

Aphid suitability and its relationship to oviposition preference in predatory hoverflies

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Summary

1. The fitness consequences of feeding on different aphids (apple, blackberry, dock, elder, nettle, pea, rose and sycamore aphids) for two species of generalist insect predator (the aphidophagous larvae of *Episyrphus balteatus* and *Syrphus ribesii* — Diptera:Syrphidae) were measured in the laboratory. The relevant literature studies on prey specialization in the Syrphidae were summarized for the first time.
2. Both the literature evidence reviewed and the data from the experiment indicated that fitness components and overall individual fitnesses are broadly similar among all aphid species, with some exceptions.
3. We correlated individual fitness to two estimates of oviposition preference, an indirect (field distribution of larvae) and a direct measure (egg distribution under laboratory conditions). In the non-resident, migratory *E. balteatus* significant correlations were absent, but there were indications of a weak preference-performance correlation in the largely resident *S. ribesii*.

Key-words: aphidophagous Syrphidae, feeding specialization, preference-performance.

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Introduction

While there is a huge literature on host-plant specialization in phytophagous insects (see Schoonhoven, Jermy & van Loon 1998), very little is known of comparable features of the interaction between predatory insects and their prey. At least some also show moderate or narrow specialization (Tauber & Tauber 1987; Bristowe 1988; Hodek 1993; Milbrath, Tauber & Tauber 1993; Rank, Smiley & Köpf 1996; Albuquerque, Tauber & Tauber 1997). Most phytophagous insects are specific in their choice of food (Berenbaum 1990; Jaenike 1990; Schoonhoven *et al.* 1998) and even generalists display a hierarchy of preferences for different hosts (e.g. Wiklund 1981).

What influences prey specificity in predators? Two aspects are known to be important determinants of specialization: the foraging behaviour of ovipositing females among available food types and the subsequent performance (biochemical and physiological specializations) of the developing larvae (e.g. Tauber & Tauber 1987). The relationship between these is a

key area of studies of host-plant specialization in herbivores (see Via 1986; Thompson 1988), since it influences how shifts onto novel hosts occur and, consequently, how insect species are distributed among potential hosts over evolutionary time. Numerous studies on a variety of phytophagous insects have estimated the preference-performance correlation, but there is no consensus, with results ranging from strong to weak values. Reasons put forward for this variation in outcome include the measures of performance used (Thompson 1988; Nylin & Janz 1993; McGraw & Caswell 1996) and differences in the ability of larvae to move to alternative food sources (Price, Craig & Roininen 1995; Price 1997). Nothing is known about this in predatory insects.

Larval performance depends on food quality and mortality due to natural enemies. There is presumably little difference between the nutritional requirements of predatory insects and the content of their prey, and as a result, the costs of capture and the toxin content of prey are probably relatively more important to the overall costs of feeding (e.g. Malcolm 1992). The potentially key role of natural enemies in moulding oviposition responses of predators has hardly been studied at all (see Berdegue *et al.* 1996). For herbivores feeding on plants, there is a

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major discrepancy between what plants provide (varying among plant species, and in time and space) and what herbivores require (Schoonhoven *et al.* 1998), particularly nitrogen (White 1993) and toxin content (e.g. Stockoff 1991).

We study here the relationship between preference and performance in two species of aphidophagous hoverflies (Diptera: Syrphidae). In hoverflies, like many other insects, ovipositing females select among food types (see Sadeghi & Gilbert 2000a; Sadeghi & Gilbert 2000b). For a polyphagous syrphid, ovipositional preference by females has a profound effect on the performance of the offspring, because syrphid larvae probably have rather limited dispersal abilities. Some indications imply larvae can move to new aphid colonies to a certain extent. From his samples, Banks (1968) suggested that even quite small syrphid larvae must move between plants and possibly 'considerable distances'; Kan (1988a,b) suggested that a single maple- or pea-aphid colony was insufficient to support larval development to maturity, and 'older larvae are observed actively migrating among maple branches' or pea plants. Most authors agree, however, that the larvae are more or less sedentary, almost completely dependent on their mothers to choose a suitable host-prey.

A number of statements in the literature about the degree of specialization of syrphid larvae derive from pure observation, without any quantitative data. In many such cases, species that from their field distribution are apparently specialized, seem to accept any aphid offered to them in the laboratory (e.g. *Dasyrphus* spp., *Eupeodes* [*Megasyrphus*] *annulipes*, *Parasyrphus vittiger*, *Platycheirus ovalis*; see Goeldlin 1974; Laska 1978). For example, *Dasyrphus* species are only found on tree aphids, and are specialized to life on bark in their dark brown colouration, spiny appearance, and sit-and-wait behaviour. However, they can be reared in the laboratory on all herb aphids that have been tried (Laska 1978). On the other hand, there are persistent reports of the larvae of some species rejecting certain aphid prey. For example, herb aphids are rejected by the pine specialists, *Eupeodes* [*Metasyrphus*] *nielsenii* and *E.[M.] nitens* (Laska 1978; Rotheray 1988), and all aphids are rejected by syrphid larvae that are specialized to non-aphid prey, such as *Xanthandrus* to caterpillars of gregarious Lepidoptera (Lyon 1968) or *Parasyrphus* species to larvae of chrysomelid leaf-beetles (Rank *et al.* 1996). *Salpingogaster nigra* larvae in Trinidad are said to 'thrive' on *Thomaspis varia*, but not on *Thomaspis pubescens* (Guppy 1914).

Rather few studies of syrphid larval development compare quantitatively any aspect of larval performance on different aphids, with the notable exceptions of Schmutterer (1972), Ruzicka (1975) and Malcolm (1976, 1992). Although involving disparate studies with different aims and very different sets of

measured variables, some generalities can be drawn. While development times and pupal weights are often unaffected (e.g. Mathur & Sharma 1973; Phoon 1973; Tawfik, Azab & Awadallah 1974a,b; Hamid 1985; Natskova 1985; Du & Chen 1993), aphid-prey species and/or prey quality does seem to affect mortality. Several aphids are probably toxic or partially toxic to the larvae of one or more species of hoverfly (Milne 1971; Schmutterer 1972; Kaufmann 1973; Ruzicka 1975; Malcolm 1976, 1992; Emrich 1991; Du & Chen 1993; Rank *et al.* 1996). Other variables have rarely been considered, but can be affected by 'food quality' (e.g. fecundity, Saidov 1969; ease of capture, Ruzicka 1976; Wnuk 1979). It is therefore unfortunate that several studies measured only development time or pupal weight. While some aphids were consistently identified as unsuitable [e.g. *Megoura viciae* aphids by Milne (1971), Ruzicka (1975) and Xiong & Dong (1992)], several aphids were deemed highly toxic in one study, but suitable in another [e.g. *Brevicoryne brassicae* by Schmutterer (1972) and Ruzicka (1975)]. A possible way of understanding these apparent contradictions lies in the fact that aphid toxins may be, at least in part, sequestered from the host plants (see Malcolm 1976, 1992; Hodek 1993), which are variable in toxin content inter- and intra-specifically, and in one plant individual through time (see Schoonhoven *et al.* 1998). There are a few explicit demonstrations of the way in which variation in host-plant chemistry affects the suitability of aphids as prey for syrphid larvae (see Kaufmann 1973; Malcolm 1976; Emrich 1991; possibly *Paragus longiventris* in Schmutterer 1972).

Two species were studied here, *Episyrphus balteatus* (de Geer) and *Syrphus ribesii* (L.), chosen deliberately to be generalists because an understanding of the basis of variation in performance of generalist predators will shed light upon the nature and evolution of more specialized predatory feeding habits. The two genera involved are not closely related (Rotheray & Gilbert 1989, 1999), and hence there is no *a priori* reason to expect either similarities or differences in their responses, beyond the fact that they are both labelled as extreme generalists (see Rotheray & Gilbert 1989). Field distributions show different patterns of prey utilization between the two study species (H. Sadeghi, F. Gilbert, G.E. Rotheray & P. Laska, unpublished data). There are varying degrees of specialization among individuals within the populations of these generalist predators (Sadeghi & Gilbert 1999); some individual females prefer particular aphids for oviposition, on which their larvae perform better when offered as prey; this specialization entails a trade-off in performance on other aphid species.

The study reported here has two aims. First, we compare the intrinsic suitability of different aphid species as food for the larvae of two species of syr-

phid under laboratory conditions, testing the null hypothesis that all aphids are equally good as food for these larvae. Secondly, we test whether there is an overall preference-performance correlation in these species, using both field distribution (H. Sadeghi *et al.* unpublished data) and egg distribution among aphids in laboratory experiments (Sadeghi & Gilbert 2000a) as our preference measures.

Materials and methods

LABORATORY STUDY ORGANISMS

The two generalist hoverfly species used in this study are very common in the UK (Gilbert 1993; Stubbs & Falk 1996). The larvae of both species have been reported from colonies of more than 100 species of aphids worldwide (F. Gilbert, unpublished data). *Episyrphus balteatus* has a single generation (occasionally two) in the UK, with adult activity in late summer. During a mild winter adult females may occasionally overwinter, but the bulk of the population migrates to southern Europe where, presumably, it breeds (Rotheray 1989; Gilbert 1993): it has very little ability to tolerate cold (Hart & Bale 1997a; Hart, Bale & Fenlon 1997). *Syrphus ribesii* is oligovoltine, with two or three generations per year, overwintering as a very cold-tolerant larva (Hart & Bale 1997b, 1998). Adult females are normally ready to lay eggs 7–8 days after emergence. The larvae of both species are very generalized in their feeding habits, but nonetheless show different field distributions on aphids (H. Sadeghi *et al.* unpublished data) and oviposition preferences (Sadeghi & Gilbert 2000a). *E. balteatus* was cultured over the winter, and was therefore available during spring for experimentation; *S. ribesii* could not be cultured reliably for long, and hence experiments were done on this species during the summer.

The following aphids were used in these experiments, chosen for their availability, and because in both field distribution (H. Sadeghi *et al.* unpublished data) and by experiment (Sadeghi & Gilbert 2000a) they form a continuum from favourite to avoided prey: *Acyrtosiphon pisum* (Harris) from stock culture on broad bean (*Vicia faba* L.), *Aphis fabae* Scopoli from dock (*Rumex obtusifolius* L.), *Microlophium carnosum* (Buckton) from nettle (*Urtica dioica* L.), *Macrosiphum rosae* (L.) from rose (*Rosa* sp.), *Aphis sambuci* L. from elder (*Sambucus nigra* L.), *Aphis ruborum* (Börner) from blackberry (*Rubus fruticosus* L.), *Drepanosiphum plantanoides* (Shrank) from sycamore (*Acer pseudoplatanus* L.), *Cavariella* sp. from hogweed (*Heracleum sphondylium* L.) and *Aphis pomi* DeGeer from apple (*Malus domestica* Borkh.).

LARVAL PERFORMANCE

Laboratory cultures of both syrphid species were established from gravid females captured in the field around woodland areas at the Nottingham University campus and kept in illuminated cages in a constant environment of $22 \pm 1^\circ\text{C}$ with 16-h day length. Adults were fed on pollen from bee hives (Sigma Ltd, Gillingham, UK) and on crystalline sugar placed on Petri dish lids on the floor of the cage. Water was placed on a soaked pad of cotton wool in a conical flask.

To obtain a group of larvae of the same age, females were induced to lay eggs on cut sections of broad bean plant (*Vicia faba* var. *Aquadulce claudia*) infested with pea aphids. For experimental purposes, a batch of eggs laid over a period of 3 h was selected and placed in a large Petri dish to hatch. The percentage mortality of the early larval instar is normally higher than the other instars, because larvae at this time are delicate and difficult to handle. In addition, in these experiments there was a low percentage of egg hatching. Together, these factors decreased the number of larvae available for study. To improve survival, larvae were left in groups for the first 3 days and allowed to feed on pea aphids (only one or two aphids are normally consumed during this time). At the beginning of the fourth day, larvae were weighed individually, transferred to experimental Petri dishes 14-cm in diameter and given aphids of the selected species.

Each day, the larvae were weighed, and the same number of similarly sized aphids were weighed and added to the Petri dishes to supply food for 24 h, the remains being weighed again the following day. Each larva received only one aphid species. As the larvae grew in size, the number of aphids offered each day increased to keep pace with their requirements; thus aphids were always in excess, but always offered in equal numbers among aphid species. Aphids are probably easier to catch in this situation than in nature and, hence, the suitability we measured did not incorporate all of the costs of capture. Depending on availability, 10–16 replicates were used, except in the case of blackberry aphid, for which only six larvae were reared because of the scarcity of this aphid in the field.

The resulting pupae were weighed, and the potential fecundity of the resulting adult females was measured by dissecting them and counting the ovariole numbers of both ovaries. In some instances the pupae could not be weighed because their strong attachment to the Petri dish meant they could not be removed without injury; this led to variable sample sizes in the data. Development time was measured to the nearest day. Given the labour involved in the experiment, it was not feasible to measure it more accurately, and in any case the exact time of pupation in syrphines is difficult to determine since

the process is gradual, with no fixed points such as the emergence of pupal spiracles through the puparial cuticle (as in cristaline syrphids).

'Performance' is a fitness measure that should include survival, growth rate, feeding efficiency, pupal mass and fecundity, as well as longevity of the resultant adult. In practice, however, offspring performance has usually been estimated from only one or two components of performance: more than 50% of studies have taken only one or two parts of the insect's life-cycle into account. It is a problem to decide which component of larval performance to use in correlation analysis, because different aspects of offspring performance can produce different results when compared to female preference (Thompson 1988). Furthermore, as noted by McGraw & Caswell (1996), different components of performance respond differently to changes in the environment. For such reasons, Janz, Nylin & Wedell (1994) recommend that oviposition preference should be correlated with total offspring fitness and not only with particular components. Therefore, individual fitness (r) was calculated as a performance measure (McGraw & Caswell 1996) by integrating development time (D), survival ($m=1$ or 0) and potential fecundity (V) via the equation: $r = [\text{Ln}(m \cdot V)]/D$, where Ln = natural logarithms.

Fitness measured in the laboratory is, of course, not the same as fitness in the field, particularly because mortality due to natural enemies is omitted; measuring fitness of individuals in the field would be almost impossible. The objective of this study was to measure the intrinsic suitability of aphids. For all these reasons, the individual fitness of McGraw & Caswell (1996) was selected as the measure of choice. Fitnesses were calculated for surviving females only and for all females including non-survivors. Because female larvae/pupae cannot be differentiated from males, we assumed half the mortality to be female, rounding up when an odd number had died. This procedure also led to variable sample sizes in the data. The sex ratio of emerging adults did not differ significantly from unity ($\chi^2_1 < 1.7$, NS).

We used Analysis of Variance for the analysis of differences in performance among aphids for all measures except mortality, where we used χ^2 , and 'individual fitness including non-survivors', where we used a non-parametric ANOVA (i.e. a Kruskal-Wallis test). Since there was no *a priori* prediction of these differences, we report only the overall variance ratio: following Day & Quinn (1989), we refrain from using multiple comparisons.

OVIPOSITION PREFERENCE

Oviposition preferences among hosts was investigated in two ways, indirectly from the field distribu-

tion of larvae (H. Sadeghi *et al.* unpublished data) and directly from egg distributions under laboratory conditions (Sadeghi & Gilbert 2000a).

Briefly, the field distribution of larvae was assessed by a regular sampling programme. From early May until late October 1996 a weekly sampling programme of aphid colonies and associated larvae of certain syrphid predators was carried out. The site of field sampling was the Nottingham University campus, a large area of about 90 ha mainly of grasslands and a few areas of woodland. Plant names used here are from Mabblerley (1997) and Clapham, Tutin & Warburg (1968). Aphid colonies (see Table 4) on plant leaves/stems were removed to the laboratory, and the type and number of each syrphid species recorded, and the aphid identified using Rotheray (1989) and Blackman & Eastop (1994). The focus of this part of the study was on only the two species considered here. In taking a sample, from every five aphid-infested leaves/stems, the fifth was picked and put into a plastic bag. As a sampling unit, 50 aphid-infested leaves were used for sycamore, beech, elm, apple and blackberry; for other plants (willow-herb, nettle, hogweed, dock, rose, and elder) ten 20-cm aphid-infested stems were used. The size of sampled aphid colonies was recorded on a 3-point scale (1 = < 5; 2 = 5–40, 3 = > 40). To give a rough estimate of the overall relative availabilities of the different aphids, the colony sizes of all samples were summed for each aphid species.

Oviposition preferences were determined in the laboratory using females of known age. Females were initially naive, having had no previous exposure to aphids. Aphids were then offered to each individual female on a newly cut section of their host-plant standing in water: great care was taken to provide equal aphid densities, by ensuring that all cut sections were about the same size (a 20-cm shoot with three small leaves) and infested with the same number of aphids (of various instars). Each day, aphids were presented in a randomized sequence to each syrphid female (i.e. a no-choice situation, with only one aphid species available at any time). Each presentation of an aphid species lasted for 30 min. The number of eggs laid in each case was counted and the aphid replaced by another aphid species, continuing until all aphids had been presented. Each day all test aphid species were offered; presentations continued until all oviposition had finished.

Results

PERFORMANCE OF *EPISYRPHUS* *BALTEATUS*

The results of measuring the components of performance of *E. balteatus* fed on various aphids are given in Table 1. The larvae of *E. balteatus* can

Table 1. The influence of the species of different aphids on various performance measures in the development of *Episyrphus balteatus* (DeGeer). Each entry in the table gives the mean \pm SEM, range and sample size (except for survival). Aphids are in order of the fitness achieved by larvae feeding upon them (last row). Differences among means are assessed by one-way ANOVA, except for 'individual fitness including non-survivors', where a non-parametric ANOVA test was used (*H*, distributed as χ^2); survival differences are tested using χ^2 . Overall fitness for each individual was calculated according to McGraw & Caswell (1996; see methods) both including and excluding non-survivors

Measure	Aphid Blackberry	Dock	Nettle	Elder	Pea	Rose	Apple	Test statistic
Development time (days)	6.8 \pm 0.2 (6-7; 11)†	7.6 \pm 0.4 (6-11; 12)	7.4 \pm 0.2 (6-8; 10)	6.9 \pm 0.2 (6-8; 10)	7.9 \pm 0.2 (7-9; 9)	7.7 \pm 0.3 (7-10; 10)	13.0 \pm 1.0 (12-14; 2)	$F_{6,50} = 13.5$ ***
Survival (%) (of larvae)	91.7 (12)	100 (12)	100 (10)	100 (10)	75 (12)	83.3 (12)	20 (10)	$\chi^2_6 = 29.7$ ***
Survival (%) (to adult emergence)	91.7 (12)	100 (12)	100 (10)	100 (10)	66.7 (12)	66.7 (12)	20 (10)	$\chi^2_6 = 25.3$ ***
Pupal weight (mg)‡	32.0 \pm 1.0 (29.7-37.5; 7)	34.8 \pm 1.9 (28-46; 10)	30.4 \pm 1.6 (25-34.6; 5)	30.2 \pm 1.4 (22.5-37.3; 9)	38.6 \pm 2.2 (29.1-44.7; 8)	32.7 \pm 2.2 (26.1-43; 7)	30.7 \pm 2.1 (28.6-32.8; 2)	$F_{6,41} = 2.70$ *
Ovariole number	67 \pm 4 (55-81; 6)	72 \pm 4 (60-88; 6)	74 \pm 4 (62-90; 6)	58 \pm 4 (46-70; 7)	63 \pm 4 (54-74; 5)	72 \pm 3 (66-77; 4)	61 (1)	$F_{6,28} = 2.37$ NS
Fitness, <i>r</i> (per day \times 100) (of survivors only)	11.1 \pm 0.2 (10.5-11.8; 6)	11.0 \pm 0.2 (10.6-11.8; 6)	11.2 \pm 0.2 (10.3-11.8; 6)	11.0 \pm 0.2 (9.8-11.7; 7)	10.7 \pm 0.2 (10.2-11.5; 5)	11.2 \pm 0.2 (10.7-11.4; 4)	8.9 (1)	$F_{6,28} = 3.33$ *
Fitness, <i>r</i> (per day \times 100) (including non-survivors)	11.1 \pm 0.2 (10.5-11.8; 6)	11.0 \pm 0.2 (10.6-11.8; 6)	11.0 \pm 0.2 (10.3-11.8; 6)	11.0 \pm 0.2 (9.8-11.7; 7)	7.6 \pm 2.0 (0-11.5; 7)	7.4 \pm 2.4 (0-11.4; 6)	1.8 \pm 1.8 (0-8.9; 5)	$H_6 = 15.2$ *

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS = not significant.

† Minimum – maximum: *sample size*.

‡ Due to the attachment of some pupae to the Petri dishes, not all individuals were weighed.

develop to maturity successfully on all the aphid species offered. The survival of larvae during development was low for those feeding on apple aphid; otherwise, apart from on pea aphids (75%), survival rates were close to 100%. The larval developmental period ranged from 6 (elder, blackberry, dock and nettle aphids) to 14 (apple aphid) days. There were significant differences among the seven aphid species in respect of larval development time. Larvae fed on apple aphid had the greatest average development time, again clearly different from all others.

The weights of pupae ranged from 22.5 mg on elder aphid to 46 mg on dock aphid. Mean pupal weights from larvae reared on different aphids differed significantly. For the resulting adults, mean head widths and wing lengths varied significantly among the experimental groups for both sexes. The number of ovarioles of adult females were not significantly different among experimental groups, but ranged from 46 (elder aphid) to 88 (dock aphid).

Individual fitnesses of *E. balteatus* developing on different aphids are given in Table 1. Except in the case of apple aphids, there were few obvious differences among mean fitnesses for the various aphid-prey treatments.

PERFORMANCE OF *SYRPHUS RIBESII*

Syrphus ribesii larvae were fed six aphid species collected from various host plants; apple aphid and elder aphid could not be used due to their scarcity in the field at the time of the experiment and were replaced by sycamore aphid. The performance measures of *S. ribesii* reared on the different aphid species are given in Table 2.

There were no significant differences in survival among treatment groups: apart from dock aphid (75%), the survival rate on all aphids was close to 100%. The larval development period ranged from 9 (rose, nettle, pea, and sycamore aphids) to 11 (dock, blackberry, nettle and pea aphids) days. The mean development times were significantly different among groups, slightly longer on blackberry and dock aphids than the very similar, but more rapid times for the other four aphid species.

Pupal weights ranged from 32.4 mg (dock aphid) to 70.8 mg (sycamore aphid), and were significantly different among aphid-prey groups. Larvae fed on rose and sycamore aphids on average resulted in heavier pupae, whereas the pupae of larvae reared on blackberry and dock were lighter. In the resulting adults, there were significant differences among treatment groups in head width and wing length for both sexes. The number of ovarioles of adult females ranged from 61 (dock aphid) to 120 (sycamore aphid), but the mean values were not significantly different.

Individual fitnesses of survivors (Table 2) differed significantly among aphid-prey treatments, with larvae fed on sycamore and rose aphids having greater fitness. The increased variance associated with the inclusion of non-survivors (i.e. individual females with zero fitness) led to no significant differences among the mean fitnesses of all females, although a non-parametric ANOVA remained significant (Kruskal-Wallis $H = 13.1$, $P < 0.05$).

COMPARISON BETWEEN SYRPHIDS

We tested the individual fitness measures (omitting non-survivors) using a two-way Anova to look for differences between the two syrphid species and for differences in response to the various aphids (the interaction term). Fitness of *S. ribesii* was consistently higher than *E. balteatus* on all aphids ($F_{1,34} = 502.5$, $P < < 0.001$) and there were differences overall among aphids ($F_{4,34} = 5.11$). The significant interaction ($F_{4,34} = 3.92$, $P = 0.01$) showed different responses of the syrphid species among aphids: *E. balteatus* had more or less equivalent fitness on all aphids (we could not provide apple aphids to *S. ribesii*), whereas the fitness of *S. ribesii* was more variable, and was particularly high on rose aphids.

PREFERENCE-PERFORMANCE CORRELATION

The assumption of the field sampling programme was that the relative frequency of larvae on particular aphid colonies would represent the relative preference of that prey by ovipositing females. The results showed a consistent pattern of preference among aphid species, detailed in Table 3. Relative frequencies and the absolute numbers of larvae were highly correlated ($r_s = 0.93$, $n = 11$, $P < 0.01$), so we concentrated on testing for correlations with the absolute numbers. The results of the oviposition preference experiments also showed that females significantly prefer some aphids over others; again, the overall preference hierarchy is given in Table 3. It is often expected that differences in oviposition preference measured in the laboratory will be reflected in the distribution of larvae among aphid colonies in the field. However, testing for a positive (rank) correlation between larval frequency among different aphid colonies and oviposition preference by females varied with syrphid species. There may have been agreement between the hierarchies of oviposition preference and larval distribution among different aphid colonies for *E. balteatus* ($r_s = 0.54$, $n = 7$, $P = 0.09$, wholly determined by the low oviposition preference for *Cavariella* aphids—without this datum, $r_s = 0.84$, $n = 6$, $P < 0.05$). There was no

Table 2. The influence of the species of different aphids on various performance measures in the development of *Syrphus ribesii* (L.). Each entry in the table gives the mean \pm SEM, range and sample size (except for survival). Aphids are in order of the fitness achieved by larvae feeding upon them (last row). Differences among means are assessed by one-way ANOVA, except for 'individual fitness including non-survivors', where a non-parametric Anova test was used (H , distributed as χ^2); survival differences are tested using χ^2 . Overall fitness for each individual was calculated according to McGraw & Caswell (1996; see Methods) both including and excluding non-survivors

Measure	Aphid Sycamore	Pea	Blackberry	Dock	Nettle	Rose	Test statistic
Development time (days)	9.7 \pm 0.2 (9–10: 10)†	9.7 \pm 0.3 (9–11: 11)	11.0 \pm 0.0 (11–11: 5)	10.8 \pm 0.1 (10–11: 9)	10.0 \pm 0.2 (9–11: 15)	9.6 \pm 0.1 (9–10: 16)	$F_{5,59} = 8.76$ ***
Survival (%) (of larvae)	100 (10)	83 (12)	83.3 (6)	75 (12)	93.7 (16)	100 (16)	$\chi^2_3 = 3.28$ NS
Survival (%) (to adult emergence)	100 (10)	75 (12)	83.3 (6)	66.7 (12)	62.3 (16)	56.3 (16)	$\chi^2_3 = 4.82$ NS
Pupal weight (mg)‡	56.1 \pm 3.4 (42–70.8: 10)	47.4 \pm 2.1 (38.9–56.0: 9)	41.5 \pm 1.1 (38.2–44.8: 5)	41.7 \pm 2.5 (32.4–54.2: 9)	53.3 \pm 1.7 (46.4–66.4: 12)	56.2 \pm 1.8 (47.2–69.0: 11)	$F_{5,50} = 7.46$ ***
Ovariole number	102 \pm 6.0 (90–120: 4)	86 \pm 8.0 (75–110: 4)	90 \pm 2.0 (88–92: 2)	73 \pm 7 (61–86: 4)	94 \pm 7.0 (75–104: 4)	102 \pm 4.0 (96–110: 3)	$F_{5,14} = 2.45$ NS
Fitness, r (per day \times 100) (of survivors)	15.9 \pm 0.6 (14.5–17.2: 4)	14.8 \pm 0.3 (14.2–15.6: 4)	14.2 \pm 0.3 (13.9–14.5: 2)	13.8 \pm 0.3 (13.2–14.4: 4)	15.0 \pm 0.4 (14.3–16: 4)	15.7 \pm 0.1 (15.6–15.9: 3)	$F_{5,14} = 3.74$ *
Fitness, r (per day \times 100) (including non-survivors)	15.9 \pm 0.6 (14.5–17.2: 4)	9.8 \pm 3.1 (0–15.6: 6)	9.5 \pm 4.7 (0–14.5: 3)	9.2 \pm 2.9 (0–14.4: 6)	8.6 \pm 3.0 (0–16: 7)	6.7 \pm 3.2 (0–15.9: 7)	$H_5 = 13.1$ *

†Minimum – maximum: sample size).

‡Due to the attachment of some pupae to the Petri dishes, not all individuals were weighed.

Table 3. Hierarchy of aphid species in relation to field distribution (H. Sadeghi *et al.*, unpublished data), oviposition preference (from Sadeghi & Gilbert 2000a) and suitability for larval development

Aphid species	Plant species	Field distribution			Suitability for larval development	
		Relative frequency*	Number of larvae†	Oviposition preference‡	All§	Survivors¶
<i>Episyrphus balteatus</i>						
<i>Acyrtosiphon pisum</i>	<i>Vicia faba</i>	–	–	32.0	7.6	10.7
<i>Aphis fabae</i>	<i>Rumex obtusifolius</i>	0.13	3	15.3	11.0	11.0
<i>Aphis grossulariae</i>	<i>Epilobium hirsutum</i>	1.38	22	–	–	–
<i>Aphis pomi</i>	<i>Malus domestica</i>	0.23	3	9.8	1.8	8.9
<i>Aphis ruborum</i>	<i>Rubus fruticosus</i>	0.05	1	2.6	9.5	11.1
<i>Aphis sambuci</i>	<i>Sambucus nigra</i>	0.13	5	13.6	11.0	11.0
<i>Cavariella</i> sp.	<i>Heracleum sphondylium</i>	0.76	16	5.1	–	–
<i>Drepanosiphum plantanoidis</i>	<i>Acer pseudoplatanus</i>	0.13	4	–	–	–
<i>Macrosiphum rosae</i>	<i>Rosa</i> sp.	0.26	9	19.4	7.4	11.2
<i>Microlophium carnosum</i>	<i>Urtica dioica</i>	0.08	2	2.3	11.2	11.2
<i>Phyllaphis fagi</i>	<i>Fagus sylvatica</i>	0.00	0	–	–	–
<i>Schizoneura ulmi</i>	<i>Ulmus</i> sp.	0.38	6	–	–	–
<i>Syrphus ribesii</i>						
<i>Acyrtosiphon pisum</i>	<i>Vicia faba</i>	–	–	18.9	9.8	14.8
<i>Aphis fabae</i>	<i>Rumex obtusifolius</i>	0.13	3	11.1	9.2	13.8
<i>Aphis grossulariae</i>	<i>Epilobium hirsutum</i>	0.09	2	–	–	–
<i>Aphis pomi</i>	<i>Malus domestica</i>	0.23	3	–	–	–
<i>Aphis ruborum</i>	<i>Rubus fruticosus</i>	0.14	3	7.0	9.5	14.2
<i>Aphis sambuci</i>	<i>Sambucus nigra</i>	0.08	3	6.9	–	–
<i>Cavariella</i> sp.	<i>Heracleum sphondylium</i>	1.19	25	9.8	–	–
<i>Drepanosiphum plantanoidis</i>	<i>Acer pseudoplatanus</i>	0.93	28	21.4	15.9	15.9
<i>Macrosiphum rosae</i>	<i>Rosa</i> sp.	0.11	4	20.3	6.7	15.7
<i>Microlophium carnosum</i>	<i>Urtica dioica</i>	0.52	13	4.6	8.6	15.0
<i>Phyllaphis fagi</i>	<i>Fagus sylvatica</i>	0.10	2	–	–	–
<i>Schizoneura ulmi</i>	<i>Ulmus</i> sp.	0.19	3	–	–	–

*Number of larvae divided by the index of aphid relative abundance (H. Sadeghi *et al.*, unpublished data).

†Absolute number of larvae found during standard sampling.

‡Mean percentage of total egg load laid on an aphid during no-choice sequential oviposition tests.

§Mean individual fitness of all individuals tested, calculated according to McGraw & Caswell (1996).

¶Mean individual fitness of those surviving to adulthood, calculated according to McGraw & Caswell (1996).

suggestion of any relationship in *S. ribesii* ($r_s = 0.37$, $n = 7$, NS).

The suitability of different aphid species as larval food showed small but significant differences for both syrphid species, summarized in Table 3. There was no discernible positive relationship between either measure of individual fitness and either measure of the frequency of larvae in field for *E. balteatus* (all rank coefficients were negative). Of the aphids studied, blackberry and nettle aphid were the least preferred by adult females in field, with only one or two larvae found in all the systematic samples. Both aphids were suitable as larval prey, however, with nettle aphid resulting in the highest measured overall fitness. In the case of *S. ribesii*, testing for a positive (rank) correlation between individual fitness and the larval numbers in the colonies of different aphids was significant ($r_s = 0.87$, $n = 5$, $P < 0.05$), showing that even for these small numbers there was agreement between performance and frequency of larvae in the field.

Testing for a positive (rank) correlation between oviposition preference and the suitability of aphids measured by individual fitness showed a similar picture. There was no suggestion of any positive relationship between oviposition preferences by gravid females and either measure of fitness in *E. balteatus* (both coefficients were negative). In *S. ribesii*, there were indications of positive relationships (in both cases $r_s = 0.60$, $n = 6$, $P = 0.09$), although the power of the test was weak because of the small number of points.

The data lead us to suggest that in *S. ribesii* there is a link among the hierarchy of oviposition preferences, larval frequencies among aphid colonies in the field and subsequent offspring fitness. In *E. balteatus*, however, the data provide no evidence of such links. We do not think this is an artefact of small sample sizes (caused by the labour-intensive nature of the experiments), in part because the sample sizes of *E. balteatus* were always larger than those of *S. ribesii*.

Discussion

Malcolm (1992) divided predators of a particular prey species into three categories: *included* (those that are unaffected by prey defences and, hence, can exploit all prey types successfully, including the one in question), *peripheral* (those that suffer significant declines in fitness when reared on the prey species in question) and *excluded* (those that cannot exploit the prey species because it kills them). Increases (or decreases) in allocation by the prey species to defensive toxins expand (or contract) enemy-free space at the expense (or to the benefit) of peripheral predators only, leaving included and excluded predators unaffected. The peripheral predators therefore constitute a potent evolutionary force on prey defences. A community approach is therefore important: each aphid species is likely to be attacked by a variety of aphidophagous predators and many aphidophagous predators attack a variety of aphid species as prey. Our results show that even generalist aphidophagous syrphids are peripheral predators on some common aphid species.

The vast majority of studies (summarized in Table 1 and including our own) use generalist species. The overwhelming pattern arising from the results is that many aphids are rather similar in their suitability as food for syrphid larvae, but often with one or two exceptions (e.g. apple aphid in our work). The rank order of aphid suitability as food differed for different components of larval performance (cf. Tables 2 and 3). This underlines the need to integrate components into a single composite measure of fitness, rather than relying on single components: we think that the individual fitness approach of McGraw & Caswell (1996) provides a better, more complete performance measure for ecological studies. A further conclusion is that in the laboratory larvae are often able to develop successfully on aphids rarely used in the field. For example, in the experiments with *E. balteatus*, nettle aphids were highly suitable as food for larvae, whereas field sampling (H. Sadeghi *et al.*, unpublished data) and oviposition preference experiments (Sadeghi & Gilbert 2000a) showed that this aphid is rarely selected for oviposition by gravid females. In the context of the hierarchy-threshold model of Courtney, Chen & Gardner (1989), nettle aphids are low in the rank hierarchy of acceptability to gravid females: why might this be the case?

A variety of factors might influence the evolved rank hierarchy of suitability: the host-plant as a habitat for larvae; the intrinsic suitability of the aphid as food may vary with host-plant (Hodek 1993), body size, normal colony size and density, the sequestration or production of toxins, defensive behaviour, recruitment of ants, season (particularly in declining colonies: Kan 1988a,b; Hodek 1993) or various other forms of low profitability; the impact

of natural enemies (which may vary with aphid species and/or host-plant); or the nature and frequency of competition among larvae within aphid colonies. Thus, in our particular case, survival of *E. balteatus* larvae on the nettle host plant in nature may be low because of the effects of the plant itself on the larvae, which must move about on its surface. Nettle aphids are known to be especially adept at avoiding capture, and hence have high costs of capture not measured in the laboratory in Petri dishes, or the mortality due to natural enemies might be unusually high when using this aphid and females have been selected to avoid using it. Most of these factors remain almost unstudied in their effects on syrphid larvae.

One well-studied aspect of prey selection in syrphids is that they prefer to lay eggs in larger (Chandler 1968a,b; H. Sadeghi *et al.* unpublished data) or developing aphid colonies (Kan 1988a,b), and they do not like declining colonies. This is probably related to the larval food requirement, and may be one reason why blackberry aphids (which often occur at very low densities) are low in the oviposition preference hierarchy. This behaviour probably ensures that newly emerged larvae have enough food to develop successfully, and is important because periods of food deprivation during the larval stage can result in dwarfed adults (Ruzicka & Gonzales Cairo 1976) with lowered fecundity or even sterility (Cornelius & Barlow 1980). Just why aphids from colonies in decline are intrinsically less suitable is hard to say. The longer development time and decrease in survival of larvae of *E. balteatus* on apple aphids could be due to this effect, since at the time of the experiment the colonies of this aphid were going into decline. For some replicates, a similar explanation was advanced for the unsuitability of *Aphis fabae* when fed to *Eupeodes (Metasyrphus) corollae* larvae (Ruzicka 1975).

Aphids show a wide range of defences against their enemies: speed and alertness (e.g. Dixon 1958; Niku 1976; Brodsky & Barlow 1986), hiding in galls or waxy secretions (e.g. Mitchell & Maksymov 1977; Evenhuis 1978), recruitment of ants that are effective deterrents (Banks 1962; Dixon 1998, p. 228), active defence sometimes by soldier castes (Ohara 1985b; Foster 1990; Dixon 1998, p. 102), and toxins (Wink & Romer 1986; Nishida & Fukami 1989; Malcolm 1990). While the impact of aphid defence has been reasonably well studied in the aphidophagous coccinellids (see Majerus 1994), there is a dearth of such work on aphidophagous syrphids. One Japanese community of aphidophagous syrphid species could be divided into three groups: generalists, specialists on ant-tended aphids and specialists on aphids that aggressively defend themselves (Mizuno *et al.* 1997). There are particular larval morphological (e.g. in *Paragus haemorrhous*: Mizuno *et al.* 1997)

or female ovipositional strategies (e.g. *Eupeodes (Metasyrphus) confrater*: Ohara 1985a) in the syrphids that mitigate the effects of these defences. Branquart (1999) came to a similar conclusion in studying European aphidophagous syrphids: 90% are oligophagous or stenophagous, and they mostly feed on well defended aphid prey. Adaptations of syrphids to aphid defences, and particularly the presence of ants, are an important and unstudied component of syrphid evolution. Because of the design of our (and most other) experiments, the measured defensive components contributing to 'suitability' consisted only of some aspects of capture efficiency together with the ability of the larvae to digest aphid tissue. However, there were differences in suitability among aphids in these components and these were related to oviposition preferences in *Syrphus ribesii*.

The role of aphid toxins in defence against their predators has been studied in only a few cases. The oleander aphid, *Aphis nerii* (Malcolm 1976, 1990, 1992), appears to synthesize its toxins, rather than deriving them from its very poisonous host-plants, but there is no doubting their effectiveness against its peripheral predators. In studies of syrphids, differences in quality among aphids are not consistent among studies even using the same syrphid species, suggesting that variable host-plant chemistry might be the source of this tri-trophic interaction. For example, our successful rearings *E. balteatus* or *S. ribesii* larvae on both elder and dock aphids contrast with those of Ruzicka (1975), who found neither aphid to be suitable food for *Eupeodes (Metasyrphus) corollae* larvae. If there was any detrimental effect of these two aphids on test larvae in this study, a possible explanation could be due to starting the experiment with 3-day-old larvae: according to Schmutterer (1972), the resistance of syrphid larvae to toxic aphids increases with larval age, although his scanty data do not provide a great deal of support for this statement. Most accounts suggest that when larval mortality is large, it occurs within the first 4 days after eclosion from the egg (Schmutterer 1972; Kaufmann 1973; Malcolm 1992). Differential early mortality on different aphids needs further investigation.

The size of prey is often considered an important characteristic in determining whether or not it can be handled by predators (Strand & Obrycki 1996); Kan (1988a,b) noted that aphid size is critical for the newly eclosed first-instar larva, and part of the reason for ovipositing in young colonies may be to make available small and tender aphids for the first few meals of the first instar. The higher mortality and longer development time for *E. balteatus* on apple aphid (*Aphis pomi*) may be related to the smaller size of this aphid, which imposes extra capture costs on older larvae. Hodek (1993) reported that apple aphids (*Aphis pomi*) were also less suitable

than other aphids as food for coccinellids and caused a decrease in the weight of larvae of *Exochomus quadripustulatus* (L.).

In this study the main unmeasured components of fitness were differences in capture efficiency among aphids on their host plants, mortality due to natural enemies, and the risk and effects of larval competition at aphid colonies. The proportion of larvae killed by specialist parasitoids can be very high (Rotheray 1989; Gilbert 1993), but no analyses of relative risks at different aphid colonies in the field have been carried out: such field measurements of susceptibility need doing. Competition between syrphid larvae can greatly influence the bionomics of the species (Benestad-Hågvar 1972, 1973). Field sampling (Mizuno *et al.* 1997; H. Sadeghi *et al.* unpublished data) generally shows a wide overlap in the ranges of prey aphid species between the studied syrphid species, but the extent to which heterospecific larvae co-occur in the same colonies has rarely, if ever, been reported in syrphid larval communities, and hence the potential for inter-specific competition remains unknown. In the population dynamics of a community of adult hoverflies, there are signs of competitive effects only among hoverfly species that are generalists as aphidophagous larvae (Gilbert & Owen 1990; Gilbert 1990). Oviposition strategies might be expected to have adapted to regular and frequent competitive interactions, and therefore the females of generalist species might avoid ovipositing in aphid colonies where eggs or larvae are present. Some observations have supported this prediction (Banks 1953; Chandler 1968a; Rotheray & Dobson 1987). However, despite some claims based purely on observational data (Hemptinne *et al.* 1993; Hemptinne, Doucet & Gaspar 1994), careful experiments (Chandler 1968b; Phoon 1973; Bargaen, Saudhof & Poehling 1998) showed no signs at all of any such avoidance of competition.

Despite the relatively small differences in fitness resulting from feeding on different aphid species and small sample sizes, there was evidence for a preference-performance correlation in one of our generalist syrphid species, *S. ribesii*, but not in the other, *E. balteatus*. As in some insect herbivores (Via 1986; Ng 1988), the existence of individual variation among females may weaken or abolish a preference-performance relationship measured at the population level. About 60% of individual female *E. balteatus* showed few oviposition preferences, whilst the remainder differed strongly from one another (Sadeghi & Gilbert 1999), associated with trade-offs in larval performance. Thus, some individuals appear to be adapted to different prey-use strategies, with preference for one aphid species entailing a trade-off in performance on another. This further underlines the fact that the relationship between

insect predators and their prey is very similar to that between insect herbivores and their host plants (Tauber & Tauber 1987; Bristowe 1988; Thompson 1988; Albuquerque *et al.* 1997).

Assuming that the difference between the two syrphid species is real, a possible explanation lies in the overwintering strategies of the two species. *E. balteatus* is the only temperate representative of a tropical genus, and migration from the South in spring and back again in autumn, is the dominating characteristic of its population ecology. Thus, *E. balteatus* has not evolved primarily to the conditions of Northern Europe and, therefore, possibly not to its aphids. In stark contrast, *S. ribesii* is the commonest representative of an overwhelmingly Northern Holarctic genus, strongly adapted to overwintering residency there, and hence to its aphids. This might also explain why the mean fitness of *S. ribesii* is consistently higher than that of *E. balteatus* and also its greater variation in fitness among aphids. One might reasonably predict greater local adaptation in the resident *S. ribesii* and greater genetic uniformity in the migrant *E. balteatus*.

In order to study evolutionary changes in diet breadth, life-history components need to be considered in a phylogenetic context: an estimate of the phylogeny now exists for the Syrphidae (Rotheray & Gilbert 1989, 1999) with which to assess such components associated with changes in diet breadth. Aside from preliminary phylogeny-free studies (Gilbert 1990; Gilbert *et al.* 1994), there are few published studies on predators with a phylogenetic focus. One exception is a pair of sister-species of aphidophagous Chrysopidae (see Tauber & Tauber 1987; Albuquerque *et al.* 1997), where one species is a generalist and the other a specialist derived from it that feeds on woolly alder aphids. Evolving to specialize on these aphids entailed the evolution of larger eggs and hatchlings, larger adults, reduced fecundity, slower development and a reduced ability to feed on the prey of the generalist. Some of these same traits may also be associated with specialization in syrphids (Gilbert 1990), a conclusion supported by the detailed phylogenetic studies of Branquart (1999).

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