Genetic relationship between olfactory response and fitness in *Cotesia glomerata* (L.)

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The flight response of the parasitic wasp *Cotesia glomerata* (L.) to semiochemicals from a plant-host complex is subject to genetic variation. The significance of additive genetic variance for the odour-guided behaviour has been demonstrated by bidirectional selection. In order to understand the potential and constraints for phenotypic evolution in olfactory response under the pressure of natural selection, this study was to investigate genetic covariation between the odour-guided behaviour and life-history traits and its genetic correlation with the efficiency of parasitism. A paternal half-sib analysis revealed that there was no significant genetic correlation between this behavioural character and any of three life-history traits examined (the development time of immature stages, the body size of female wasps, the number

of female wasps per brood). Comparisons between the selected high and low olfactory-response strains showed the lack of correlated responses in these life-history traits to bidirectional selection on the odour-guided behaviour. On the other hand, genotypic differences in the ability of olfactory response significantly affected the efficiency of parasitism. In comparison with the low olfactory-response strain, female wasps from the high olfactory-response strain were able to parasitize more host larvae in a wider area of habitats. This study provides the first evidence of links between olfactory response and population success in parasitoids from a genetic perspective.

Heredity (2004) 92, 579–584. doi:10.1038/sj.hdy.6800464

Keywords: parasitoid; *Cotesia glomerata*; olfactory response; life-history traits; parasitism; genetic covariation

Introduction

Parasitic wasps (parasitoids) rely to a larger degree on chemical signals in search for hosts in the field, although visual, acoustic and tactile stimuli are also involved in the host-location process (Vet and Dicke, 1992; Tumlinson *et al.*, 1993). The volatiles emitted from the plants infested by host herbivores represent the most prevalent form of information about the presence of herbivore hosts, as such semiochemicals can be conveyed through air over distances (Vet, 1999). Since olfactory response plays an essential role in the survival and reproduction of individuals and hence population success in parasitoids, it will be subject to natural selection (Vet, 2001).

Empirical studies have shown that a significant proportion of phenotypic variation in odour-guided behaviours of parasitoids is genetic in origin (Prevost and Lewis, 1990; Gu and Dorn, 2000; Campan *et al.*, 2002). Additive genetic variance in flight response to semiochemicals from a plant-host complex has been demonstrated directly by laboratory selection (Wang *et al.*, 2003). The existence of additive genetic variance in a population predicts the potential of a character to respond to selection (Falconer, 1989). However, single characters will evolve together if they are correlated genetically with one another and either or both are correlated genetically with fitness (Stearns, 1976; Bell, 1997). Therefore, the knowledge of not only genetic variation for this

behavioural character but also the genetic covariation with other fitness traits is essential to address the issue of evolutionary changes in the olfactory response of parasitoids to the environment.

This study was to address two questions: (1) is olfactory response genetically correlated with other fitness components in parasitoids? (2) do genotypic differences in the ability of olfactory response influence the efficiency of parasitism? For these purposes, a sib analysis was conducted to investigate genetic correlations between flight response to semiochemicals from a plant-host complex and three life-history traits (the development time of immature stages, the body size of female wasps, and the number of female wasps per brood) in the parasitic wasp *Cotesia glomerata* (L.). Correlated responses in these life-history traits to bidirectional selection on flight response to semiochemicals from a plant-host complex were also examined by multigenerational comparisons of the two strains that were genetically differentiated in the odour-guided behaviour (Wang *et al.*, 2003). Furthermore, the two selected strains were evaluated for their habitat colonization capability and host location efficiency.

Materials and methods

Sib analysis

Parasitoids originated from a Swiss field population of *C. glomerata*. The population samples were obtained from the host larvae (*Pieris brassicae*) parasitized by field wasps. In total, 52 potted cabbage plants (*Brassica oleracea* var. *capitata* cv. Mezzo) were distributed in cabbage fields at Feldi in Canton Zurich. Each of these potted plants

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Received 24 October 2003; accepted 19 February 2004

carried 5–15 neonate larvae of *P. brassicae*. After exposure to field wasps for 2 days, these plants were brought back to an insectary. The recovered *P. brassicae* larvae were fed with cabbage leaves in insect cages (30 × 30 × 30 cm) within a climate chamber at 25°C, 70% RH and L16:D8. Cocoon clusters of *C. glomerata* from the parasitized hosts were collected and kept at 21°C, 70% RH and L16:D8.

Six cocoons were separated from each of the 97 field-derived broods, and each of these cocoons was placed singly in a small vial for emergence. From the wasps obtained from each brood, either one male or one female was randomly chosen. The selected individuals were mixed as a group according to sex. Male and female groups were reared separately in nylon gauze cages (30 × 30 × 30 cm) and fed with honey and water. Three days later, 12 male and 60 female wasps were randomly taken from the respective group. Each male (sire) was allowed to mate with five females (dams). The females were placed one after another together with the male in a small transparent vial (4 × 2 cm) that allowed direct observation of the mating process. A female was considered as having successfully mated only if copulation lasted for longer than 5 s. After copulation, the mated female wasp was removed from the vial and transferred to a cylinder cage (12.5 × 16 cm). The five dams (females) mated to the same sire (male) were kept together in a cylinder cage with honey and water.

Five 2nd-instar *P. brassicae* larvae were offered to each mated female wasp for parasitism 1 day after copulation. To avoid superparasitism (Gu *et al.*, 2003), only one oviposition was allowed in each caterpillar. One host caterpillar was placed in a glass tube that held a female wasp, and immediately removed from the tube after completion of the first oviposition. The five *P. brassicae* parasitized by the same female wasp were reared together on cabbage leaves in a plastic box (20 × 10 × 8.5 cm). The duration of development before egression of parasitoid offspring was observed for each brood.

Two days after egression and pupation of parasitoids, the cocoon clusters (broods) were collected and placed separately in vials (3 × 5.5 cm) according to hosts, with one cluster per vial. Emergence of each brood was checked for the number of male and female wasps. Wasps were fed with honey and water in a cylinder cage (12.5 × 16 cm), but deprived of any contact with cabbage- or host-related cues. Four to five days after emergence, 30 female wasps were randomly taken from different broods produced by a single dam, and tested for flight response to hexane extract from a plant-host complex in a wind tunnel, as described in Wang *et al.* (2003). The flight test was conducted at a temperature of 20 ± 1°C, relative humidity of 50–60%, wind speed of 30–35 cm/s and light intensity at 640–650 lux. Each individual was given a chance to take off from a release platform. After release, the wasp was observed for its behaviour within a maximum of 2 min. A straightforward or zigzagging flight towards an odour source, which was set up upwind at a distance of 50 cm from the release platform, was recorded as 'flight response'. A random flying performance was considered failure in flight response to the odour source. The bioassay was conducted during 3 consecutive days. The same number of individuals from each dam was tested on each day as the wasps became

available. Random samples were also taken from the broods derived from each dam to check the body size of female wasps. The body size of wasps was measured as the mean tibia length of the hind legs.

In total, 11 of the 12 sires used in the experiment had at least two dams that produced enough female offspring for the bioassay. The parasitoid offspring of each dam constituted a full-sib family and those from the different dams sharing the same sire comprised half-sib families. The percentage of flight response was calculated for each family since the odour-guided behaviour is a binary character. Percentages of flight response were subject to arcsine-square-root transformation prior to the correlation analysis. Product-moment correlations between the odour-guided behaviour and each of the three life-history traits (the development time of immature stages, the body size of female wasps, and the number of female wasps per brood) were calculated based on the mean values of paternal half-sib families, as such estimates are not confounded with the nonadditive genetic components such as dominance and maternal effects (Falconer, 1989). All analyses were performed with the statistical program StatView 5.0.1.

Examination of correlated responses in life-history traits

Bidirectional selection led to significant divergence in flight response to semiochemicals from the plant-host complex between the two selected strains (Wang *et al.*, 2003). Correlated responses to selection on the odour-guided behaviour in three life-history traits (the development time of immature stages, the body size of female wasps and the number of female wasps per brood) were examined for the high and low olfactory-response strains in each generation of selection. As in the sib analysis, the development time of immature stages was recorded as the time from oviposition to egression from the host. The body size of female wasps was measured as the mean length of the two hind tibiae, as described above. The number of female wasps per brood was obtained by counting the wasps from a single host. To test for differences between the two strains, an analysis of variance (ANOVA) with repeated measures (ie the generation) was conducted using the program StatView.

Evaluation of the efficiency of parasitism for the two selected strains

The efficiency of parasitism for the two selected strains was evaluated in a greenhouse experiment. After four generations of selection, the progeny of the high and low olfactory-response strains were used for this experiment. Releases were carried out in neighbouring greenhouse compartments with the same environmental conditions: 24 ± 3°C, 60% RH and L16:D8. A cabbage plant patch with four rows of 10 plants was established in each compartment, using 2-month old potted plants (*B. oleracea* L. var. *capitata* cv. Mezzo). At 24 h before wasp release, 12 plants, each infested by five 2nd instar *P. brassicae* caterpillars, were randomly arranged among the 28 uninfested plants within the patch. Plants were positioned 10 cm apart from each other. In one experimental set-up, wasps from each strain were released in the centre of the plant patch, and in another set-up, they were released at a distance of 80 cm away from the cabbage patch. In each scenario, the two strains were

released simultaneously, each in a separate compartment, and the release was replicated by changing compartments.

From each strain, 20 mated female wasps, aged 3–5 days, were randomly selected for each experimental replicate. They were released at 10:00 am. Every 3 h thereafter, four caterpillar-infested cabbage plants were randomly taken from the plant patch and replaced by uninfested plants. The distance of each sampled plant from the wasp-releasing point was noted. Sampling was made 3, 6 and 9 h after wasp release, respectively. To determine parasitism, all caterpillars on the same plant were reared within a single box (20 × 10 × 8.5 cm) in an insectary at 21 ± 1°C, 40–60% RH and L16:D8 until pupation of the parasitoids. The product of parasitism rates on individual host-infested plants and their distances to the wasp release point was used to define the efficiency of parasitism. Thus, this efficiency index measures the capability of both habitat colonisation and host location. To test for differences in the efficiency of parasitism between the two selected strains, an ANOVA with repeated measures (ie the sampling time) was conducted for each release scenario, using the program StatView.

Results

Paternal half-sib analysis for genetic correlations

The odour-guided behaviour was positively correlated with the development time of immature stages and the number of females per brood and negatively with the tibia length of female wasps (Table 1). However, none of these correlation coefficients differed significantly from

zero. Thus, there were no significant genetic correlations between olfactory response and these life-history traits in *C. glomerata*.

Examination of correlated responses in life-history traits

After the first generation of selection on flight response to semiochemicals from the plant-host complex, the upward-selected strain already differentiated significantly from the downward-selected strain in the odour-guided behaviour, and their divergence continued with further selection in subsequent generations. The data were shown in a previous paper (Wang *et al.*, 2003). Changes in the three life-history traits also occurred during the four generations of selection (Table 2). The mean development time of immature stages in both strains decreased from the first to fourth generation of selection. The mean body size of female wasps, measured as the mean length of the two hind tibiae, increased from the first to the third generation, and then remained unchanged in the fourth generation. The mean number of females per brood increased from the first to the second generation of selection and then decreased in the third and fourth generations. However, these changes were not caused by selection on the odour-guided behaviour, as generational differences in none of these life-history traits were significant between the two strains, though the development time of immature stages and females per brood showed interactions between strain and the generation of selection (Table 3).

Evaluation of the efficiency of parasitism for the two selected strains

The two strains differed in the host-foraging activity of female wasps with respect to time elapse after release. When released in the middle of a cabbage plant patch, wasps from both strains parasitized host caterpillars close to the release point within the first 3 h. As time elapsed, the patch area colonized and the number of hosts parasitized by female wasps from both strains increased. In comparison to the low olfactory-response strain, however, female wasps from the high olfactory-response strain parasitized more hosts in larger areas with processing time (Figure 1). In the case where wasps were released outside a plant patch, differences in the performance of the two strains were also evident. At 3 h

Table 1 Genetic correlations between olfactory response and life-history traits (development time of immature stages, tibia length of female wasps, number of females per brood), based on mean values of paternal half-sib families

Life-history trait	Correlation coefficient	n	P-value
Development time	0.191	11	0.584
Female tibia length	−0.219	11	0.530
Females per brood	0.402	11	0.229

Table 2 Mean values and standard deviations of life-history traits (development time of immature stages, body size of female wasps, number of females per brood) in the high and low olfactory-response strains of *Cotesia glomerata* with regard to different generations of selection (sample size shown in parentheses)

Generation of selection	Strain	Life-history trait		
		Development time (days)	Female tibia length (mm)	Females per brood
1	High	13.83 ± 1.49 (76)	0.787 ± 0.079 (175)	16.4 ± 14.1 (42)
	Low	13.80 ± 1.55 (120)	0.801 ± 0.068 (200)	17.5 ± 15.8 (48)
2	High	13.15 ± 0.39 (93)	0.824 ± 0.067 (250)	19.8 ± 15.4 (80)
	Low	13.44 ± 0.66 (110)	0.829 ± 0.060 (300)	20.9 ± 16.8 (69)
3	High	12.42 ± 0.76 (103)	0.861 ± 0.056 (300)	13.2 ± 11.0 (87)
	Low	12.64 ± 0.79 (138)	0.842 ± 0.061 (235)	16.9 ± 16.6 (70)
4	High	11.96 ± 0.82 (115)	0.842 ± 0.061 (204)	11.2 ± 10.3 (81)
	Low	11.84 ± 0.91 (118)	0.844 ± 0.053 (115)	6.5 ± 9.5 (89)

Table 3 Analysis of variance for differences in life-history traits (development time of immature stages, tibia length of female wasps, number of females per brood) between the high and low olfactory-response strains, using the general linear model with repeated measures (ie generations)

Source of variation	Life-history traits								
	Development time			Female tibia length			Females per brood		
	df	F	P	df	F	P	df	F	P
Strain	1	1.96	>0.05	1	0.03	>0.05	1	0.72	>0.05
Generation	3	137.42	<0.001	3	59.52	<0.001	3	16.09	<0.001
Strain × generation	3	2.72	<0.05	3	0.68	>0.05	3	3.31	<0.05

Figure 1 Temporal-spatial distribution of the host *Pieris brassicae* parasitized by the high and low olfactory-response strains of *Cotesia glomerata*, released in the centre of a cabbage plant patch. The data pooled from two replicates are presented since no significant differences were shown between replicates. The circle size indicates the number of parasitized host caterpillars (1, 2, 3, 4 or 5) on the plant (⊙ — different levels of parasitism on a plant of the same position sampled in two replicates, ● — the same level of parasitism on a plant of the same position sampled in two replicates).

after release, female wasps from the high olfactory-response strain had already parasitized some hosts whereas those from the low olfactory-response strain appeared to have not colonized the plant patch yet (Figure 2). In both replicates of release, the differences between the two strains continued as time elapsed.

The differences between the two strains are quantified using an index for the efficiency of parasitism (Figure 3). The analysis of variance showed that the efficiency of parasitism was significantly different between the two strains ($F=7.60$, $df=1$, 12 , $P<0.02$) when wasps were released within plant patches, though strain × replicate interaction was also significant ($F=5.61$, $df=1$, 12 , $P<0.05$). Despite clear differences between the two strains during the first 3 h after wasps were released outside plant patches, the mean values for the efficiency of parasitism were overlapped between the two strains after 6 and 9 h of release; thus their general efficiencies of parasitism were not statistically significant ($F=2.46$, $df=1$, 12 , $P>0.05$). In both release scenarios, no significant differences were observed between replicates of release ($F=0.16$, $df=1$, 12 , $P>0.6$ for release within

Figure 2 Temporal-spatial distribution of the host *Pieris brassicae* parasitized by the high and low olfactory-response strains of *Cotesia glomerata*, released outside a cabbage plant patch. The data pooled from two replicates are presented since no significant differences were shown between replicates. The circle size indicates the number of parasitized host caterpillars (1, 2, 3, 4 or 5) on the plant (● — the same level of parasitism on a plant of the same position sampled in two replicates).

plant patches; $F=2.82$, $df=1$, 12 , $P>0.1$ for release outside plant patches).

Discussion

The paternal half-sib analysis revealed no significant correlation between the odour-guided behaviour and the development time of immature stages, the body size of adults or the number of female wasps per host in *C. glomerata*. It should be pointed out, however, that the structure of genetic covariation among different characters could vary with the environmental conditions under which the experiment was carried out or due to sampling errors (Service and Rose, 1985). This is exemplified in a quantitative genetic study with the light brown apple moth, *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae). In this herbivore insect, the structure of genetic covariations between flight capacity

Figure 3 The efficiency of parasitism of the high and low olfactory-response strains of *Cotesia glomerata* (the upper part presents the data from the experimental scenario where female wasps were released in the centre of a cabbage plant patch, and the lower part the data from the experimental scenario where wasps were released outside a cabbage plant patch).

and life-history traits (Gu and Danthanarayana, 1992) and among life-history traits (Gu and Danthanarayana, 2000) were shown to differ at two laboratory temperatures. The present experiment was carried out under constant laboratory conditions, which are different from the environmental conditions that *C. glomerata* experience in the field. In view of the possible environmental effect, caution must be taken when interpreting genetic correlations estimated from laboratory analyses and when extrapolating these results to different situations.

In comparison to sib analysis, selection experiments are considered to be more powerful tools to probe into the genetic architecture of organisms (Scheiner, 2002). Bidirectional selection on flight response to semiochemicals from the plant-host complex in *C. glomerata* diverged the two selected strains in opposite directions, demonstrating the presence of additive genetic variance in the odour-guided behaviour (Wang *et al.*, 2003). However, the two selected strains did not show consistent differences in the life-history traits examined in different generations of selection. The lack of correlated responses in these life-history traits validated the results derived from the sib analysis. Therefore, there is no evidence for genetic covariation between the odour-guided behaviour and life-history traits in this parasitoid species. The absence of significant genetic covariation between the odour-guided behaviour and other fitness traits supports that the ability of flight response to the herbivore-induced plant odour is located at the sensory level rather than in flight capacity (Wang *et al.*, 2003). Although the empirical data obtained from this study do not warrant a generalization that olfactory response is not correlated with life-history traits in parasitoids, a genetic analysis for a natural population of *Drosophila*

melanogaster also showed that genetic correlations between an odour-guided behaviour (ie benzaldehyde avoidance) and fitness traits were not significantly different from zero (Mackay *et al.*, 1996). It has been interpreted that the odour-guided behaviour shows low significant genetic correlations with fitness traits if the number of loci affecting olfactory response is low compared to the number of loci affecting total fitness (Mackay *et al.*, 1996). Whether this interpretation applies to the case of *C. glomerata* remains to be answered.

The odour-guided behaviour directly influenced the efficiency of parasitism in *C. glomerata*. The strain with high olfactory response was more capable of habitat exploitation and host location than the strain with low olfactory response. Clearly, these differences resulted directly from genetic differentiation in the odour-guided behaviour, since the two strains were not significantly different in life-history traits, including the body size of female wasps (this study) and flight capacity (Wang *et al.*, 2003). Apparently, the positive relation between olfactory response and host-foraging performance in parasitoids is in contrast to the relationship between olfactory response and prey-searching activities in predators. In the predatory mite, *Phytoseiulus persimilis* (Athias-Henriot), the strain with strong olfactory response tended to have a shorter residence time on infested leaf disks, leading to less efficacy in exploiting a local prey patch in comparison to the strain with weak olfactory response (Margo-lies *et al.*, 1997). Nevertheless, the apparent trade-off between patch location and patch residency in predatory mites was compounded by phenotypic correlation between patch residency and prey consumption (Jia *et al.*, 2002).

Previous studies have demonstrated that there is significant additive genetic variance for olfactory response to semiochemicals in the natural populations of *C. glomerata* (Gu and Dorn, 2000; Wang *et al.*, 2003). In theory, the existence of genetic variance in a character can be due to the antagonistic pleiotropy manifested as negative genetic correlations between the character in question and fitness (Rose and Charlesworth, 1981; Rose, 1982) and/or result from disruptive selection in a variable environment through genotype-environment interaction (Ewing, 1979; Gillespie and Turelli, 1989). Comparisons of the two selected strains in three life-history traits and the efficiency of parasitism do not suggest that there are negative genetic correlations between the odour-guided behaviour and other fitness traits in this parasitoid. These findings imply that the habitat heterogeneity of this generalist parasitoid might play a major role in the maintenance of genetic variance in the odour-guided behaviour within natural populations, as has been suggested previously (Wang *et al.*, 2003). Since the life-history traits, such as the development time of immature stages and the number of females per brood, in different olfactory response strains varied differently with different generations of selection, such interaction could also contribute to the presence of genetic variance for olfactory response in the parasitoid populations.

In summary, the genotypes of *C. glomerata* that show a higher response to semiochemicals from the plant-host complex are more efficient in exploiting habitats and locating hosts than those with a lower olfactory response, though the life-history traits appeared not to be

correlated with the odour-guided behaviour. This is the first evidence showing a genetic relationship between olfactory response and the efficiency of parasitism and hence with population success in parasitoids, although the link between olfactory response and the host-location capability was demonstrated by various studies on conditioning or associative learning in other parasitoids (Papaj and Vet, 1990; Turlings *et al*, 1993). Empirical studies on the subject in more species will advance our understanding of the tri-trophic interactions involving plants, herbivorous insects and parasitoids from a genetic perspective. Concurrently, the knowledge based on further empirical data may point to new possibilities of improving parasitoids as biological control agents by genetic manipulation of their behavioural response to herbivore-induced plant chemicals. In addition, the study of possible interaction with learning of host-finding cues can precisely evaluate the advantages of improved olfactory response through genetic selection.

Acknowledgements

Thanks are due to Henry Wöhrnschimmel, David Wettstein, Lena Obrist and Tanja Christoffel for assistance with insect cultures. We are grateful to Dr Anja Rott, Dr Kathrin Tschudi-Rein and Dr Jörg Samietz for helpful comments on the manuscript. The comments and suggestions from an anonymous reviewer improved the manuscript.

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