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Oviposition preferences of aphidophagous hoverflies

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Abstract. 1. Oviposition preferences of two predatory hoverflies, *Episyrphus balteatus* and *Syrphus ribesii* (Diptera, Syrphidae), were studied in the laboratory.

2. There was broad agreement between the two species: two of the top three preferred prey for oviposition in both hoverflies were pea and rose aphids; nettle aphids were consistently the least preferred.

3. Discrimination decreased with age.

Key words. Aphidophagous hoverflies, diet breadth, hierarchy threshold model.

Introduction

Oviposition behaviour is central to investigations of many aspects of insect biology, e.g. insect population dynamics, life-history evolution, and biological control of insect pests. One crucial aspect of oviposition behaviour is host choice, especially in insects where the newly hatched offspring are relatively sessile and are unable to move any great distance to search for another appropriate host. Such offspring must often feed on the host chosen by their mother. Choices of the proper hosts for larval growth and development are therefore made by the ovipositing female, resulting in a distribution of larvae on different hosts. The relationship between female oviposition preference and larval performance is a vital component of current ideas about the evolution of host choice (Thompson, 1988; Singer *et al*., 1994; Thomas & Singer, 1998).

It is often believed that females display a hierarchy of preference for different hosts (e.g. Wiklund, 1981; Courtney *et al*., 1989; Nylin & Janz, 1993; Thomas & Singer, 1998). The outcome of such preferences is not fixed because the distribution of eggs varies among and within individuals in response to a variety of factors (see Fitt, 1986; Minkenberg *et al*., 1992). For example, it is usually found that female age affects the oviposition behaviour of insects, with females becoming less selective with increasing age, thus broadening their diet width. There is plenty of evidence for this pattern: Singer (1982) showed that butterflies increased the range of acceptable hosts with increasing time since the last oviposition; Fitt (1986) found that older females of the highly polyphagous *Dacus tryoni* broadened their diet to include hosts that had previously been unacceptable, whereas in specialist tephritid flies, diet breadth did not expand.

Various models incorporate the feature that older females are less selective in placement of their eggs (e.g. Courtney *et al*., 1989; Mangel, 1989). In their hierarchy threshold model, Courtney *et al*. (1989) formalised this and a number of other ideas on host choice by individual insects. They made a number of assumptions, among which were the following: that females possess an intrinsic evolved degree of preference for each host, producing a rank order of preference among hosts that does not change throughout an individual's lifetime; that individuals accepting a low-ranking host will also accept all higher-ranking hosts; and that actual acceptance of an encountered host depends on whether the stimulus of that host exceeds the current motivational threshold (which can vary with factors such as age or egg load), and thus is not affected by variation in host-specific factors.

The study reported here investigated host preferences for oviposition among aphidophagous hoverflies (Diptera, Syrphidae) as part of an integrated study of the relationship between preference and performance (Sadeghi & Gilbert, 1999a,b; H. Sadeghi and F. Gilbert, unpublished; H. Sadeghi *et al*., unpublished). Hoverflies are one of the largest families of flies, 33% of which are homopteran (usually aphid) predators classified in the subfamily Syrphinae (see Rotheray, 1989; Gilbert, 1993). Host choice in this subfamily is determined largely by the oviposition behaviour of females. Some factors involved in selecting the oviposition site (Table 1) include aphid-associated chemical stimuli, aphid colony size, the spatial position of the aphid colony (Chandler, 1968d; Sanders, 1980), and host-plant characteristics (Dixon, 1959; Chandler, 1968a; Sanders, 1983a,b). There is some evidence (Table 1), largely anecdotal, that as syrphine females age they become less selective about where they lay their eggs.

Specifically, the study reported here tested an assumption and a prediction arising from the hierarchy threshold model of host choice: (1) that there will be a rank-order hierarchy of preference of aphid prey species by gravid females, and (2) that ageing will decrease the motivational threshold of females, and thus the potential diet breadth of larvae will increase and the discrimination between highly preferred and less-preferred hosts will decrease, but the rank order will not change.

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Table 1. Main literature studies on influences on the oviposition behaviour of aphidophagous hoverflies, or those that compare oviposition on different aphid species. Names of the Syrphidae follow Pek (1988); those of the aphids follow Eastop and Hille Ris Lambers (1975); and those of the plants follow Mabberley (1997).

Syrphid	Prey	Plant	Author	Findings
Eupeodes (Metasyrphus) corollae	*Aphis fabae*	*Vicia faba*	Bombosch (1962)	Aphids and/or volatile components of honeydew (probably siphuncular secretions) were the main stimuli for oviposition, perceived mainly via the antennae, but also via the tarsi and/or mouthparts.
Episyrphus balteatus *Platycheirus albimanus*	*Sitobion avenae* aphids Honeydew of *Acyrthosiphon pisum* *Metropolophium dirhodum* *Microlophium carnosum*	*Triticum* sp.	Budenberg & Powell (1992)	*Episyrphus* females landed on plants and oviposited in response to honeydew rather than to the plants or aphids themselves. They responded to *Metopolophium* and *Acyrthosiphon* honeydew, but not *Microlophium.* *Platycheirus* oviposited on wheat irrespective of the presence of aphids or honeydew.
Episyrphus balteatus *Platycheirus peltatus*	Not reported	Not reported	Chandler (1966)	Young female *E. balteatus* did not oviposit on uninfested plants, but as they aged they lost this discrimination. Even young female *P. peltatus* lay eggs on uninfested plants.
Eupeodes (Metasyrphus) luniger	*Brevicoryne brassicae*	*Brassica oleracea*	Chandler (1967)	Precision of oviposition (distance between nearest aphid and location of egg) decreased with female age.
Many species	*Brevicoryne brassicae* *Aphis fabae*	*Brassica oleracea* *Vicia faba*	Chandler (1968a)	Most species laid single eggs in response to aphids, but some (*Platycheirus peltatus, Melanostoma* spp.) laid a substantial proportion of eggs on aphid-free plants in larger batches.
Many species	*Brevicoryne brassicae* *Aphis fabae*	*Brassica oleracea* *Beta vulgaris* *Vicia faba*	Chandler (1968b)	Oviposition in most species increased with aphis infestation up to a maximum, then declined. Species differed in the level of infestation eliciting maximal oviposition
Many species	*Brevicoryne brassicae* *Aphis fabae*	*Brassica oleracea* *Vicia faba*	Chandler (1968c)	*Platycheirus manicatus* females laid eggs on uninfested plants, but were situated by nearby aphis colonies. No effect on oviposition of nearby flowers was detected. No effects of prior eggs, larvae, or evidence of larval feeding was detected on subsequent oviposition.
Eupeodes (Metasyrphus) luniger	*Acyrthosiphon pisum*	*Vicia faba*	Dixon (1959)	More eggs were laid in denser aphid colonies. Gravid females responded mainly to olfactory stimuli.
Pipizella varipes	*Anuraphis subterranea*	*Pastinaca sativa*		Females could retain mature eggs for several weeks in the absence of suitable oviposition sites.
Many species	*Brevicoryne brassicae*	*Brassica oleracea*	Guest (1984)	More eggs were laid at higher aphid densities such that a fixed ratio of eggs to aphids is maintained. *Melanostoma* and some *Platycheirus* spp. were much less dependent on the presence of aphids, laying in batches.

Syrphid	Prey	Plant	Author	Findings
Episyrphus balteatus				Female *E. balteatus* laid further away from aphids as they aged. Response to aphid density reached a maximum at 200 aphids per plant, then declined. Behaviourally the probability of landing at an aphid colony was related to aphid density, but the probability of approach was random, and the number of eggs laid and length of each visit were fixed.
Episyrphus balteatus	*Periphyllus californiensis* *Yamatocallis tokyoensis*	*Acer palmatum*	Kan (1988a)	Females oviposited without showing any preference between colonies of the two aphid species.
Betasyrphus serarius *Eupeodes (Metasyrphus) nitens* *Syrphus vitripennis*	*Acyrthosiphon kondoi* *Acyrhosiphon pisum* *Megoura crassicauda*	*Vicia angustifolia*	Kan (1988b)	Females selected young colonies without winged adults for oviposition. Most (81%) colonies had eggs of only a single syrphid species.
Episyrphus balteatus *Eupeodes (Metasyrphus) corollae*			Lyon (1965)	Aphids needed for oviposition, unlike in *Sphaerophoria* and especially *Platycheirus peltatus*; in absence of aphids, eggs were retained, eventually being resorbed. Prolonged retention reduced fecundity but increased longevity.
Eupeodes (Metasyrphus) luniger *Syrphus ribesii* Others, including *Episyrphus balteatus* (not common)	*Acyrthosiphon pisum* *Aphis fabae* *Megoura viciae*	*Vicia faba*	Milne (1971)	All the common syrphids laid more eggs on beans infested with *Aphis*, and to a lesser extent *Megoura*, than they did on beans infested with *Acyrthosiphon*.
Eupeodes (Lapposyrphus) lapponicus	*Adelges piceae* *Adelges cooleyi* *Adelges tsugae*	*Abies* spp.	Mitchell (1962)	Eighty-five per cent of eggs laid on *A. tsugae*, none on *A. piceae*
Field data from all species *Eupeodes (Metasyrphus) corollae*	Many aphids *Aphis fabae* (mostly)	Many plants *Vicia faba*	Peschken (1964)	No influence of plant species, colour, height or plot size was detected, but females preferred the interior of dense stands (90–100% ground cover), and large aphid colonies.
Dideopsis aegrota *Ischiodon scultellaris*	Various *Aphis citricola* *Aphis fabae*	Various	Phoon (1973)	Female *Dideopsis* used olfaction since they find concealed aphid colonies. *Ischiodon* females required gustatory stimuli from aphid cornicle secretion, refusing to oviposit just with olfactory cues.
	Rhopalosiphum maidis			Oviposition was close to aphids, usually less than 3 mm away. Older females lost discrimination. Fifty-six per cent of eggs were laid on *A. fabae*, 31% on *R. maidis*, and only 13% on *A. citricola*. The presence of eggs or larvae did not deter females from oviposition.
Parasyrphus melanderi	*Chrysomela aeneicollis*	*Salix* spp.	Rank & Smiley (1994)	Specialist predator of chrysomeline leaf beetle eggs and larvae defended against predators by a glandular secretion of salicylaldehyde derived from salicin of the willow. *Parasyrphus* females preferred to oviposit on beetles feeding on salicin-rich willow species.

Syrphid	Prey	Plant	Author	Findings
Eupeodes (Metasyrphus) corollae	Various	Various	Reepmeyer (1969)	The number of eggs laid depended on the number of aphids in a colony, up to a maximum beyond which no further stimulation was apparent. Adult aphids stimulated females more than nymphs. Using no-choice tests on nine aphid species, there was a gradual increase in preference, from avoided (*Eucallipterus tiliae* on *Tilia platyphyllos*) to preferred (*Aphis craccivora* on *Vicia faba*). Using binary choice tests, relative to *Aphis craccivora*, Rhopalosiphum padi was equally preferred, *Tuberolachnus salignus* rather less, and *Myzus persicae* definitely avoided. Different host plants had no effect on the relative preference of *Myzus pericae*, but avoidance could be reduced by increasing numbers relative to *Aphis craccivora*.
Platycheirus fulviventris	*Hyalopterus pruni* *Cavariella* sp. *Macrosiphum* sp.	*Phragmites communis* *Angelica sylvestris* *Heracleum sphondylium* *Filipendula ulmaria*	Rotheray & Dobson (1987)	Oviposition only occurred in *Hyalopterus* colonies on *Phragmites*. In Scotland, batches contained 2–15 eggs, with a mean colony size of 35 aphids. Larger aphid colonies were more likely to have egg batches, which also contained more eggs. Ninety-five per cent of colonies only had a single egg batch, and females were seen rejecting colonies already containing an egg batch.
Eupeodes (Metasyrphus) corollae	*Aphis craccivora*	Plant models	Sanders (1979)	Experimental studies show females always preferred larger colonies when given a choice. Colonies 2 cm in diameter were most effective in stimulating oviposition, eliciting on average one egg per visit; a small colony of three aphids only elicited one egg every 10 visits.
Eupeodes (Metasyrphus) corollae	*Aphis fabae*	*Vicia faba*	Volk (1964)	Volatile chemical stimuli from aphid honeydew and/or siphuncle secretion were the main stimulus for oviposition, supplemented by visual and tactile cues.
Episyrphus balteatus	*Aphis fabae*	*Vicia faba*	Wnuk (1979)	More eggs were laid when there were more aphids per plant, but the egg : aphid ratio decreased.
Episyrphus balteatus *Eupeodes (Metasyrphus) corollae* *Syrphus vitripennis*	*Aphis fabae*	*Vicia faba*	Wnuk & Starmach (1977)	In all three syrphids there was an increase in the number of eggs laid with greater aphid densities, but all three relationships were asymptotic, saturating at about 500 aphids per plant.

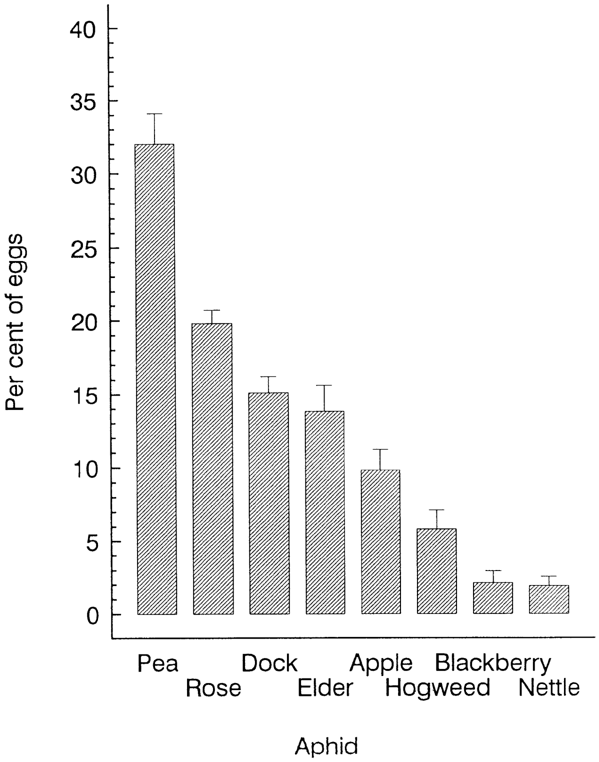

Fig. 1. Percentage of lifetime fertility of female *Episyrphus balteatus* (± SE) laid in response to particular aphid species, averaged across females ($n = 12$). The differences are highly significant (KW = 83.7, $P < 0.001$).

Materials and methods

Study organisms

The two hoverfly species chosen for use in this study, *Episyrphus balteatus* (DeGeer) and *Syrphus ribesii* (L.), are very common in the U.K. *Episyrphus balteatus* has a single (occasionally two) generation in the U.K., with adult activity in late summer; adult females may overwinter occasionally but the bulk of the population migrates to southern Europe where, presumably, it breeds or overwinters (Rotheray, 1989; Gilbert, 1993). *Syrphus ribesii* is oligovoltine, with two or three generations per year, overwintering as an exceptionally cold-tolerant larva (Hart & Bale, 1997a). Adult females are normally ready to lay eggs 7–8 days after emergence.

The pea aphids *Acyrthosiphun pisum* (Harris) used in these experiments were from stock cultures on broad bean *Vicia faba* L. All other aphids were collected from the field: *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 sambuci* L. from elder *Sambucus nigra* L., *Aphis ruborum* Börner from blackberry *Rubus fruticosus* L., *Drepanosiphum plantanoidis* Schrank from sycamore *Acer pseudoplatanus* L., *Cavariella* sp. from hogweed *Heracleum sphondylium*, and *Aphis pomi* deGeer from apple *Malus domestica* Borkh. All are known to be natural prey of larvae of these hoverflies (H. Sadeghi *et al.*, unpublished).

Depending on availability, stock cultures of *Syrphus ribesii* (from April) and *Episyrphus balteatus* (from June) were established from gravid females captured at the Nottingham University Campus. The culturing system followed Frazer (1972) and Hart and Bale (1997b), with some changes. Adult cages (60 × 60 × 100 cm) were made of an aluminium frame with acrylic sides, top, and front, and plywood floor and back; a sliding door and 15-cm holes in the front and top provided access. All holes were covered with muslin, fixed by Velcro® fastening. Adults lived in a constant environment of 22–23 °C and 16-h photoperiod, and were provided with bee-collected pollen (Sigma Ltd, Gillingham, U.K.), 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. The pollen and water were changed every 2–3 days. To supply aphids as food for larvae, broad beans were sown densely (about 100 seeds) in small plastic trays in a greenhouse. Newly sprouted beans were placed in the aphid cages at a rate of at least two trays per week. To have enough flies when necessary, adult females in the stock culture were stimulated to oviposit by presenting cut sections of broad bean infested with pea aphids. A batch of eggs laid over a 2–3-h period provided a cohort of flies with a synchronous adult emergence to within 48–72 h.

Experimental design and assay method

Oviposition preferences were investigated under laboratory conditions. Singer (1986) discussed different techniques for measuring preference, concluding that many insects cannot perceive more than one host at a time, encountering them sequentially even when they are presented simultaneously. Courtney *et al.* (1989) followed this idea and proposed either no-choice or sequential-choice tests as the best design for testing the predictions of diet choice models.

Oviposition preference experiments used females of known age. On the day of eclosion, an equal number of females and males were transferred to the adult rearing cages. Under these conditions, mating occurred after 3–4 days, and the ovaries began to enlarge about a week after emergence. When the majority of females contained some mature eggs (easily seen through the transparent abdominal pleurites), individual gravid females were transferred into separate cages of the same design. Females were initially naive, having had no previous exposure to aphids. Aphids were 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, with the same number of aphids (of various instars). Each day, aphids were presented in a randomised 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 30 min. The number of eggs laid in each case was counted, and the aphids were replaced by another

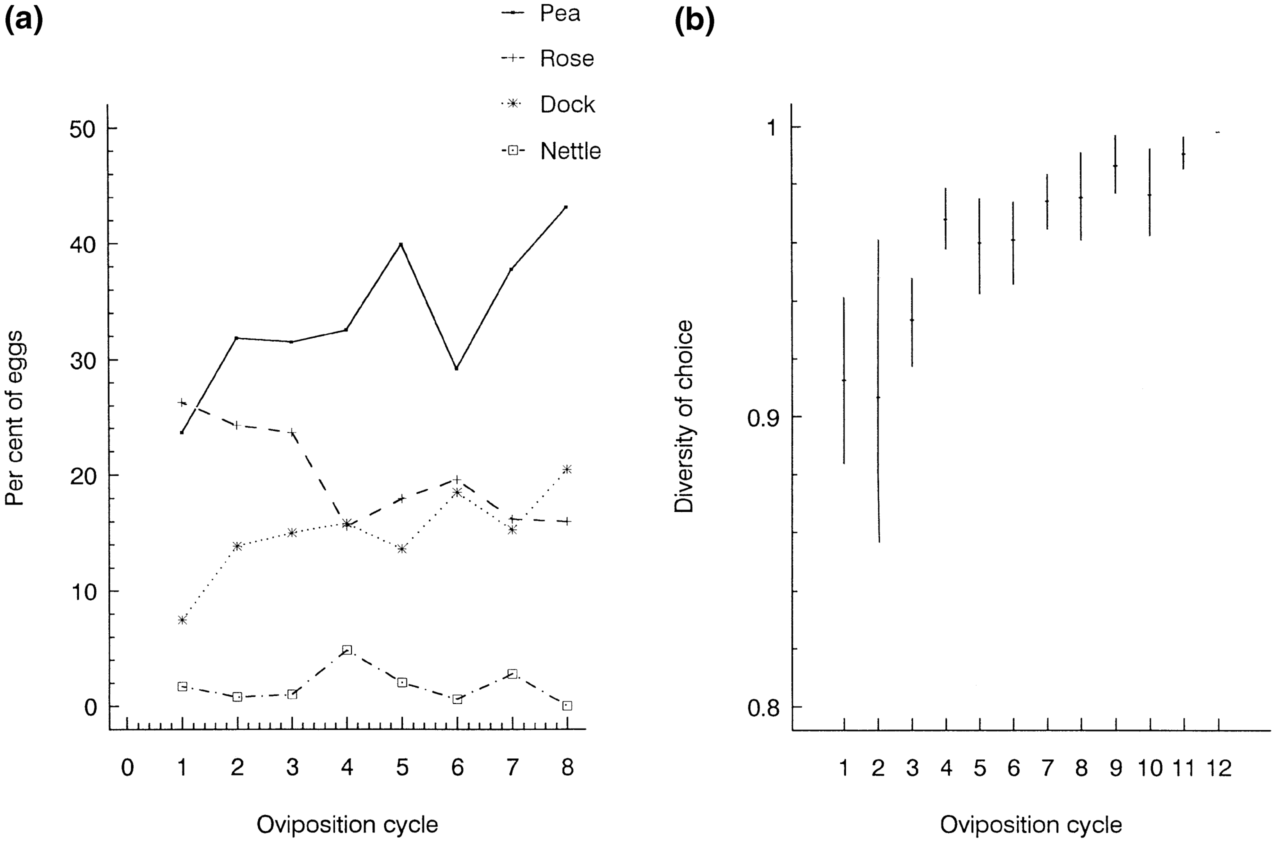

Fig. 2. (a) The three most preferred and the least preferred (nettle) aphids by female *Episyrphus balteatus*. The percentages of the total eggs deposited during each oviposition cycle are plotted against the successive oviposition cycles. Note that the trends are different in each aphid species. (b) The overall diversity of choices made by female *E. balteatus* plotted against successive oviposition cycles: there is a highly significant positive correlation ($r_s = 0.36$, $n = 96$, $P < 0.001$). More cycles are used here because, unlike in (a), the data were not split into different subsets, so sample sizes were adequate to use the larger number of cycles.

aphid species, continuing until all aphids had been presented. Each day, all test aphid species were offered, and presentations continued until all oviposition had finished.

Analysis

As for *Eupeodes corollae* (Volk, 1964), it was clear from the cyclical patterns of egg deposition that there was a rhythm of oviposition, typically with 1–3 days' recovery and further egg maturation after a peak of oviposition. Superimposed upon this was the variability of individual females. Rather than using days as a measure of time, therefore, the time course of egg deposition for each female was separated into oviposition cycles to allow for this variation. Such cycles were normally obvious from the data, but occasionally they were not so clear, usually because for some reason few eggs were laid.

The relative preferences of ovipositing females were expressed as the mean percentage of eggs laid in response to each aphid species, expressed on a per-cycle or overall per-female basis. Percentages were not transformed because nonparametric methods were used. A nonparametric one-way ANOVA (Kruskal–Wallis) test was used for detecting differences among relative preferences for different aphids, with the test statistic denoted by KW. Kendall's coefficient of concordance *W* (Sokal & Rohlf, 1981) was used to measure the consistency of the rank order of preference either between females or between days for each female through the oviposition period. A concordance value of 1 indicates perfect agreement in rankings; a value of 0 indicates that the rankings being compared are independent.

To measure potential diet breadth, the Simpson diversity index was calculated (see Lande, 1996). This is an estimate of the probability that any two eggs chosen randomly from those laid by an individual female were laid on different aphid colonies. A value of 0 indicates that females only oviposit on one aphid species; a value of 1 indicates that every egg was laid on a different aphid species. The prediction is that as females age, they will be less selective, broadening their host range by laying more eggs on low-ranking hosts; the Simpson diversity index should therefore increase with age (i.e. with age measured in oviposition cycles), and there should be a positive rank correlation between diversity and age.

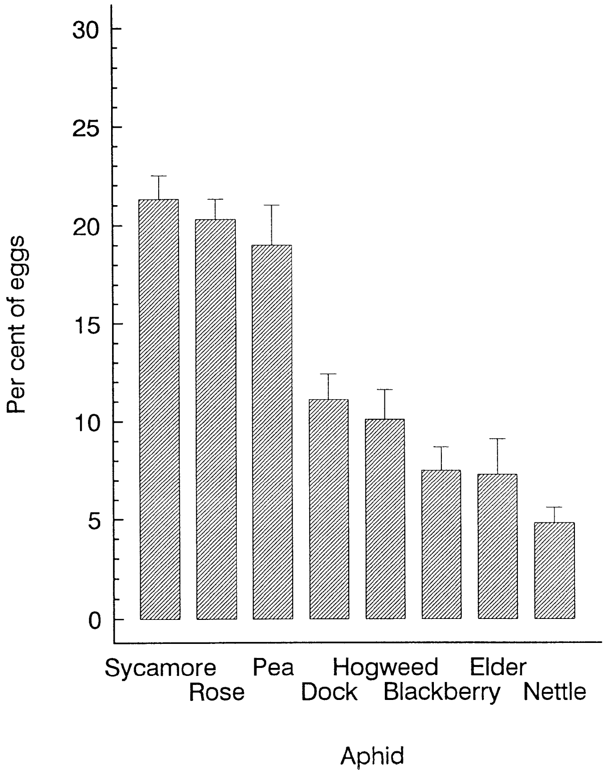

Fig. 3. Percentage of lifetime fertility of female *Syrphus ribesii* (± SE) laid in response to particular aphid species, averaged across females ($n = 13$). The differences are highly significant (KW = 76.5, $P < 0.001$).

Results

Episyrphus balteatus

Overall, all females preferred pea aphid the most, with on average about 32% of eggs; the lowest preference was for nettle aphid, with only 2.3% of eggs (Fig. 1). There were large fluctuations in the daily proportion of eggs laid on each aphid, especially towards the end of the oviposition period, but much less variation when the data were expressed per oviposition cycle. The percentage of eggs laid on the most and the least preferred aphids in successive cycles is shown in Fig. 2(a). With increasing age, there was a slight increase in the proportion of eggs laid on nettle, the least preferred aphid. Furthermore, the Simpson diversity index increased with age, as predicted (Fig. 2b).

With respect to the rank order of oviposition preference, there was a high level of agreement among females in their overall ranking of different test aphids ($W = 0.91$, $\chi^2_7 = 76.4$, $P < 0.001$). All females had the highest preference for pea and rose aphids, followed by dock aphid. There was greater variation among females in ranking elder, apple, and hogweed, but the majority of females ranked blackberry and nettle aphids as the least preferred hosts.

To test whether there was agreement in the ranking of aphid species throughout the oviposition period by individual females, Kendall's coefficient of concordance was calculated for each individual female across all the cycles of the oviposition period. The resulting values of W (0.41–0.64, $\chi^2_7 > 15.7$, $P < 0.05$) were all significant, usually very highly significant, suggesting consistency in the ranking of aphids by individual females through time. Inconsistencies were usually produced when few eggs were laid during an oviposition cycle, rendering the preference rank orders unreliable, and making it difficult to distinguish the cycle itself.

Syrphus ribesii

The distribution of eggs among aphids showed significant differences in relative preference of aphids by females (Fig. 3). With a few exceptions, sycamore aphid was ranked the highest by all females, with on average about 21% of eggs, followed by rose aphid (20.3%) and pea aphid (18.9%). The lowest preference was for nettle aphid, with about 4.6% of the eggs. There were some differences among different aphids in terms of acceptability by individual females. For example, only two of 13 females laid eggs on nettle aphid on the first day of oviposition, but the majority oviposited on the colonies of this aphid after 3 or 4 days of the experiment. All the other aphids were used for oviposition by females from the first day of oviposition.

The distribution of eggs clearly changed with female age (Fig. 4a), with the most preferred declining in preference and the least preferred increasing in preference. The diversity of choice increased with age, as predicted (Fig. 4b).

There was good agreement among females in their overall ranking of different aphids in this experiment ($W = 0.77$, $\chi^2_7 = 70.1$, $P < 0.001$). The consistency with which females ranked aphids through time (oviposition cycles) was significant (usually very highly significant) in 10 of the 13 females ($W = 0.24$–0.64, $\chi^2_7 > 14.6$, $P < 0.05$). In three females, W failed to reach significance: one of these ($W = 0.76$) was due to an abnormally low egg load and short lifespan (only two oviposition cycles); in the other two females, one laid consistently and similarly to all other females for the first five cycles ($W = 0.73$, $\chi^2_7 = 25.6$, $P < 0.001$) but then appeared to switch preference away from pea and rose aphids. These results indicate that most females have a consistent ranking of aphids through time. Concordance values were significantly lower in *S. ribesii* than in *E. balteatus* (Kruskal–Wallis test, KW = 7.0, $P < 0.01$).

Discussion

The results of the work presented here show that even in these very generalised predators, there were significant differences in the distribution of eggs among various aphids. This supports the literature suggesting selectivity of oviposition (Mitchell, 1962; Reepmeyer, 1969; Milne, 1971; Phoon, 1973; Niemczyk & Pruska, 1986; Budenberg & Powell, 1992). Even greater selectivity might reasonably be predicted in specialist syrphid predators, as found in *Xanthandrus* (Lyon, 1968) and

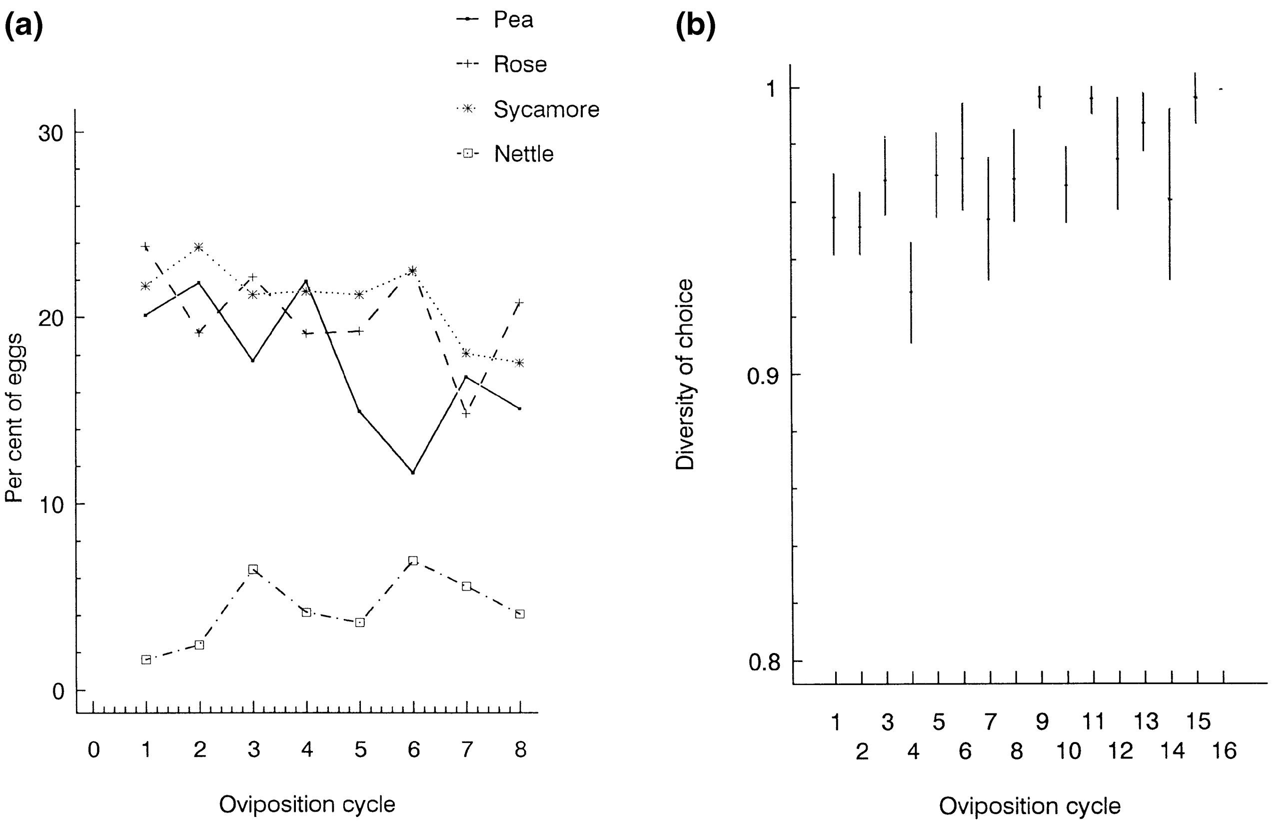

Fig. 4. (a) The three most preferred and the least preferred (nettle) aphids by female *Syrphus ribesii*. The percentages of the total eggs deposited during each oviposition cycle are plotted against the successive oviposition cycles. Note that the preferred aphids decline in preference, whereas the least preferred aphids increase in preference with age of the female. (b) The overall diversity of choices made by female *S. ribesii* plotted against successive oviposition cycles: there is a highly significant positive correlation ($r_S = 0.36$, $n = 109$, $P < 0.001$). More cycles are used here because, unlike in (a), the data were not split into different subsets, so sample sizes were adequate to use the larger number of cycles.

Platycheirus fulviventris (Rotheray & Dobson, 1987). Because most syrphids are oligophagous (Gilbert, 1990; Gilbert *et al.*, 1994), syrphid predators are clearly like insect herbivores in that most species are relatively specialised (Schoonhoven *et al.*, 1998). A reason for this might be the selective attention hypothesis, which states that there are costs for generalists of making decisions among potential hosts that are avoided by specialists concentrating attention on just one cue (Kotler & Mitchell, 1995; Bernays, 1996, 1998; Dall & Cuthill, 1997; Janz & Nylin, 1997).

The relative percentage of eggs on any particular aphid is considered to be the relative preference of an ovipositing female for that aphid. Based on the percentage of eggs laid on each aphid, pea and rose aphids were clearly more preferred hosts of *E. balteatus* females; nettle and blackberry were least preferred aphids. Other aphids with some variation were placed in mid rank order. For *S. ribesii,* sycamore, rose, and pea aphids were ranked highest, and nettle was the least preferred aphid. These results are reasonably consistent with the natural distribution in the field but it is difficult to interpret field distributions of syrphid larvae because of the many other influences that come into play. Certainly, *E. balteatus* is rarely found in nettle-aphid colonies in the field, but in contrast *S. ribesii* is very often found there (H. Sadeghi *et al.*, unpublished). Singer (1986) stated that because all factors involved in host selection may influence the result of preference tests, testing the effect of single oviposition stimuli (here, aphids) may be misleading because of the interaction between insect responses and different stimuli. Moreover, Singer believes that captive insects are often less discriminatory than those in the field.

Considering the effect of age on oviposition behaviour, the results of experiments with both syrphid species are generally in line with results from other insects. This pattern is so general that it is incorporated into the hierarchy threshold model (Courtney *et al.*, 1989). The syrphid species studied here do indeed lose discrimination as they age, broadening the range of acceptable prey. This agrees with the indirect data from syrphids of other authors, e.g. it is the implication of the increase with age of the egg-to-aphid distances measured by Chandler (1967), Phoon (1973), and Guest (1984). As females age, they discriminate less among different aphid prey.

Although discrimination reduces with age, results presented here show that there is a high degree of consistency in the ranking of different aphids through time by both syrphid species. This agrees with the prediction of the hierarchy threshold model, that the rank order of hosts should not change with age, even though the absolute acceptability of the host may change. Nettle aphids were always poorly accepted even though syrphid response varied with female age. The reasons why the consistency of ranking should be lower in *S. ribesii* than in *E. balteatus* are unclear, but may be connected with the fact that the first generation of gravid female *S. ribesii* derived from overwintering larvae is ovipositing in spring, when aphid availability is highly variable among years. The vast majority of *E. balteatus* females oviposits in midsummer when year-to-year variation in aphid phenologies is much lower.

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