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Individual variation in oviposition preference, and its interaction with larval performance in an insect predator

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Abstract Individual female *Episyrphus balteatus* (De-Geer) (Diptera: Syrphidae) show different oviposition preferences when presented with two aphid prey species, *Aphis sambuci* L. and *A. fabae* (Scop). After larvae were reared on those aphids, some fitness components indicated that individual females were adapted to different host-use strategies, with preference for one aphid prey species entailing a trade-off in poorer performance on another. We interpret the pattern of significant interactions as suggesting that natural selection has responded to the nutritional value of prey.

Key words Predators · Individual variation · Preference-performance interaction · Syrphidae

Introduction

Often adult females exhibit a hierarchy of preference among hosts (e.g. Wiklund 1981; Courtney et al. 1989; Nylin and Janz 1993), but whether this is correlated with the performance of their offspring is a controversial point (Thompson 1988). In insects sedentary as larvae, we would expect a female's decision about where to lay her eggs to be related to subsequent offspring performance, and thus that there would be a preference-performance linkage. Several studies have tested for this linkage using survival, growth rate and reproduction as performance measures. In a number of cases a strong association has been found (e.g. Rausher 1982; Rausher and Papaj 1983; Via 1986; Singer et al. 1988; Nylin and Janz 1993; Barker and Maczka 1996), but surprisingly often the relationship has been poor (e.g. Wiklund 1975; Rausher 1979; Williams 1983; Roininen and Tahvanai-

nen 1989; Courtney and Kibota 1990; Burstein and Wool 1993; review in Thompson and Pellmyr 1991). The concordance between oviposition preference and offspring performance is clearly complex (Janz et al. 1994), perhaps due to inadequate measures of performance (Thompson 1988), other unmeasured ecological factors, such as selection for enemy-free space, that may be more important in promoting specialization than nutritional value (Nylin and Janz 1993), or other ecological factors (see reviews by Thompson and Pellmyr 1991; Singer et al. 1994; Schoonhoven et al. 1998).

Individual variation is a basic feature of insect-plant relationships (Schoonhoven et al. 1998), but has not been studied as often as perhaps is required for proper understanding of different host selection strategies and the selection pressures that generate them (Janz et al. 1994). Several studies have shown variation in host selection behaviour or performance among and within populations of phytophagous insects (e.g. Fox and Morrow 1981; Tabashnik et al. 1981; Wiklund 1981; Papaj and Rausher 1983; Jaenike 1990; Scriber et al. 1991; Bernays et al. 1992). Within a population of an insect species, there may also be individual variation in the relationship itself between adult oviposition preference and consequent larval performance. In a study of a natural population of the butterfly *Euphydryas editha*, Ng (1988) found that oviposition behaviour differs among individual females and that oviposition preference by individual females and their offspring's performance was correlated, and equivalent to different host-use strategies. Some females preferred certain plants for oviposition, and their larvae survived better on these plants. Other females showed no preferences (i.e. were generalists), and their larvae showed no differences in survival on different plants. This interaction between genotype and environment reflects specialization via adaptation, and has been demonstrated in several other systems (e.g. leaf miners, Via 1984, 1986; aphids, Via 1990).

In the case of predatory insects, such investigations are limited to one or two studies at the species or pop-

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ulation level. For example, in two sister species of chrysopids, the generalist *Chrysopa quadripunctata* was able to reproduce regardless of prey type, but the specialist *C. slossonae* did not lay fertile eggs in the absence of its own prey (woolly alder aphid); the larvae also differed in their response to different prey types, although less than the adults (Tauber and Tauber 1987). The larvae of both the generalist and the specialist developed more slowly and suffered higher mortality when offered their less preferred prey. Genetic crosses showed that the underlying differences are genetic. In a further comparative study of these two chrysopids, Albuquerque et al. (1997) demonstrated the physiological trade-offs associated with the evolution of feeding specialization: the specialist was unable to reproduce on the generalist's prey, and its rate of oviposition, adult size, and egg fertility were reduced. At the population-level comparison, larvae from three populations of the generalist predator, *C. quadripunctata*, when reared under common environmental conditions, showed significant geographic variation in quantitative aspects of feeding and defensive behaviour (Tauber et al. 1995).

During a study of the overall pattern (across individuals) of oviposition preference and larval performance in an aphid predator, *Episyrphus balteatus* (DeGeer) (Diptera: Syrphidae; H. Sadeghi and F. Gilbert, unpublished work), we noticed substantial differences among individual females in their oviposition preferences. While on average across all females there were no major differences in larval performance among aphid prey species, this may mask substantial individual variation. In addition, in our earlier experiments 3-day-old larvae were transferred to different aphid prey species, possibly obscuring very early effects of prey taxon.

This study aims to investigate individual variation in oviposition preference and the degree of concordance between maternal preference and offspring performance in *E. balteatus*. We do this by looking for a genotype \times environment interaction in components of fitness in the offspring of individual females reared from eclosion feeding on different aphid prey species.

Materials and methods

Study organisms

E. balteatus is one of the commonest hoverflies during the summer in the United Kingdom. Its larvae have been reported from colonies of more than hundred aphid species worldwide (F. Gilbert, unpublished work). However, field sampling (H. Sadeghi, unpublished work) showed that the larval distribution is far from random among different aphid species. We investigate here the consequences of discrimination between elder aphid (*Aphis sambuci* L., collected from the field from elder, *Sambucus nigra* L.) and bean aphid (*A. fabae* Scopoli, fed on laboratory-cultured broad bean plants, *Vicia faba* L.). Both aphids are among the hoverfly's natural prey in the Nottingham area (H. Sadeghi, unpublished work), although since it is a migrant, the implications of local prey availability are unclear.

Experimental procedure

To investigate possible variation in oviposition preferences among syrphid females and consequently categorize them into different groups, a large number of females were used initially. These females originated from a laboratory culture established from wild-caught females for no more than three generations.

To have a group of females of the same age, females were induced to lay eggs on cut sections of broad bean plant infested with pea aphids. Eggs laid over 5–6 h were placed in several petri-dishes and kept till hatching. Larvae were fed with pea aphids until adult. All newly emerged adults were kept in a large illuminated cage in constant conditions of $21 \pm 1^\circ\text{C}$ and daylight of 15 h; they were fed on bee pollen (Sigma, Cat. No. P-8753), crystalline sugar placed on petri-dish lids on the floor of the cage, and water provided on a soaked pad of cotton wool placed in a bottle. During the preoviposition period, cut sections of broad bean plant infested with pea aphids were frequently placed in the cage as an oviposition stimulant. Under these conditions, usually 14 days after emergence the majority of females are ready to lay eggs. Nevertheless, to be certain, all females were allowed access to pea aphids for another 5 days, and hence oviposition preference tests began 19 days after eclosion.

Oviposition preference was assessed by offering the two test aphids in random order on cut sections of their host-plant in a no-choice situation (each aphid offered one after the other, not simultaneously) to singly caged females for 1 h each per day. Great care was taken to ensure that all cut sections were of about the same size and with the same number of aphids of various instars. The number of eggs laid in response to the subject aphid was counted, and the aphid replaced by the other aphid species. This procedure lasted 4 days for each female. Based on the total percentage of eggs laid on each aphid during these 4 days, each female was transferred into one of three large cages: cage A (females laying $> 60\%$ of their eggs on elder aphids); cage B (females laying $> 60\%$ of their eggs on black bean aphids) and cage C (females showing no or weak preference between elder and black bean, with neither receiving more than 60% of the total eggs laid by the female: we did no further experiments with this group). The procedure of categorizing females into groups continued until 15 females had been placed in each group, A or B: at this time there were 60 females in group C. All test females were kept in constant conditions, similar to the stock culture.

To investigate whether oviposition preferences by individual females are in concordance with their offspring performance, 11 females of group A or B were selected randomly and put singly in small cages. Individual females were induced to lay eggs by offering both test aphids simultaneously for several hours. After obtaining enough eggs from each female, two sets of 20 eggs were selected from each female and placed separately in petri dishes to hatch. Subsequent larvae were allocated either elder or bean aphids throughout their larval development. Since generally the percentage of hatching was low (in some cases around 30%), the number of larvae (replicates) in each petri dish differed. The number of larvae in each petri dish was counted 72 h after eggs had been laid and unhatched eggs discarded. Immediately after hatching, larvae were fed with the specified aphid prey until pupation. Each day, enough aphids to supply food for 24 h were added to each petri dish and the dead larvae along with remainder of the previous day's food discarded. The following components of performance were measured: larval development time, larval mortality, puparial weight, head width of resulting adults and the potential fecundity of females (measured by dissecting them and counting the ovariole numbers in both ovaries).

Fitness was calculated from these data according to the method of McGraw and Caswell (1996), via the equation: $r = [\ln(mV)]/D$, where r = fitness (growth rate per day), m = survival (1 or 0), V = potential fecundity and D = development time in days. The sex ratio in this study was assumed to be 0.5 in order to calculate fitness. Since only females are used for this calculation, half of the dead larvae/puparia were assumed to have been female, rounding up in the case of uneven numbers. Mean values are cited ± 1 SE.

Analysis

There were three factors in the experimental design: *preference* of females (a fixed factor with two levels: elder or bean), *prey* of larvae (a fixed factor with two levels: elder or bean) and *female* (a random factor with 11 levels, nested within the preference factor). No effects of *sex* (male or female offspring) were detected for any target variable, and hence this was omitted from the analyses. Therefore, to test for significant differences between mean values, and also to detect the preference \times prey interaction of interest, a 3-way nested ANOVA was used, with female nested within preference. The prediction is that females that prefer elder aphids should produce larvae that perform better when feeding on elder aphids, and similarly for those that prefer bean aphids, generating a significant preference \times prey interaction. The calculations were done using the statistical package Statistica (StatSoft, Tulsa, Okla., USA).

We are not interested in *any* preference \times prey interaction, but in the occurrence of a specific form, i.e. we have an a priori prediction that where preference and prey coincide, performance is enhanced. This is not testable within a nested ANOVA since the nesting factor (female) is a random factor, but we are able to test it using contrasts within a preference (elder/bean, E/B) \times prey (elder/bean, e/b) two-way ANOVA using as the raw data the mean values for the offspring of each female in each block, and ignoring the within-subjects nature of the paired means (which decreases the power of the test). Since performance in the combinations Ee and Bb are predicted to be high, and Eb and Be low, the actual prediction tested is that $Ee - Eb > Be - Bb$.

Results

The result of the nested ANOVA for offspring puparial weight (Table 1) demonstrates the details of the analysis. It shows that there is a very significant preference \times prey interaction, indicating the occurrence of some sort of interaction; the contrast is also very significant, indicating that the interaction does indeed follow the predicted pattern: the data are plotted in Fig. 1c. There was a small but significant main effect of prey, with a higher mean puparial weight (33.2 ± 0.7 mg) on elder than bean (32.0 ± 0.6 mg). There was no effect of preference (elder = 33.1 ± 0.6 mg, bean = 32.2 ± 0.7 mg). There were strong differences among females in their offsprings' growth response to prey types (the prey \times female interaction) and among females overall (the female-within-preference main effect).

Table 1 Result of a three-way nested analysis of variance for puparial weight of offspring of female *Episyrphus balteatus* (DeGeer) (Diptera: Syrphidae). Females were divided on the basis of oviposition tests into two *preference* types (preferring elder aphids, or bean aphids), and their offspring were fed on two *prey* types (elder or bean aphids). The factor *female* is therefore nested within the

Effect	df	SS	MS	F	P
Preference (of female)	1	91.0	91.04	0.9	ns
Prey (fed to offspring)	1	138.6	138.62	4.6	< 0.05
Female (within preference)	20	2089.2	104.46	22.0	\ll 0.001
Preference \times prey	1	426.9	426.95	14.2	< 0.002
Prey \times female	20	600.8	30.04	6.0	\ll 0.001
Residual	439	2186.5	4.98		

Table 2 summarizes the results of testing all fitness components separately, and overall individual fitness itself; the preference \times prey interaction in each case is plotted in Fig. 1. Puparial weight turned out to be the only statistically significant component to show the predicted pattern of interaction: for survival, development time, head width and potential fecundity, the preference \times prey interaction within the nested ANOVA was not significant, and the more powerful contrast method was also not significant. Even after allowing for the six tests of this hypothesis (using the Bonferroni procedure), puparial weight remains a significant contrast. There were usually significant main effects of female-within-preference, and often of preference and prey also. For potential fecundity, there was a very significant prey \times female interaction, and significant main effects of preference, prey, and female-within-preference. The integrated measure of performance, individual fitness, showed no significant effect for any factor or interaction, possibly in part because of the greater variance introduced by mortality, which generates individuals with zero fitness.

Even though only puparial weight significantly showed the predicted effect, the means also more or less followed the predicted pattern for head width (Fig. 1d). Surprisingly, survival was lower for the offspring of bean-preferring females fed on bean aphids (Fig. 1a), which strongly influenced the pattern of individual fitness (Fig. 1f), although neither was a significant difference. The head width of resulting adults (Fig. 1d) was lower in larvae fed on bean aphids, and was higher for offspring of elder-preferring females, the same pattern as for potential fecundity (Fig. 1e).

Discussion

We found substantial individual variation among females in their oviposition preferences between two test aphids, and these differences had important consequences for the performance of their offspring. This variation occurred in about one-third of females from the tested population: the other two-thirds either had weak or no preference between the offered aphids. These

factor *preference*. Preference and prey are treated as fixed factors and female as a random factor: hence the main effect of preference is tested using the female-within-preference MS as the error term; the main effect of prey and the preference \times prey interaction, are tested using the prey \times female interaction MS as the error term; other terms are tested using the residual MS as the error MS

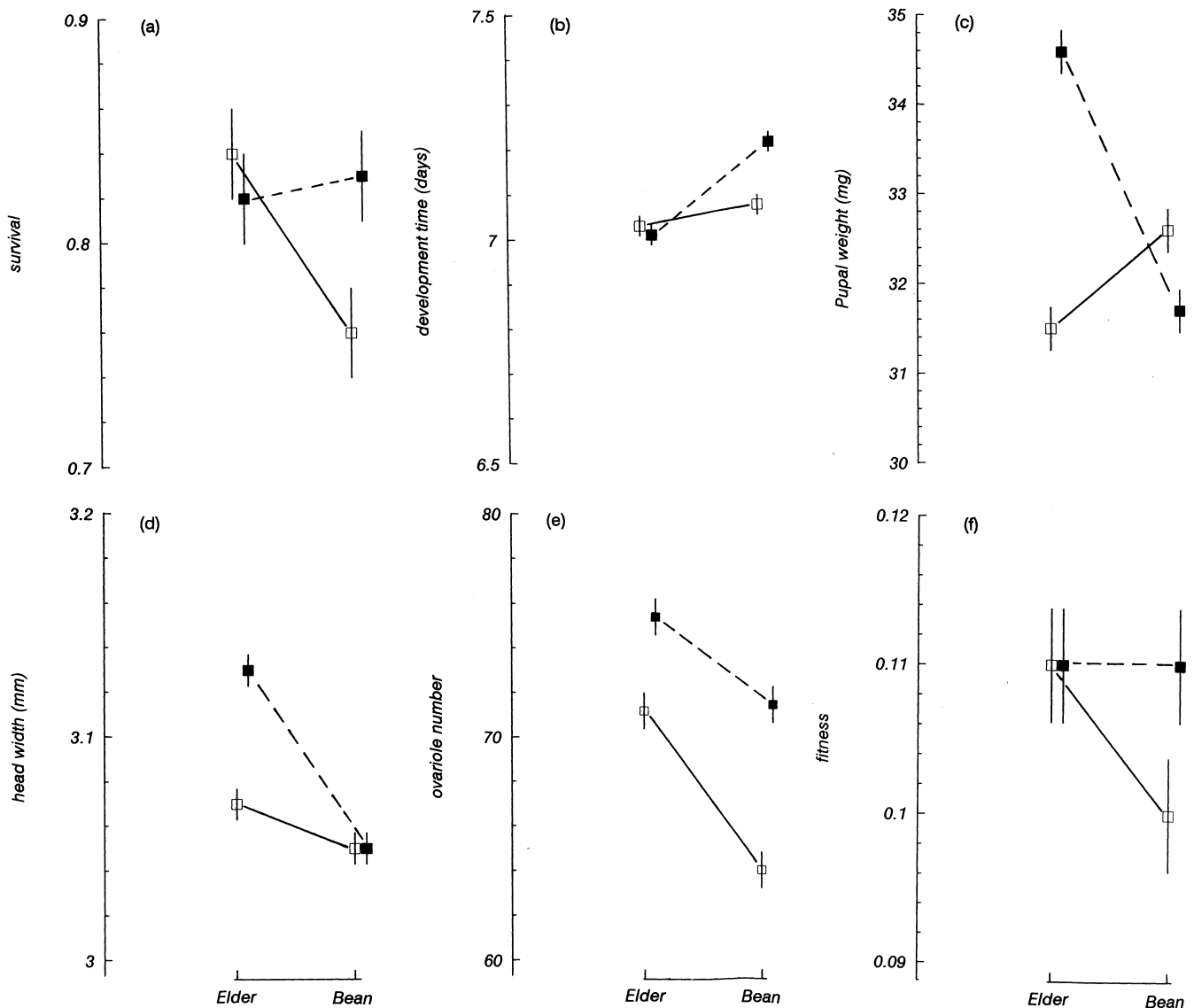


Fig. 1a-f Plot of the mean values of fitness components and of individual fitness itself (calculated according to the method of McGraw and Caswell 1996) for the preference \times prey interaction. The prediction is that offspring performance should be better when feeding on the prey type preferred by their mothers – see Table 2 for the results of testing this prediction. *Error bars* show SE, calculated from the residual mean square of the three-way nested analysis of variance (e.g. that for puparial weight, in Table 1) Variables plotted are: **a** survival (as a proportion); **b** larval development time (days); **c** puparial weight (mg); **d** head width of adults (mm); **e** potential fecundity (number of ovarioles); **f** individual fitness (per day). In each plot, the *x*-axis denotes the preferred prey of the female, the *solid squares* the means for offspring fed on elder aphids and the *open squares* the means for offspring fed on bean aphids

differences should be seen in the context of the fact that this particular species overall is an extreme generalist amongst the aphidophagous syrphids (Gilbert 1990; Gilbert et al. 1994), possibly a critical factor in its very high abundance. We looked for concordance between the oviposition preferences of females and components of the performance of their offspring (i.e. survival, devel-

opment time, puparial weight, adult size and potential fecundity), and the results varied according to the fitness component analysed. There was evidence for different adaptations (Gotthard and Nylin 1995) among females in the trade-off in puparial weight: females choosing to oviposit on one of the two test aphids produced heavier puparia when their larvae were actually fed on that aphid than when they were fed on the non-preferred aphid.

A number of studies have investigated these relationships in phytophagous insects (reviewed by Thompson 1988), but often have relied on only one or two particular measures of performance (e.g. Wiklund 1981; Via 1986; Ng 1988; Nylin and Janz 1993; Barker and Maczka 1996). The results of these studies range from good to poor concordance, and the problem is to decide which components of performance represent performance best, and what the results mean in evolutionary terms (Janz et al. 1994). Our findings highlight the conclusion of Thompson (1988) that larval performance components are not always positively correlated with

Table 2 Results of testing for the presence of the preference \times prey interaction for the various components of fitness in *E. balteatus*; details of the experiment are as in Table 1. Each line represents results from a single nested ANOVA, whose degrees of freedom are described in Table 1. The “contrasts” column tests for the specific

type of preference \times prey interaction expected, i.e. that the pattern is exactly like that of Fig. 1c: note that the data for the contrasts are means for offspring groups, rather than (as for all the other tests) the raw data for individuals (and hence the different degrees of freedom)

Fitness component	Preference $F_{1,20}$	Prey $F_{1,20}$	Female $F_{20,439}$	Preference \times prey $F_{1,20}$	Contrast $F_{1,40}$	Prey \times female $F_{20,439}$
Survival	0.4	0.5	2.3***	1.4	1.1	1.5
Development time	1.0	0.5	8.1***	0.8	0.5	3.6***
Pupal weight	0.9	4.6*	21.0***	14.2**	6.8**	6.0***
Head width	5.8*	6.0*	2.1***	2.3	1.6	1.1
Potential fecundity	7.0*	7.0*	1.8*	0.5	0.5	2.0**
Fitness	1.3	1.4	1.0	0.7	0.6	0.6

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

each other, and may respond differently to changes in the larval environment (McGraw and Caswell 1996) or have different genetic bases (Thompson 1994).

In our study the predicted pattern of concordance between oviposition behaviour and offspring performance did occur for puparial weight, and possibly head width, but for other components such as survival or overall fitness no such relationship was apparent. However, there is an overall pattern to the results. Significant effects of preference type and prey type are concentrated in variables that record the efficiency with which larvae convert food into biomass (i.e. weight of puparia, size of resulting adults, reproductive resources of female offspring), rather than apparently toxic effects (i.e. on survival, development time). There may be a strong effect of both female preference and aphid prey on the efficiency of larval digestion, evident in the preference \times prey interaction for puparial weight, weakening with time (since head width and then ovariole number are probably determined sequentially in the pupal stage) as further environmental variation influences development. Our experiments are extremely labour-intensive, resulting in small numbers of females being used: larger sample sizes might have resulted in the detection of a significant preference \times prey interaction for the head-width variable (cf. Fig. 1d). Thus nutritional value may well be an important selective force moulding female oviposition preferences and larval digestive efficiencies.

Not too much evolutionary significance can be attached to the survival data, since these measured one small component of mortality, the degree to which aphid species were toxic. In the field, very high proportions of syrphid larvae can be parasitized by specialist dip-lazontine parasitoids (see Gilbert 1993). We need field data on mortality risks related to oviposition choices. As in our earlier study (H. Sadeghi and F. Gilbert, unpublished work), offspring survival was high, and there was no significant effect of aphid species on offspring survival. This contrasts with the results of Ruzicka (1975), who reported that both elder and bean aphids were unsuitable food for the larvae of another generalist syrphid, *Eupeodes (Metasyrphus) corollae*, reducing early survival, especially elder aphids. Different syrphid spe-

cies may respond to particular foods very differently, as in the case of the coccinellids *Adalia bipunctata* and *Coccinella 7-punctata* (Blackman 1967). Overall, the evidence suggests that, in line with other studies (e.g. Wiklund 1981; Smiley 1978; Rausher 1983; Roininen and Tahvanainen 1989), syrphid larvae are able to develop successfully on a wider range of prey than those selected by ovipositing females. Furthermore, the suitability of aphids as prey differs among different components of larval performance.

In insect-host relationships, variation arises at many different levels: in stochastic environmental conditions; among patchy host populations together with the nature of their spatial distribution (Thomas and Hanski 1997; van der Meijden and van der Veen-van Wijk 1997); in host quality among populations, individuals (Singer and Parmesan 1993; Schoonhoven et al. 1998) and the same individuals through time (Slansky and Scriber 1985); and in insect preference and performance among populations (Singer and Parmesan 1993), individuals (Ng 1988) and of the same individual through time (e.g. Courtney et al. 1989; Schoonhoven et al. 1998). The resulting mosaic is an important element of the coevolutionary process (Thompson 1994): since individuals of every species encounter unfavourable conditions from time to time, the existence of individual variation in host-use strategy may minimize the risks of coping with fluctuations in the environment (Schoonhoven et al. 1998), and the minimization of risk may be a better way of thinking about the way natural selection operates than many of our current scenarios (Yoshimura and Shields 1987; Hengeveld 1989; Yoshimura and Clark 1991; Yoshimura and Jansen 1996).

The causes of variation in this study were not established, but both genetic (e.g. Futuyma and Peterson 1985; Courtney and Chen 1988; Ng 1988; Thompson 1988; Singer et al. 1988; Via 1990; Schoonhoven et al. 1998) and non-genetic factors such as egg load (e.g. Papaj and Rausher 1983; Courtney and Chen 1988; Papaj and Prokopy 1988; Jaenike 1990) have been proposed as causes of individual variation within populations. Genetic variation may cause serious problems in applied breeding programmes (Via 1984; Ng 1988). Similarly,

variation in response to the environment within a population of a biocontrol agent such as the aphidophagous hoverflies may result in the undesirable situation for biological control programmes of the risk of shifts to non-target organisms (Strand and Obrycki 1996).

In conclusion, interactions between insect predators and their prey are homologous to those of herbivorous insects to a much greater degree than we thought. Rank et al. (1996) recently made this same point in the context of the study of a specialized group of syrphid predators, *Parasyrphus* spp., that have switched prey from aphids to the eggs and larvae of chrysomeline leaf beetles. They list seven criteria where the evolution of prey specialization parallels that of host-plant specialization: host-finding, larval efficiency, specificity, diversity of natural enemies, physiological dependency, efficacy of defensive chemicals, and specialization being the derived trait. For most of these criteria there are direct parallels for the *Parasyrphus*/chrysomeline interaction, as there are for the chrysopid/aphid interaction (Tauber and Tauber 1987; Tauber et al. 1993; Albuquerque et al. 1997) and the syrphid/aphid interactions (Gilbert 1990; Gilbert et al. 1994).

Among individual females of the aphidophagous predatory insects that we studied, substantial variation exists in oviposition preferences and the performance of their larvae. Our data suggest that preference and at least one component of performance, digestive efficiency, are linked. About one-third of individual females appear to be specialized to prefer to oviposit in response to particular aphid species that are better nutritionally for their offspring, and this entails a trade-off in efficiency of utilization of other aphid prey species. We did no experiments with the two-thirds of individuals that had weak or no oviposition preferences between the test aphids: like some of the butterflies studied by Ng (1988), these may have been true generalists with no preferences at all, or they may have been specialized to prefer aphids not used in the test. Two lines of further research may prove fruitful: first, a comparison between *Episyrphus balteatus*, a migrant to the United Kingdom which therefore spends only part of its life-cycle here, and *Syrphus ribesii*, equally an extreme generalist, but resident throughout the year in the United Kingdom; and second, an exploration of the sources of variation listed by Singer and Parmesan (1993) – in our system consisting of the effect of different aphid species feeding on the same host-plant, single aphid species feeding on different host-plants, different populations of syrphids and different individuals within populations.

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References

- Albuquerque GS, Tauber MJ, Tauber CA (1997) Life-history adaptations and reproductive costs associated with specialization in predacious insects. *J Anim Ecol* 66:307–317

- Barker AM, Maczka JM (1996) The relationships between host selection and subsequent larval performance in three free-living graminivorous sawflies. *Ecol Entomol* 21:317–327
- Bernays EA, Bright K, Howard JJ, Raubenheimer D (1992) Variety is the spice of life: frequent switching between foods in the polyphagous grasshopper *Taeniopoda eques* Burmeister (Orthoptera, Acrididae). *Anim Behav* 44:721–731
- Blackman RL (1967) The effects of different aphid foods on *Adalia bipunctata* L. and *Coccinella 7-punctata* L. *Ann Appl Biol* 59:207–219
- Burstein M, Wool D (1993) Gall aphids do not select optimal galling sites. *Ecol Entomol* 18:155–164
- Courtney SP, Chen GK (1988) Genetic and environmental variation in oviposition behaviour in the mycophagous *Drosophila suboccidentalis* Sp. *Funct Ecol* 2:521–528
- Courtney SP, Kibota TT (1990) Mother does not know best: selection of hosts by ovipositing insects. In: Bernays EA (ed) *Insect-plant interactions. II*. CRC, Boca Raton, pp 161–188
- Courtney SP, Chen GK, Gardner A (1989) A general model for individual host selection. *Oikos* 55:55–65
- Fox LR, Morrow PA (1981) Specialization: species property or local phenomenon? *Science* 211:887–892
- Futuyma DJ, Peterson SC (1985) Genetic variation in the use of resources by insects. *Annu Rev Entomol* 30:217–238
- Gilbert F (1990) Size, life history, phylogeny and feeding specialization in insect predators. In: Gilbert F (ed) *Insect life cycles: genetics, evolution and coordination*. Springer, Berlin Heidelberg New York, pp 101–124
- Gilbert F (1993) *Hoverflies*, 2nd edn (Naturalists handbooks 5). Richmond, Slough
- Gilbert F, Rotheray GE, Zafar R, Emerson P (1994) The evolution of feeding strategies. In: Eggleton P, Vane-Wright R (eds) *Phylogenetics and ecology*. Academic Press, London, pp 324–343
- Gotthard K, Nylin S (1995) Adaptive plasticity and plasticity as an adaptation: a selective review of plasticity in animal morphology and life history. *Oikos* 74:3–17
- Hengeveld R (1989) Caught in an ecological web. *Oikos* 54:15–22
- Jaenike J (1990) Host specialization in phytophagous insects. *Annu Rev Ecol Syst* 21:243–273
- Janz N, Nylin S, Wedell N (1994) Host plant utilization in the Comma butterfly: source of variation and evolutionary implications. *Oecologia* 99:132–140
- McGraw JB, Caswell H (1996) Estimation of individual fitness from life-history data. *Am Nat* 147:47–64
- Meijden E van der, Veen-van Wijk CAM van der (1997) Tritrophic metapopulation dynamics: a case study of ragwort, the cinnabar moth and the parasitoid *Cotesia popularis*. In: Hanski IA, Gilpin ME (eds) *Metapopulation dynamics*. Academic Press, New York, pp 387–406
- Ng D (1988) A novel level of interactions in plant-insect systems. *Nature* 334:611–613
- Nylin S, Janz N (1993) Oviposition preference and larval performance in *Polygonia c-album* (Lepidoptera: Nymphalidae): the choice between bad and worse. *Ecol Entomol* 18:394–398
- Papaj DR, Prokopy RJ (1988) The effect of prior adult experience on components of habitat preference in the apple maggot fly (*Rhagoletis pomonella*). *Oecologia* 76:538–543
- Papaj DR, Rausher MD (1983) Individual variation in host location by phytophagous insects. In: Ahmad S (ed) *Herbivorous insects: host selecting behaviour and mechanisms*. Academic Press, New York, pp 77–124
- Rank N, Smiley J, Köpf A (1996) Natural enemies and host plant relationships for chrysomeline leaf beetles feeding on Salicaceae. In: Jolivet PHA, Cox ML (eds) *Chrysomelidae biology, vol 2. Ecological studies*. SPB Academic, Amsterdam, pp 147–171
- Rausher MD (1979) Larval habitat suitability and oviposition preference in three related butterflies. *Ecology* 60:503–511
- Rausher MD (1982) Population differentiation in *Euphydryas editha* butterflies: larval adaptation to different hosts. *Evolution* 36:581–590

- Rausher MD (1983) Ecology of host-selection behavior in phytophagous insects. In: Denno RF, McClure MS (eds) Variable plants and herbivores in natural and managed systems. Academic Press, New York, pp 223–257
- Rausher MD, Papaj DR (1983) Demographic consequences of discrimination among conspecific host plants by *Battus philenor* butterflies. *Ecology* 64:1402–1410
- Roininen D, Tahvanainen J (1989) Host selection and larval performance of two willow-feeding sawflies. *Ecology* 70:129–136
- Ruzicka Z (1975) The effects of various aphids as larval prey on the development of *Metasyrphus corollae* (Diptera: Syrphidae). *Entomophaga* 20:393–402
- Schoonhoven LM, Jermy T, Loon JJA van (1998) Insect-plant biology. Chapman Hall, London
- Scriber JM, Giebink BL, Snider D (1991) Reciprocal latitudinal clines in oviposition behavior of *Papilio glaucus* and *P. canadensis* across the Great Lakes hybrid zone: possible sex linkage of oviposition preferences. *Oecologia* 87:360–368
- Singer MC, Parmesan C (1993) Sources of variations in patterns of plant-insect association. *Nature* 361:251–253
- Singer MC, Ng D, Thomas CD (1988) Heritability of oviposition preference and its relationship to offspring performance within a single insect population. *Evolution* 42:977–985
- Singer MC, Thomas CD, Billington HL, Parmesan C (1994) Correlates of speed of evolution of host preference in a set of twelve populations of the butterfly *Euphydryas editha*. *Ecoscience* 1:107–114
- Slansky F, Scriber JM (1985) Food consumption and utilization. In: Kerkut GA, Gilbert LI (eds) Comprehensive insect physiology. *Biochem Pharmacol* 4:87–164
- Smiley J (1978) Plant chemistry and the evolution of host specificity: new evidence from *Heliconius* and *Passiflora*. *Science* 201:745–747
- Strand MR, Obrycki JJ (1996) Host specificity of insect parasitoids and predators. *BioScience* 46:422–429
- Tabashnik BE, Wheelock H, Rainbolt JD, Watt WB (1981) Individual variation in oviposition preference in the butterfly, *Colias eurytheme*. *Oecologia* 50:225–230
- Tauber CA, Tauber MJ (1987) Food specificity in predacious insects: a comparative ecophysiological and genetic study. *Evol Ecol* 1:175–186
- Tauber MJ, Tauber CA, Ruberson JR, Milbrath LR, Albuquerque GS (1993) Evolution of prey specificity via three steps. *Experientia* 49:1113–1117
- Tauber CA, Tauber MJ, Milbrath LR (1995) Individual repeatability and geographical variation in the larval behaviour of the generalist predator, *Chrysopa quadripunctata*. *Anim Behav* 50:1391–1403
- Thomas CD, Hanski IA (1997) Butterfly metapopulations. In: Hanski IA, Gilpin ME (eds) Metapopulation dynamics. Academic Press, New York, pp 359–386
- Thompson JN (1988) Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. *Entomol Exp Appl* 47:3–14
- Thompson JN (1994) The coevolutionary process. The University of Chicago Press, Chicago
- Thompson JN, Pellmyr O (1991) Evolution of oviposition behavior and host preferences in Lepidoptera. *Annu Rev Entomol* 36: 65–89
- Via S (1984) The quantitative genetics of polyphagy in an insect herbivore. I. Genotype-environment interaction in larval performance on different host plant species. *Evolution* 38:881–895
- Via S (1986) Genetic covariance between oviposition preference and larval performance in an insect herbivore. *Evolution* 40:778–785
- Via S (1990) Ecological genetics and host adaptation in herbivorous insects: the experimental study of evolution in natural and agricultural systems. *Annu Rev Entomol* 35:421–446
- Wiklund C (1975) The evolutionary relationship between adult oviposition preference and larval host plant range in *Papilio machaon* L. *Oecologia* 18:186–197
- Wiklund C (1981) Generalist vs. specialist oviposition behaviour in *Papilio machaon* (Lepidoptera) and functional aspects on the hierarchy of oviposition preferences. *Oikos* 36:163–170
- Williams KS (1983) The coevolution of *Euphydryas chalcedona* and their larval host plants. III. Oviposition behavior and host quality. *Oecologia* 56:336–340
- Yoshimura J, Clark CW (1991) Individual adaptations in stochastic environments. *Evol Ecol* 5:173–192
- Yoshimura J, Jansen VAA (1996) Evolution and population dynamics in stochastic environments. *Res Popul Ecol* 38:165–182
- Yoshimura J, Shields WM (1987) Probabilistic optimization of phenotype distributions: a general solution for the effects of uncertainty on natural selection? *Evol Ecol* 1:125–138