, behaviours relating to instar preference were recorded, including antennation and oviposition attempts. Oviposition attempts were further classified as a successful or failed oviposition. Antennations were defined as the parasitoid draping its antennae over the aphid, which often preceded the initial attack. Attempted oviposition consisted of a strike with the ovipositor, regardless of the contact made with the aphid. Successful oviposition was defined as an attack that resulted in the ovipositor making contact with the aphid. Failed ovipositions were most commonly owing to aphid defences (aphids moving away, dropping, kicking or raising the body to avoid the ovipositor) and were defined by the parasitoid striking at, but not making contact with, the aphid. Differences in instar preference were determined for parasitoids from the two rearing populations and host species exposure groups using a log linear type 3 generalized estimating equation (GEE) analysis, which takes into account pooling across females in each treatment group (SAS Statistical Package v. 8.2; SAS Institute, Cary, NC, USA). Missed attacks, by instar, were compared across rearing and exposure groups using a multivariate analysis with an identity response design (JMP v. 5.0; SAS Institute, Cary, NC, USA).

(c) Mechanism of host size selection

To determine whether adult parasitoid size influenced host size selection criteria, we correlated parasitoid female body weight with preferred aphid size. This experiment was performed with parasitoids reared on and exposed to pea aphids, to remove the effect of host species on size selection. In order to eliminate constraints on oviposition, such as differences in instar defensive capabilities, aphids were anaesthetized with CO_2 for both the pre-treatment and actual trials (Gerling *et al.* 1990). Aphids were anaesthetized, but not killed, by sealing them in a dram vial for 1–2 min with CO_2 . Individual females were given a pre-treatment of eight aphids, two of each of the four instars, in order to acclimatize the parasitoids to the range

of host sizes. Upon stinging three hosts, the aphids were removed from the vial and the parasitoids were then transferred to the trial arena. Parasitoids were then given access to 16 pea aphids, selected to represent a full range of sizes, randomly placed in a circle around a hole cut in the centre of the trial arena. Parasitoids entered through the hole and were allowed to attack only three aphids, which were removed. Test parasitoids were placed in a $60 \pm 2^\circ\text{C}$ drying oven for 72 h prior to being weighed using a Cahn microbalance. The three stung aphids were adhered to a glass slide and measured. Dorsal measurements of aphid length (vertex to base of cauda) and width (distance between cornicles) were taken using a dissecting scope with an ocular micrometre. Total aphid size was calculated as the volume of a cylinder ($L\pi r^2$). The mean volume of the three aphids that were attacked by the wasp was compared to parasitoid weight using a linear regression (JMP v. 5.0).

3. RESULTS

(a) Adult morphological plasticity

Parasitoid size was limited by host size, resulting in substantially larger adults emerging from *A. pisum* compared to adults that developed in the smaller host species *A. solani* (mean female parasitoid weight (mg): 0.103 ± 0.0016 and 0.0454 ± 0.0015 for hosts *A. pisum* and *A. solani*, respectively; ANOVA: $F_{1,446} = 637.34$, $p < 0.0001$).

(b) Host size preference

Oviposition attempts (successful and unsuccessful) were used to determine parasitoid instar preference as this removed biases in success rate caused by constraints imposed by aphid species and instars, e.g. degrees of defensive capabilities. The aphid host species in which the parasitoid developed had an effect on the instar that parasitoids preferred to attack (log linear: $\chi^2_3 = 9.55$, $p = 0.0229$). Parasitoids which had developed in pea aphids preferred larger instars on average than those reared in foxglove aphids. Exposure to different aphid species was significant (log linear: $\chi^2_3 = 7.98$, $p = 0.0464$). There was no interaction among rearing host species, exposure species and instar preference (log linear: $\chi^2_3 = 4.19$, $p = 0.2414$). When comparing the instar preference regimes of each rearing–exposure combination, parasitoids demonstrated a consistent instar preference only when reared and then exposed to the same aphid species. Furthermore, parasitoids demonstrated a parallel deviation in instar ranking when reared and then exposed to the alternate host, in that parasitoids reared on foxglove aphids preferred smaller pea aphids and those reared on pea aphids preferred larger foxglove aphids (figure 1).

(c) Missed attacks owing to aphid defence

The mean number of missed attacks increases with host age across all rearing–exposure groups owing to the superior defensive capabilities of the mature third and fourth instar aphids (figure 2). The interaction between rearing and exposure groups indicates a divergence in the number of missed attacks across instars (MANOVA: $F_{4,106} = 3.649$, $p = 0.008$). This deviation is most probably owing to the foxglove aphid-reared parasitoids that were exposed to pea aphids, which resulted in a much greater number of missed attacks when attempting to attack third and fourth instar pea aphids. Pea aphids, being a large,

Figure 1. Host size preference of *A. ervi* after developing in two different natal hosts, displayed as the mean instar preferred per female when exposed to the foxglove aphid, *A. solani*, or the pea aphid, *A. pisum*. The dotted line represents the optimal instar preference for highest reproductive returns. Elevations of the exposure lines demonstrate a general preference for larger *A. solani* and smaller *A. pisum*. Natal host development induces a shift in overall host size preference.

Figure 2. Preferred aphid size correlated to parasitoid weight when parasitoids were reared and exposed to *A. pisum*. Aphid size is displayed as the mean volume of the first three aphids selected by each parasitoid female.

well-defended aphid species, generated a substantially greater number of missed attacks by parasitoids (MANOVA: $F_{4,106} = 5.1445$, $p = 0.0008$). The superior defences of pea aphids compounded with a marginal increase in the number of missed attacks owing to being reared in foxglove aphids (MANOVA: $F_{4,106} = 2.47$, $p = 0.0489$) resulted in the substantial increase in missed attacks in the foxglove-reared, pea aphid-exposed group.

(d) Mechanism of host size selection

Parasitoid weight was positively correlated with aphid size preference (linear regression: $F_{1,33} = 22.19$, $p < 0.0001$; figure 3). The coefficient of variation determination indicated that parasitoid weight accounts for 40% of the variation in the observed aphid size preference ($R = 0.402$).

4. DISCUSSION

Parasitoids provide an exceptional system for examining questions about adaptive behaviour (Godfray & Shimada

Figure 3. Instar-specific mean missed attacks per female parasitoid after developing in two different natal hosts and then exposed to either pea aphids, *A. pisum*, or foxglove aphids, *A. solani*.

1999). A substantial body of research has focused on causes and consequences of parasitoids' host-choice behaviour and the influence of natal host on adult traits (reviewed in Godfray 1994). Natal host has been shown to influence odour preference, handling time and sex allocation behaviour, and to modify adult parasitoid morphology (Morris & Fellowes 2002; Fellowes *et al.* 2005). Adult size is a highly flexible trait in many parasitoids that is determined by host size (Sequeira & Mackauer 1992b; Harvey *et al.* 1994). This allows generalist parasitoids to use a broad range of host species. Variability in adult size has been demonstrated in several Aphidiinae wasps, using a broad range of host species of diverse sizes (Elliot *et al.* 1994; Honek *et al.* 1998; Nicol & Mackauer 1999; Ode *et al.* 2005), and in other koinobiont parasitoid systems (Harvey & Vet 1997; Mohamed *et al.* 2003; Abe 2006). The maintenance of growth plasticity has been demonstrated with *A. ervi* in two host species populations where adult parasitoid size correlated with host species size, irrespective of natal host population (Daza-Bustamante *et al.* 2003; L. M. Henry 2004, unpublished data). Body size has been shown to influence foraging behaviour, which, in turn, affects niche partitioning (Wang & Messing 2004b). In predator-prey systems, predator-to-prey size ratio has been shown to influence handling time, foraging success and subsequent prey preference (Lafferty & Kuris 2002). However, the consequences and covariance of adult size on host selection behaviour are topics that have received little attention in host-parasitoid systems.

When considering the attempted attacks on each instar, i.e. the biological preference excluding factors such as host defence, the results of our experimental manipulations indicated that natal host affects the way females choose between host size classes. Assuming that the parasitoids are still attempting to select the highest quality host for their offspring, we can infer that natal host influences a female's host assessment criteria in that it changes the ranking of perceived host quality with relation to host size. For aphid parasitoids, which attack all stages of their hosts, selecting the highest quality host for larval development involves selecting an instar that is allocating all of its resources towards growth, yet can handle the damage

ensued by an oviposition (Vinson & Iwantsch 1980). This typically results in intermediate hosts being the most suitable for larval development, owing to young hosts being limited in resources and adult aphids declining in quality through superior physiological defences against parasitism or competition for host resources with embryos (Colinet *et al.* 2005). Intermediate instars have been reported yielding the highest fitness returns in many aphid parasitoid systems. Instar quality for *A. ervi* larval development was shown to drop dramatically from 18% to 1% for second to fourth instar *A. solani* (Henry *et al.* 2005). Per cent parasitism of *A. ervi* exposed to instars of *A. pisum* (20 individuals) resulted in second instar hosts producing the highest reproductive returns, with declining returns from younger and older instars (McBrien 1991). Similar patterns have been demonstrated with *Lipolexis oregmae* and *Lysiphlebia mizari* using *Toxoptera citricida* (Tsai & Wang 2002; Walker & Hoy 2003), *Monoctonus paulensis* using *A. pisum* (Chau & Mackauer 2001) and *A. ervi* using *Myzus persicae* (Colinet *et al.* 2005). Intermediate instars represent a high-quality pool of future resources for koinobiotic parasitoids, because the larva continues to grow and develop with their hosts after parasitization. Therefore, the developmental stage of a host becomes far more important for larval survival than the actual size of the host at parasitization. Generalist parasitoids that attack a wide range of species of variable sizes can have their host size selection criteria complicated, given that the optimal second and third instars may have a two- or threefold deviation in size between host species. The two hosts used in this experiment presented such a contrast, in that *A. pisum*, the pea aphid, is on average twice as large as *A. solani*, the foxglove aphid.

Parasitoids reared and then exposed to instars of the same host were able to accurately select the highest quality instar for larval development. This was true for both natal host treatments, with the distributions of attacks resulting in second and then third instar aphids being preferred in both rearing and exposure groups (figure 1). However, when parasitoids were exposed to the alternate host from which they were reared, there was a deviation from the optimal behaviour. When the larger parasitoids (*A. pisum* reared) were exposed to *A. solani*, the smaller host species, they preferentially selected the larger, lower quality, *A. solani* instars for oviposition. A consistent deviation from the optimal behaviour was demonstrated by parasitoids reared on *A. solani* and then exposed to the larger host *A. pisum*, which preferentially selected smaller instars of this host species. This pattern suggests that adult parasitoid size is influencing instar preference behaviour in *A. ervi*. However, we could not rule out the possibility that some aspects of the natal host other than the changes in adult size may have contributed to the observed preference.

In order to examine the mechanism of host size selection and to determine whether adult parasitoid size is the primary factor influencing host size selection, we investigated the relationship between adult size and host size preference within a single rearing/exposure host species, *A. pisum*. Aphids were anaesthetized to remove any factors that may have influenced the parasitoid's foraging behaviour. Parasitoid size correlated with host size preference (figure 2). This suggests that the plasticity in host size selection behaviour between natal host species groups is most probably caused by the size differentiation

that results from parasitoids developing in different hosts. Even when hosts were anaesthetized to remove many constraints on oviposition success, such as accessibility and aphid defences, parasitoids still preferred to oviposit in hosts that correlated with their own body size. This suggests a behavioural trait that has been evolutionarily conditioned to perform in conjunction with the size of the adult.

Size and fitness are generally correlated in the parasitic Hymenoptera and, as a result, a female's choice of hosts directly affects the fitness of her offspring (Lampson *et al.* 1996; Morris & Fellowes 2002). Larger female parasitoids often have higher egg loads, live longer and have higher dispersal capabilities (Eijs & van Alphen 1999). Consequently, selecting the largest host in order to maximize offspring size is a trend that is commonly seen among many parasitoids, especially idiobiotic parasitoids (Wang & Messing 2004a). However, to benefit from having a large-bodied offspring, there must exist a greater advantage than cost in achieving a large body (Leather 1988). Factors that may decrease the overall returns of selecting a larger host include a prolonged developmental time, which increases the chance of offspring predation, and increased juvenile mortality, which is commonly observed in koinobiotic parasitoids selecting the largest host instars (Sequeira & Mackauer 1992b; Harvey *et al.* 1994).

Perhaps the most important factors influencing overall reproductive returns are demonstrated by the mother parasitoid in terms of foraging success and capture efficiency. Research using *Dirhinus giffardii*, a generalist ectoparasitoid of many tephritid flies, has demonstrated that variation in female parasitoid body size, as a result of natal host development, influences host selection behaviour in that parasitoid size is positively correlated with host puparia size selection (Wang & Messing 2004a). This is thought to be owing to a trade-off between attempting to select the largest host for offspring development countered by an increased handling time in smaller wasps drilling through the thick puparia of larger host (Morris & Fellowes 2002; Wang & Messing 2004b). Consequently, smaller wasps are thought to gain greater reproductive returns from selecting a greater number of smaller hosts. A similar pattern is seen in instar-specific defences of many koinobiotic parasitoids, such as caterpillar and aphid parasitoids. Host instar-specific physical defences typically increase with age, and female parasitoids must make a choice between an increased handling time and risking injury in attempting to oviposit in a larger host (Gerling *et al.* 1990). Our study suggests that success rate is further influenced by parasitoid size, given that small parasitoids (i.e. foxglove-reared) miss more attacks, thereby wasting more time and energy when attacking larger aphids (i.e. pea aphids; figure 3). Accordingly, if handling time and capture efficiency are influenced by the ratio of parasitoid to host size, then this may have contributed to the evolution of a size-based preference policy.

The relationship between body size and capture efficiency of natural enemies is important in understanding the evolution of prey preference. The attack success of many predators is predicated on having a substantial size advantage over prey, although this is not always the case in highly specialized solitary killers and

facultative social predators (Lafferty & Kuris 2002). For aphid parasitoids that must gain control over hosts and cope with their defences, there is clearly a parasitoid to host size threshold that dictates attack success. Consequently, it is not surprising that host size selection covaries with body size in aphid parasitoids, given the existence of host-determined body growth. An asymmetry that exists within this system is that aphid defences impede the attack success of small parasitoids to a greater extent than large parasitoids. Therefore, although the small, foxglove-reared parasitoids exhibited a suboptimal instar selection regime, by selecting small instars of the larger host species they may in fact be optimizing their reproductive returns when aphid defensive behaviour is included. However, size selection behaviour in small-sized parasitoids was not provisionally based on host defensive capabilities as a suboptimal instar regime was still chosen when aphids were anaesthetized, removing instar-specific defences (figure 2). In contrast, large-sized, pea aphid-reared parasitoids preferentially attacking third and fourth instar foxglove aphids are indeed maladaptive, given that they thus preferred the lowest quality instars within that host species (Henry *et al.* 2005). Our work demonstrates how a behavioural policy may be required to maintain a certain level of flexibility when an organism has a plastic developmental strategy in order to increase oviposition accuracy, thereby optimizing reproductive returns.

Evaluation of host size in relation to one's own body size involves relative measurements that can correlate parasitoid to host size ratios. The ability to measure absolute host size has been demonstrated using *Trichogramma* egg parasitoids, which use short time-intervals when crossing a host's surface to determine host volume and subsequent egg deposition (Schmidt & Smith 1987). The aforementioned experiment demonstrated that parasitoids did not use relative measures, given that small and large parasitoids laid the same number of eggs per host volume. Our results show that *A. ervi* and possibly all aphid parasitoids rely on some aspects of their own body size to dictate which host is most profitable to attack. It is possible that the antennation process that often precedes initial attacks is a method of comparative measuring, given that antennal length generally correlates with overall parasitoid size.

The adaptive nature of a trait depends on the trait's flexibility and on the variability of the environment in which the organism lives (Kawecki & Stearns 1993). A behavioural policy that is fixed upon emergence can lead to erroneous decisions when a parasitoid is confronted by an alternate host species (Henry *et al.* 2005). This brings up interesting questions about the evolution of such linked plastic traits, given that a maladaptive policy should be selected against in a non-adapted environment (Ernande & Dieckmann 2004). Having traits fixed by the natal host for an individual's life but flexible between generations would suggest that this policy evolved under conditions where the parasitoid would have a higher probability of encountering the same host species within an individual lifetime, but possibly encounter several host species across generations. As relatively small-sized and short-lived animals, with a life expectancy in nature that may be hours rather than days, parasitoids may sample only a few host patches within their lifetime (Ellers & Jervis 2003). Owing to the parthenogenetic nature of aphid reproduction, it is quite probable that a parasitoid

will emerge within or, at least, at a short distance from the same host species patch. Consequently, a fixed behavioural policy within an aphid parasitoid's lifetime may optimize the individual's reproductive strategy, but still allow population movement between host species, suffering only a one-generation lag in performance.

In conclusion, adaptation through phenotypic evolution often involves trade-offs between traits in order to maximize fitness returns. This is especially true when traits are directly associated with reproductive success. Both host selection behaviour and adult body size are correlated with reproductive fitness in parasitoids, yet are not mutually exclusive traits. Flexibility in adult body size allows generalist parasitoids to use many host species at a cost of producing a range of adult sizes. Consequently, host selection behaviour must also maintain a level of flexibility as adult size is related to capture efficiency. These types of coadapted gene complexes allow generalist parasitoids to effectively use multiple host species over several generations. However, the fixed nature of the behavioural response, within a parasitoid's lifetime, suggests that these traits may have evolved in a patchy heterogeneous host species environment.

We thank James Page for all his hard work, the BC Greenhouse growers and NSERC for financial support. Thanks also to the Roitberg laboratory group and Carl Schwartz for statistical advice.

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