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Assortative mating and the role of phenotypic plasticity in male competition: implications for gene flow among host-associated parasitoid populations

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Local adaptation is promoted when habitat or mating preferences reduce gene flow between populations. However, gene flow is not only a function of dispersal but also of the success of migrants in their new habitat. In this study I investigated mating preference in conjunction with phenotypic plasticity using *Aphidius* parasitoids adapted to different host species. Males actively attempted to assortatively mate, but actual mating outcomes were strongly influenced by the relative size of the adult males. Results are discussed in the context of assortative mating in combination with the success of migrant males in mitigating gene flow between host-associated parasitoid populations.

Keywords: *Aphidius ervi*; local adaptation; body size

1. INTRODUCTION

The diversity of parasitic insects is often attributed to the intimate relationship they share with their host species, and the potential for disruptive selective pressures associated with different hosts to drive ecological divergence (Drès & Mallet 2002). Population divergence is further promoted if selection on traits between host-associated populations leads directly or indirectly to a reduction in gene flow between populations, thereby facilitating reproductive isolation (Mopper 1996). Reproductive isolation can evolve indirectly as a by-product of selection on individual traits, or through direct selection on premating isolation, in which case host specialization on patch or assortative mating may be favoured (Schluter 2001).

Development in contrasting environments can lead to phenotypic differences that influence the acquisition of resources, such as food or mates. For example, divergence in body size has been shown to contribute to premating isolation through mechanisms such as size-assortative mating (Nagel & Schluter 1998). Body size is positively correlated with mating success and is a predictor of mate quality in a wide range of organisms (Peters 1983). In insects, body size, among other things, is an indicator of fecundity in females and is positively correlated with mating success in males (Bonduriansky 2001).

In this paper I investigate the influence of adaptation to different host species on the development of mating outcomes in aphid parasitoids. Mating behaviour in Ichneumonid and many Braconid wasps typically involves a pre-copulatory struggle, with larger males having greater success (Teder 2005). Once a female is subdued copulation proceeds. However, when multiple males are present, as is often the case with *Aphidius* parasitoids, they frequently compete for copulatory privileges. Laboratory-reared populations of *Aphidius ervi* (Haliday) were maintained on pea *Acyrthosiphon pisum* (Harris) or foxglove aphids *Aulacorthum solani* (Kaltenbach) for a period of 2 years, by which time the populations diverged in several traits including reproductive fitness (Henry *et al.* 2008). Furthermore, parasitoids maintained plasticity in traits such as adult body size. Adult body size is a highly flexible trait in *Aphidius* parasitoids, which is determined by the size of their natal host (Godfray 1994). Male size influences mating success in many parasitoid systems (Teder 2005); however, this is the first study addressing the influence of determinant growth on mating success between host-associated populations. The objectives of the study were to determine the following:

(i) Does adaptation to different host species influence mating preference in *A. ervi*?
(ii) How does adult body size influence mating success between host-associated parasitoids?

2. MATERIAL AND METHODS

(a) *Insect stock and selection lines*

Aphidius ervi were maintained in isolation on foxglove or pea aphids, hereby denoted as F-line and P-line parasitoids, respectively. Eight F-line populations were maintained on *A. solani* feeding on *Capiscum annuum* (Solanaceae) and 12 P-line populations were maintained on *A. pisum* on *Vicia fabae* (Fabaceae). For more information on the initiation and maintenance of host selection lines, please refer to Henry *et al.* (2008).

(b) *Mating experiment*

Parasitoids were 1- to 2-day-old virgins, isolated in emergence containers, given access to only dilute honey and water. Individual females were placed in an arena with one natal host male and one non-natal host male ($n=66$). The mating arena consisted of a 40 mm aerated Petri dish with the floor cut out, resting on a leaf corresponding to the female's natal host plant. Females only ever mated once within the 15 min mating trial.

Mating events were partitioned into (i) female individual interactions with a single male (female receptiveness), (ii) male preference for female by host type, and (iii) males competing for mating events when the female had arrested and remained passive (male competition). Female receptiveness was measured as the latency from initial mount to female arrestment (pre-copulatory struggle) (ANOVA) and the probability of a male type being rejected (chi-square). Male preference was measured as the number of attempted and successful mounts combined (chi-square). Male competition occurs after female arrestment, at which time both males compete for copulatory privileges. To account for the sizes of competing males, the difference in their dry weights was compared with the probability of mating successfully (logistic regression). The probability of a male usurping another mounted male to win a mating contest was investigated (chi-square). Overall mating outcomes were compared with female host, male host and female–male interaction as factors influencing the outcome (log linear). All chi-square analyses included the four possible host population mating combinations.

One possible confound in my analysis of size is the host species effect *per se*. Thus, to determine the influence of male size on competition without the influence of different host species, the above experiment was repeated using a range of parasitoid sizes reared in pea aphids only ($n=30$; size range: 0.05–0.32 µg).

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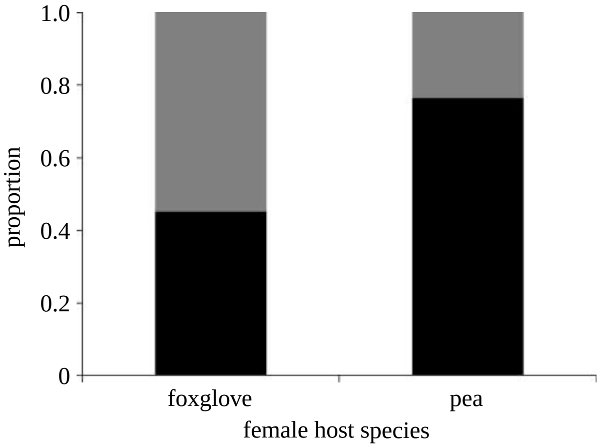

Figure 1. Proportion of assortative (black) and disassortative (grey) mate pairing outcomes by female host species (*x*-axis) when two males (one natal host species and one non-natal host species) compete for access to a single virgin female.

(c) *Insemination*

Production of female offspring was used to confirm successful insemination and that females were not cryptically choosing males. *Aphidius* parasitoids are haplodiploid, thus female wasps can choose whether or not to fertilize an egg: females develop from fertilized eggs, males from unfertilized. Post-copulation females foraged on 40 natal host aphids (3 h). Proportion insemination was analysed for the four possible mate pairings (chi-square). Analyses were performed using JMP 6.0 statistical software (SAS Institute, Cary, NC, USA).

3. RESULTS

(a) *Mating experiment*

The log-linear analysis indicated that male host species contributed the greatest amount of variance to mating success (log-linear likelihood ratio, $\chi^2_2=3.55$, $p=0.169$; male host, $\chi^2_1=6.908$, $p=0.009$). Female host and female–male host interaction did not significantly influence mating success. P-line males won more mating outcomes, 67 per cent, compared with F-line males, 33 per cent, irrespective of female host population (figure 1). To determine whether females were preferentially selecting P-line males, pre-copulatory struggle latency was analysed for each male by host species (ANOVA: male host, $F=1.53$, $p=0.23$; female host, $F=0.26$, $p=0.61$; male–female, $F=1.19$, $p=0.28$). Furthermore, failed mounts by males did not differ ($\chi^2_{1,26}=0.22$, $p=0.64$). These results indicate that female mate choice is not responsible for P-line males winning more mating events.

Variation was found in male mating attempts ($\chi^2_{1,125}=7.734$, $p=0.0054$), with parasitoids attempting to mate assortatively 69 and 88 per cent for F- and P-lines, respectively. P-line males on average were much larger than F-line males (mean dry weight: F-line, 0.053±0.015 μg; P-line, 0.11±0.041 μg). Size differences between males influenced the probability of a P- or F-line male successfully mating (logistic regression: $\chi^2_{1,45}=11.09$, $p=0.0009$; figure 2*a*). Female size did not influence P- or F-line males successfully mating ($\chi^2_{1,39}=0.041$, $p=0.84$). The ability to usurp a mounted male was influenced by male host species ($\chi^2_{1,23}=3.89$, $p=0.048$). P-line males usurped F-line males 40 per cent of the time; F-line males usurped P-line males 7.1 per cent of the time.

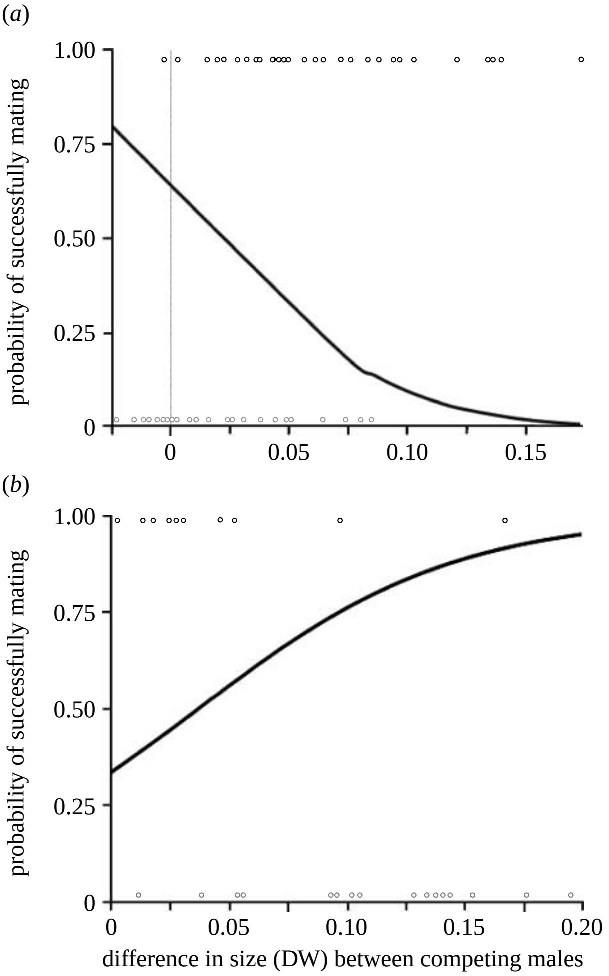

Figure 2. Logistic regression plot describing the probability of winning a mating contest in relation to the difference in size (DW, dry weight) between the two competing males (*x*-axis), for competing (*a*) F-line and P-line males and (*b*) males reared only in pea aphids. Weight difference = (F-line) − (P-line). The zero line in (*a*) represents parasitoids of equal size, with values to the right indicating P-line males are larger and to the left F-line males are larger. Circles represent individual successful mating events; (*a*) black circles, pea reared; grey circles, foxglove reared; (*b*) black circles, small male successes; grey circles, large male successes.

The second mating experiment using pea aphid reared parasitoids only revealed that body size positively influenced a male's ability to win male competitions for mating events (logistic regression, $\chi^2_{1,25}=4.81$, $p=0.028$; figure 2*b*).

(b) *Insemination*

Post-copulated females produced female offspring 81.43±8.65% of the time. No difference was found in the number of female offspring produced from the four mating pairs ($\chi^2_{3,39}=1.428$, $p=0.69$). This confirmed that there was no cryptic mate choice by females.

4. DISCUSSION

Parasitoid host selection lines differed in the proportion of successful mate pairings (figure 1). Female mate choices, as evaluated by the number of rejected males and latency of the pre-copulatory struggle, indirectly indicate that females are not actively

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choosing males. Furthermore, following the pre-copulatory struggle, females remained passive during which time males frequently competed for access to the female by grappling until one male successfully acquired a copulatory lock with the female. This suggests that female mate choice within this system is most likely superseded by male competition. It is possible that females may exhibit cryptic male choice, in that they have the option to use a male's sperm to manipulate sex ratios. The insemination results, however, indicate that females were equally likely to use sperm to produce female offspring irrespective of the male's natal host population.

Males attempted to assortatively mate with females from their natal host population more frequently than from the non-natal host population (69 and 88% for F- and P-lines, respectively). Male mate choice is widespread in insects and is predicted to be favoured when there is high variance in quality among individual females (Parker 1983). In parasitoid systems where reproductive success of males is completely mediated by the female's ability to successfully oviposit daughters, preferentially selecting high-quality females may have evolved as a means of maximizing male fertilization success (Bonduriansky 2001). Assortative mating is an important mechanism contributing to the reproductive isolation of diverging populations (Drès & Mallet 2002). Host-associated assortative mating has been shown in a number of phytophagous insect species, which is a process thought to speed the evolution of specialization and potentially facilitate speciation (Schluter 2001).

Although males actively attempted to mate assortatively, the asymmetric skew of the mating outcomes suggests that there is more to mating success than purely male choice. P-line males mated assortatively 74.2 per cent of the time, compared with F-line males that successfully mated assortatively only 45.1 per cent of the time (figure 1). When considering the probability of successful mating based on male body size (figure 2*a*), coupled with the average size deviation between the larger P-line compared with the smaller F-line males, it appeared that male body size was a factor contributing to P-line males winning a greater number of competitive mating events. The role of body size was demonstrated using males reared on a single host species (pea aphids), in that similar-sized males have an equal probability of winning a mating event (figure 2*b*, x-axis); however, as the deviation in sizes increased between the two competing males, the larger male increased its probability of successfully mating. Larger P-line males also had a greater proportion of usurping events where the male physically removed the other, previously mounted male, or in several cases actually mated overtop the smaller F-line males to win the mating event. These results demonstrate that body size plays a key role in *A. ervi* male competition, which has also been demonstrated in several other parasitoid systems (e.g. Teder 2005). Furthermore, this shows how assortative mating in F-line individuals can be decreased by the competitive advantage that larger P-line males have when competition occurs.

Previous studies have suggested that *Aphidius* parasitoids exhibit some mate choice, in that mating success has been shown to be the greatest when individuals are from the same host species population (Powell & Wright 1988). This study demonstrates that it is male *A. ervi* that actively attempt to mate assortatively. In addition, the influence of host-determined body size presents a layer of complexity, unique to parasitoids, that has important implications for gene flow between host-associated parasitoid populations. Parasitoids like many insects are known to exhibit different degrees of host fidelity; however, in most parasitoid species at least a portion of males disperse to local patches (Hardy *et al.* 2005). My results suggest that when host-associated conspecific parasitoid populations exist in sympatry, a male's natal host will undoubtedly influence its ability to exploit neighbouring female populations. This presents an interesting scenario wherein the potential for asymmetric gene flow between populations could exist due to the success of migrant males. Parasitoid populations associated with large natal hosts are likely to resist gene flow from parasitoids immigrating from smaller host species, due to the advantage large males have in competitive mating on their natal host patch. Furthermore, large males gain an advantage when dispersing as they can outcompete smaller males for access to females in a non-natal host patch. Parasitoids using smaller host species are therefore more susceptible to having local adaptation slowed or disrupted by gene flow from neighbouring populations.

Host-associated genetic divergence has been reported in many insect species, including sympatric aphid parasitoid populations (Vaughn & Antolin 1998). A substantial amount of research has focused on host preferences and host fidelity in females (Godfray 1994), which are mechanisms that potentially conserve host-adapted gene pools. Although the aforementioned processes theoretically contribute to local adaptation in host-associated insect populations (reviewed in Mopper 1996), the impact of mating preference coupled with the success of migrant males has virtually been ignored in parasitoids, despite its importance in mitigating gene flow. Assortative mating in conjunction with phenotypic plasticity in male mating success thus represents a novel mechanism influencing the movement of genes between host-associated parasitoid populations.

Although male-based assortative mating occurred within this study, under the present experimental design it was not possible to determine the signal dictating the male response. Males may have been size assortatively mating, have evolved mating preferences as a by-product to different selective regimes, or may have conditioned responses based on preimaginal or early emergence learning. Further research is required to determine whether male mating preference is due to genetic changes brought about by adaptation to a host species, or preference for a particular phenotype induced by developing in a host for a single generation.

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