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The Relationship Between Oviposition Preference and Larval Performance in an Aphidophagous Hover Fly, *Syrphus ribesii* L. (Diptera: Syrphidae)

H. Sadeghi[1]

ABSTRACT

The relationship between female oviposition preference and offspring performance is a key area of study on the evolution of host specificity. This study investigates host preference of the polyphagous hover fly *Syrphus ribesii* (Diptera: Syrphidae) and compares it with some components of its offspring's performance. Females and offspring were tested on six naturally used aphid hosts (blackberry, dock, nettle, pea, rose, and sycamore aphids). In the laboratory, larvae were able to develop successfully on aphids which were rarely selected for oviposition by gravid females. Despite the relatively small differences in performance resulting from feeding on different aphids, there was evidence for a preference-performance correlation in the generalist *S. ribesii.*

Keywords: Host choice, Host specificity, Fitness, Preference-performance.

INTRODUCTION

In many insects where the newly hatched offspring are relatively sessile and are not able to move any great distance to search for another appropriate host, host choice is made by the ovipositing female. In such cases, offspring must often feed on the host chosen by their mother. Whether or not the mother knows the best food for further development of her offspring is a controversial point (7). As a result of natural selection, one might expect a positive correlation between female oviposition preference and offspring performance. A good correlation between these suggests that host characteristics including host chemistry and nutritional value, are key factors that influence offspring performance, determine host range, and promote host specificity. Conversely, poor correlations are used as evidence that other ecological factors, such as the selection of enemy-free space are of greater importance in the evolution of host choice and specialization [3].

Numerous studies on a variety of phytophagous insects have investigated the preference-performance correlation, but there is no consensus, with the results ranging from strong [2, 29] to weak correlation [6, 7, review in 48]. Reasons put forward for the variation in outcome of these experiments include variation among the measures of performance used [24, 29, 47] and differences in the ability of larvae to move to alternative food sources [30, 31]. Nothing is known about this matter in predatory insects.

Larval performance depends mainly on food quality and mortality due to natural enemies. There is presumably little difference between the nutritional requirments of predatory insects and the contents of their prey [4] and, as a result, the cost of capture and the toxin content of prey are probably relatively more important to the overall costs of feeding [23].

In this research, the relationship between preference and performance in a predatory

[1] Department of Plant Protection, College of Agriculture, Ferdowsi University, Mashhad Islamic Republic of Iran.

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hover fly (Diptera: Syrphidae) was investigated. In hover flies, like many other insects, ovipositing females select among food types [41]. For a polyphagous syrphid, ovipositional preference by females may have a profound effect on the performance of the offspring, because syrphid larvae probably have rather limited dispersal abilities, although some indications imply larvae can move to new aphid colonies to a certain extent. For example, Banks [1] suggested that even quite small syrphid larvae must move between plants and possibly 'considerable distance'. Kan [19, 20] suggested that a single maple- or pea aphid-colony was insufficient to support larval development to maturity, and noted that 'older larvae are observed actively migrating among maple branches' or pea plants. However, most authors agree that the larvae are more or less sedentary (e.g. F. Gilbert; G. Rotheray, personal communication), and almost completely dependent on their mothers to chose a suitable host prey.

Rather few studies of syrphid larval development compare quantitatively any aspect of larval performance on different aphids, with the notable exceptions of Schmutterer [43], Ruzicka [38] and Malcolm [22, 23]. Although involving disparate studies with different aims and very different sets of measured variables, some generalities can be drawn. While development time and pupal weights are often unaffected [8, 27], aphid-prey species and/ or prey quality do seem to affect mortality. Several aphids are probably toxic or partially toxic to the larvae of one or more species of hover fly [8, 9, 21, 22, 32, 38, 43]. Other variables have rarely been considered, but can be affected by food quality (e.g. ease of capture) [39, 52]. 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 studied by Milne [25], Ruzicka [38] and Xiong and Dong [53]), several aphids were deemed highly toxic in one study, but suitable in another (e.g. *Brevicoryne brassicae* by Schmutterer [42] and Ruzicka [38]). A possible explanation for these apparent contradictions lies in the fact that aphid toxins may be, at least in part, sequestered from the host plants [17, 22, 23], which are variable in toxin content inter- and intra-specifically and, in one individual plant, through time [see 44]. 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 [9, 21, 22, possibly *Paragus longiventris* in 43].

This study aims firstly, to compare the effect of different aphid species as larval food on the performance of *Syrphus ribesii* under laboratory conditions, testing the null hypothesis that all aphids are equally good as food for the larvae. Secondly, we test whether there is an overall preference-performance correlation in this species, using egg distribution among aphids in laboratory experiments as our preference measure.

The hover fly chosen for use in this study is a widespread and very common species [14, 37]. The larvae are often the most common predators and have been reported from colonies of more than 100 species of aphids worldwide (F. Gilbert unpublished data). It is oligovoltine, with 2-3 generations per year, overwintering as an exceptionally cold-tolerant larva [15]. Adult females are normally ready to lay eggs 7-8 days after emergence. The larvae of this syrphid are very generalized in their feeding habits, but nonetheless show different oviposition preferences and field distributions on different aphid species [40] and oviposition preferences [41].

MATERIALS AND METHODS

Study Organism

The individuals of the *syrphus ribesii* L. (Diptera: Syrphidae) used in the experiment came from gravid females collected from Nottingham University Campus. The aphids used in this experiment were chosen for their availability, and because in both field and by

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experiment [40] they form a continuum from good to poor prey. Pea aphids *Acyrthosiphun pisum* (Harris) were obtained from stock cultures on broad bean (*Vicia faba* L.). All other aphids were collected from the University Campus including *Aphis fabae* L. from dock (*Rumex crispus* L.), *Microlophium carnosum* (Buckton) from nettle (*Urtica dioica* L.), *Macrosiphum rosae* (L.) from rose (*Rosa canina* L.), *Aphis ruborum* Börner from blackberry (*Rubus fruticosus* L.), and *Drepanosiphum plantanoidis* Schrank from sycamore (*Acer pseudoplatanus* L.). All are known to be the natural prey of larvae from this hover fly; the larvae have been found in colonies of all these aphid species [40].

Oviposition Preference

For experimenting on oviposition preference, females of known age were used. Females were initially naive, having had no previous exposure to aphids. On the day of eclosion, an equal number of females and males were transferred to the adult rearing cages. Mating was completed after 3-4 days, and the ovaries began to enlarge about a week after emergence. Once the majority of females contained some mature eggs (easily seen through the transparent abdominal pleurites), individual gravid females were transferred to separate cages. Aphids were then offered to each female on a newly-cut section of their host-plant standing in water; great care was taken to ensure that all cut sections were about the same size and 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 minutes. The number of eggs laid in response to the presented aphid were counted, and the aphid replaced by another aphid species, continuing until all aphids had been presented. Each day females had the choice of ovipositing in any of the test aphid colony; presentations continued throughout the oviposition preiod of 14–38 days. 13 syrphid females were used in the oviposition preference experiment.

Larval Performance

The culturing of *Syrphus ribesii* follows the methods of Frazer [11] and Hart and Bale [15, 16] with slight modifications. Adults were kept in a constant environment of 22-23°C with a 16 hour photoperiod, and were provided with bee-collected pollen (Sigma Ltd, Cat. No.P-8753), crystalline sugar placed on petri-dish lids on the floor of the cage, and water on a soaked pad of cotton wool in a conical flask. Both pollen and water were changed every 2-3 days.

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 three hours 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 our experiments there was a low percentage of egg hatch, and together, these factors decreased the number of larvae available for study. To counter this, for the first three days, larvae were left in groups and allowed to feed on pea aphids (during this period, only one or two aphids are normally consumed). At the beginning of the fourth day, larvae were weighed individually, transferred to experimental Petri dishes, and given aphids of the selected species.

Each day, the larvae were weighed, and enough similarly-sized aphids to supply food for 24 hours were weighed and added to the Petri dishes, the remains being weighed again the following day. Each larva received only one aphid species. Depending on availability, 10 to 16 replicates were used, except in the case of blackberry aphid, for which only 6 larvae were reared because of the

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scarcity of this aphid in the field. The resulting pupae were weighed, and the potential fecundity of the resulting adult females measured by dissecting them and counting the ovariole numbers of both ovaries.

Individual fitness was calculated (r) as a performance measure [24] by integrating development time (D: egg - pupa), survival (m=1 or 0) and potential fecundity (V) via the equation: r = [Ln (m.V)] / D, where Ln = natural logarithms. Fitness was calculated twice, once for surviving females only, and then for all females including non-survivors. In the latter, because female larvae cannot be differentiated from males, I assumed half the mortality to be female, rounding up when an odd number of larvae had died.

Differences among means were assessed using a one-way Anova, except for individual fitness including that of non-survivors, where a non-parametric Anova test was used (H, distributed as χ^2); survival differences were tested using χ^2.

RESULTS

Oviposition Preference

The distribution of eggs among aphids showed significant differences in the relative preference of aphids by females (KW = 76.5, P< 0.001; Fig. 1). With a few exceptions, sycamore aphid was ranked the highest by all females, with on average about 26.6% of eggs, followed by rose aphid (24.5%) and pea aphid (20.8%). The lowest preference was for nettle aphid, with about 5.9% of the eggs. There were some differences among different aphids in terms of acceptability by individual females. For example, only two out of 13 females laid eggs on nettle aphid colonies on the first day of oviposition, but the rest oviposited on the colonies of this aphid after days 3 or 4 of the experiment. All the other aphids were used for oviposition by females from the first day of oviposition.

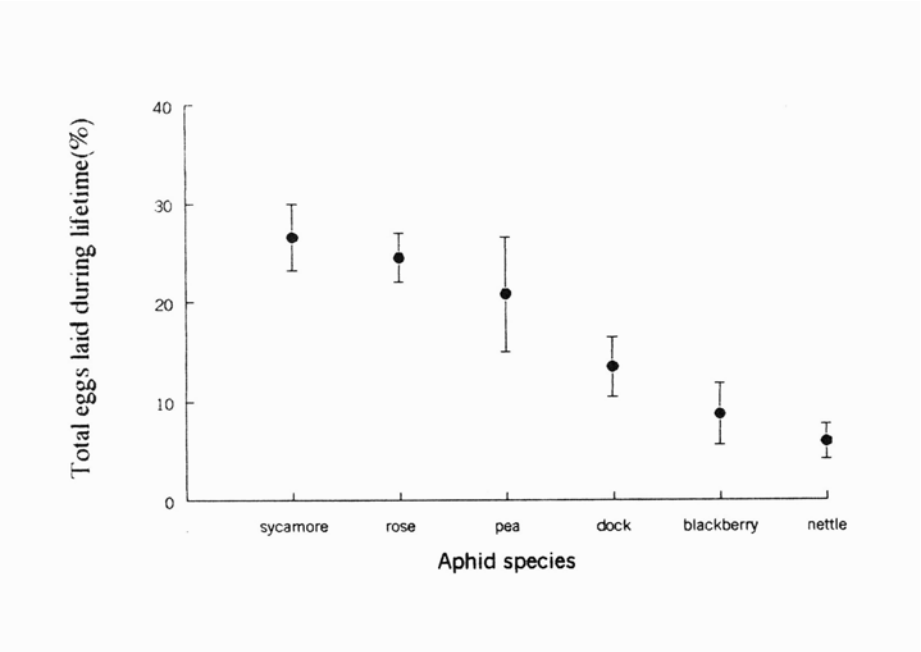

Figure. Percentage (± se) of lifetime fertility of female *Syrphus ribsii* laid in response to particular aphid species averaged across females (n=13). The differences are highly significant (KW= 76.5, P< 0.001).

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Table 2. Hierarchy of aphid species in relation to oviposition preference and suitability for larval development (from 41).

Aphid species	Plant species	Oviposition preference[a]	Suitability for lavral development	
			all[b]	survivors[c]
Acyrthosiphon pisum	*Vicia faba*	18.9	11.8	14.8
Apbis fabae	*Rumex obtusifolius*	11.1	8.3	13.8
Aphis grossulariae	*Epilobium hirsutum*	-	-	-
Aphis pomi	*Malus domestica*	-	-	-
Aphis ruborum	*Rubus fruticasus*	7.0	9.5	14.2
Aphis sambuci	*Sambucus nigra*	6.9	-	-
Cavariella sp	*Haracleum sphondylium*	9.8	-	-
Drepanosiphum plantanoidis	*Acer pseudoplantanus*	21.4	15.9	15.9
Marasipbum rosae	*Rasa* sp	20.3	15.7	15.7
Microlophium carnosum	*Urtica dioica*	4.6	12.0	15.0
Phyllaphis fagi	*Fagus sylvatica*	-	-	-
Schizoneura ulmi	*Ulmus* sp	-	-	-

[a] Mean percentage of total egg load laid on an aphid during no-choice sequential oviposition tests
[b] Mean individual fitness of all individuals tested, calculated according to McGraw and Caswell (25).
[c] Mean individual fitness of those surviving to adulthood, calculated according to McGraw and Casweel (25).

Larval Performance

The performance measures of *S. ribesii* reared on the different aphid species are given in Table 1. The results showed only relatively small but nevertheless significant differences in the suitability of most aphid species as larval food.

There were no significant differences in survival among treatment groups. The survival rate until pupation ranged from 75 % for dock aphid to 100% for sycamore and rose aphids. Substantial mortality occurred during the pupal period, particularly on rose aphids. The mean larval development period ranged from 9.6 to 11.6 days. The mean values were significantly different among groups ($F_{5,59}$= 8.76; p<0 .001), being 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 (on dock aphid) to 70.8 mg (on 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. The number of ovarioles of adult females ranged from 61 to 120, but the mean values were not significantly different.

Individual fitness of survivors (Table 1) 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, $p < 0.05$).

Oviposition Preference Versus Larval Performance

Testing for a positive (rank) correlation between oviposition preference and the performance of offspring measured by individual fitness (data in Table 2), there were indications of a positive relationship between oviposition preference versus larval performance (r_s=0.60, n=6, p=0.09).

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DISCUSSION

A number of factors, including those mentioned by Thompson and Pellmyr [48], may be the cause of a weak correlation between oviposition preference and larval performance in the syrphid studied here.

In the field, it is possible that the relationship between oviposition preference and performance is influenced by differential levels of attack by natural enemies on preferred or non-preferred aphid species: the proportion of syrphid larvae killed by specialist parasitoids can be very high [14, 37]. However, the effect of natural enemies on host choice by ovipositing females was not investigated in the present study. Studies have also shown that factors such as egg load and age may affect a female's oviposition preference [e.g. 10]. Earlier works [41, 42] showed that, as a female ages or when she has accumulated eggs, the discrepancy among preferred and less preferred aphid species decreases.

One important point to be mentioned is the possible effect of host plant on the oviposition preference of females. The treatments in oviposition preferences were aphids with a cut section of their host plant. Consequently, there is the possiblity that the significant differences among treatments were due to different aphids, plants, or both. For example, plant traits such as the presence of trichomes and many others [see 44] are often assumed to influence the host plant selection behaviour. As a result, it is possible that the oviposition preferences observed could be due either to the aphid or plant effect.

There is plenty of evidence on the effect of learning on host selection by adult females [see 7], but very little is known of the effect of prior experience of larvae on their performance. Without providing data, Schmutterer [43] notes that small larvae of *Afrosyrphus varipens* collected from *dactynotus compositae* on *Vernomia lasiopus* developed normally when transferred to *Toxoptera citricidus,* but were killed by *Aphis fabae solanella*. However, if there was any effect of early feeding on the performance of the test larvae in this study, one might expect to see a better performance in the larvae fed on pea aphids.

The results showed that even in this very generalized predator, there are significant differences in the distribution of eggs among various aphids. This supports suggestions in the literature of selectivity of oviposition [5, 25, 26, 29, 35].

As in other studies[33, 34, 36, 45, 50, 51], the evidence suggests that the larvae of this syrphid species are able to develop successfully on nearly all aphid species offered to them. In other words, the host range of the larvae, as measured by different components of larval performance, is wider than that of the ovipositing females.

Larval conservatism (i.e. being generalist in feeding behaviour) along with the results of studies on host shifts [18, 46] are used as evidence that host shifts only involve a behavioural change in host preference. It has been argued that, in general, behavioural (i.e. preference) flexibility should be more evolutionarily labile than morphological or physiological (i.e. performance) traits, and for this reason, the more labile characters should be the initiators of new directions in the evolution of host utilization [49]. Other authors [12,13, 36, 44, 45] have also stressed the role of behavioural adaptation in the specialization process, and the leading role of the behaviour of ovipositing females in evolution of host utilization [18]. The behavioural sequence followed by gravid females during oviposition may shed more light on syrphid specialization, especially in the light of the hypothesis of selective attention (i.e. the costs associated with obtaining and assessing information for generalists are avoided by specialists, so the specialist species will make faster and more accurate decisions than generalists). This could be the next study to be undertaken in unravelling the evolution of prey specialization in the aphidophagous Syrphidae.

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رابطه بین رجحان تخم ریزی و رشد و نمو لاروها در یک گونه مگس گل
Syrphus ribesii L. (Diptera: Syrphidae)

ح. صادقی

چکیده

رابطه بین رجحان تخم‌ریزی مگس گل ماده و رشد و نمو نتاج یکی از عرصه های اصلی مطالعات مرتبط با فرآیند تکاملی استفاده از تخصص در میزبان‌یابی است. این مطالعه رجحان میزبانی را در مگس پلی فاژ *Syrphus ribesii* بررسی و آنرا با برخی اجزا رشد و نمو نتاج مقایسه می‌کند. حشره ماده و لاروها روی شش گونه از شته‌های میزبان طبیعی آنها: شته تمشک، رز، نخود، افرا، ترشک و گزنه مورد آزمایش قرار گرفتند. در شرایط آزمایشگاهی لاروها با موفقیت بیشتری روی شته‌هایی که بندرت برای تخم‌ریزی انتخاب می‌شوند رشد یافتند. علیرغم اختلاف جزیی در رشد و نمو در نتیجه تغذیه از شته‌های مختلف، شواهد حاکی از وجود یک همبستگی بین رجحان تخم‌ریزی و رشد و نمو لاروها در مگس سیرفیده *Syrphus ribesii* بود.

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