

The effect of egg load and host deprivation on oviposition behaviour in aphidophagous hoverflies

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Abstract. 1. Two species of aphidophagous hoverfly, *Episyrphus balteatus* and *Syrphus ribesii*, were tested for the effects of egg load and host deprivation on oviposition choices.

2. Egg load affected the total number of eggs laid in *E. balteatus* but not in *S. ribesii*, however it did not affect the proportion laid on any one aphid in *E. balteatus* but did affect the proportion laid on any one aphid in *S. ribesii*. The rank order of preferences remained unchanged by age or host deprivation.

3. The dominant effects on host choices were aphid species (in both syrphids) and presentation order (in *E. balteatus*).

4. Being deprived of hosts increased egg load substantially in *E. balteatus*, and increasing time of deprivation also had an effect on discrimination; there was no effect of host deprivation in *S. ribesii*.

5. Reasons for these patterns are discussed.

Key words. Diet breadth, egg number, host shortage, predatory insects, Syrphidae.

Introduction

Insect oviposition behaviour is a vital component in understanding a great many elements of insect evolutionary biology. Oviposition behaviour is known to vary in response to many factors: changes in environmental factors, learning or previous experience, marking pheromones, genetics and phylogenetic inheritance, and internal physiological state (Minkenberg *et al.*, 1992; Schoonhoven *et al.*, 1998). Understanding this behaviour is particularly important to theories of diet breadth (e.g. Futuyama & Peterson, 1985; Futuyama & Moreno, 1988; Courtney *et al.*, 1989; Jaenike, 1990; Bernays & Chapman, 1994; Schoonhoven *et al.*, 1998).

The importance of egg load (i.e. the number of mature eggs in the ovaries) as a source of variation in host choice by ovipositing females has often been noted, and in their review Minkenberg *et al.* (1992) concluded that '... consideration of the role of egg load, egg-load dynamics, and the function of the egg-load response will lead to a more complete understanding of variation in oviposition behaviour'. Host deprivation is often used to investigate the effect of egg load on oviposition behaviour (e.g. Fitt, 1986; Harris & Miller, 1988; Pilson & Rausher, 1988), however the effect of deprivation itself on the oviposition behaviour of insects has received little attention. Fitt (1986) pointed out that such studies can enhance

knowledge of host utilisation in the field, where there may often be temporal shortages in the availability of hosts, depriving gravid females of preferred hosts. The hierarchy threshold model of host choice (Courtney *et al.*, 1989) has two components: an inherent, fixed (in each individual) rank-order of preference of hosts, and a variable threshold of acceptability that depends in part on internal factors such as egg load. The model predicts that 'diet breadth should increase with factors increasing egg load: increasing inter-host period, decreasing host density etc.'.

There is a massive gap in knowledge of diet breadth in insects because there is virtually no information on predators (Tauber & Tauber, 1987; Bristowe, 1988; Albuquerque *et al.*, 1997), perhaps because predators are assumed to be generalists. This assumption is false: in many predatory insect groups there are both generalists and specialists (Tauber & Tauber, 1987; Hodek, 1993; Gilbert *et al.*, 1994). Using a well-known group of insect predators, the hoverflies (Diptera, Syrphidae), the aims of the study reported here were to test the following predictions: that host deprivation increases egg load and diet breadth; and that rank-order preferences will not change with age or host deprivation. There is already some evidence of changes in oviposition behaviour with deprivation in this group. For example, Dixon (1959) showed that female *Eupeodes corollae* could retain mature eggs in the absence of aphids, but eventually some eggs were laid; a similar result was obtained by Phoon (1973) when depriving female *Ischiodon scutellaris* of aphids.

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Materials and methods

Study organisms

The hoverflies (Diptera, Syrphidae) are a well-known very large family of true flies (see Gilbert, 1990, 1993; Gilbert *et al.*, 1994). One monophyletic clade (Rotheray & Gilbert, 1999) consists of homopteran predators as larvae, with most members concentrating on aphid prey. The two aphidophagous hoverflies chosen for use in this study, *Episyrphus balteatus* (deGeer) and *Syrphus ribesii* (L.), are polyphagous as larvae, and are two of the commonest species in Britain (Gilbert, 1993; Stubbs & Falk, 1996). Individuals of both species for this experiment came from cultures established less than 12 months previously, based on gravid females collected from the field, and kept in illuminated cages at a constant temperature of 20 °C and 16 h photoperiod. The stock cultures were reared on pea aphid (*Acyrtosiphon pisum* Harris). Adults were fed on pollen from bee hives (Sigma-Aldrich Ltd, Catalogue Number P-8753) and solid sugar placed on Petri dish lids on the floor of the cage. Water was provided on cotton wool placed in conical flasks.

Three aphid species were used in the experiments. Two were cultured in the laboratory: *Acyrtosiphon pisum* on broad bean (*Vicia faba* L.) and *Aphis fabae* L. on dock (*Rumex* sp.); the third, *Microlophium carnosum* (Buckton), was collected from the field from nettle plants (*Urtica dioica* L.). These aphids were chosen because the results of previous work (Sadeghi & Gilbert, 1999, 2000; H. Sadeghi and F. Gilbert, unpublished; H. Sadeghi *et al.*, unpublished) showed that pea aphid was a preferred prey, dock aphid had a moderate degree of preference, and nettle aphid was the least preferred of all the studied aphids.

Experimental procedures

Each experiment commenced with a large number of flies, at least 80 or 40 females of *E. balteatus* and *S. ribesii* respectively, reared in the laboratory from eggs laid over 1–2 days to ensure that they were the same age. After the larval and pupal stages, newly emerged flies of both sexes were transferred to a large rearing cage and fed on pollen, solid sugar, and water. A previous study of oviposition preferences (Sadeghi & Gilbert, 2000) showed that the majority of *E. balteatus* and *S. ribesii* females is usually ready to lay eggs 14 or 7 days after emergence respectively. To be certain that ovaries had entered in a regular schedule of oocyte maturation and oviposition, all females were given continuous access to the test aphids for 5 days. To avoid the potentially confounding effects of prior contact, for the first 3 days, each day one aphid species was offered and was changed the following day for another aphid species. For the last 2 days, each day all three test aphid species were presented to syrphid females in a randomised sequence. After this 5-day period, flies were divided into two equal-sized groups. Flies in the control group had continuous access to aphids; flies in the experimental (deprived) group had no physical access to any aphid for varying periods of time (see

below). Because both groups were held in the same room where there were stock cultures of pea and dock aphids, all flies could perceive olfactory stimuli.

The oviposition preferences of females from each group were assayed 1, 4, 8, or 16 days after the females in the experimental group had been deprived of aphids. On the day of assay, two batches of 10 (*E. balteatus*) or five (*S. ribesii*) were taken at random from each group and placed individually in small cages (36 × 24 × 18 cm). All three aphid species were presented to individual females as oviposition stimuli, sequentially in random order, for 2 h each. The order of presentation was recorded for inclusion in the analysis. A standard oviposition stimulus consisted of a group of ≈ 30 aphids (of various instars) offered on a cut section of their own host plant, standing in water. The number of eggs laid in response to each aphid was recorded. These two species of aphidophagous hoverfly lay the vast majority of their eggs singly (Chandler, 1968a,b; Guest, 1984; Gilbert, 1990) so each egg laid was considered to be an independent oviposition decision.

To determine egg load, at the end of each day of testing for oviposition preferences, all tested females from both treatments (control and deprived) were frozen, dissected, and the number of mature eggs remaining in their ovaries was counted. Following Minkenberg *et al.* (1992), the total egg load at the time of oviposition was determined by summing the number of remaining mature eggs and the number of eggs deposited in response to all three aphid species during the assay. A dye was used to distinguish mature from immature eggs in the ovaries; both ovaries of each dissected female were immersed in a 1% suspension of trypan blue (Telfer & Anderson, 1968) for a few minutes, then rinsed with a few drops of distilled water. Mature eggs remained clear whereas immature eggs were stained.

Analyses

Because there were four categories (i.e. eggs laid on pea, dock, and nettle aphids, and unlaied eggs), the proportions laid on each of the aphids during the 6-h test were regarded as independent of one another. Three analyses were performed. In the first, total egg load (square-root transformed) was analysed in a three-way ANOVA with species (*E. balteatus*, *S. ribesii*), deprivation treatment (undeprived control, deprived), and days of deprivation (1, 4, 8, or 16 days) as fixed factors.

In the second analysis, the numbers of unlaied eggs were converted into a proportion of total egg load for each individual, and the influences on it were analysed in a three-way ANOVA with species, deprivation treatment, and days of deprivation as fixed factors, and total egg load as a covariate (square-root transformed, with one outlier excluded). The proportions were not angular-transformed because they were adequately normally distributed.

Finally, the numbers of eggs laid in response to each aphid were converted into proportions of the total egg load, and a five-way ANOVA was performed initially, with species (*E. balteatus*, *S. ribesii*), aphid (pea, dock, nettle), deprivation treatment, days of deprivation, and order of presentation of the

aphids (first, second, third) as fixed factors, and total egg load as a covariate (square-root transformed, with one outlier excluded). Because the covariate affected each species in a different way (see Results), each species was then analysed separately in a four-way ANOVA with factors of aphid, deprivation treatment, days of deprivation, and order of presentation. The proportions were not angular-transformed because they were adequately normally distributed.

The statistical software programs StatGraphics 7 Plus (Manugistics Inc., Rockville, Maryland, U.S.A.), Statistica (StatSoft Inc., Tulsa, Oklahoma, U.S.A.), and GLIM4 (NAG Ltd, Oxford; see Crawley, 1993) were used.

Results

Episyrphus balteatus females had greater egg loads overall than *S. ribesii* females, and also increased their egg loads much

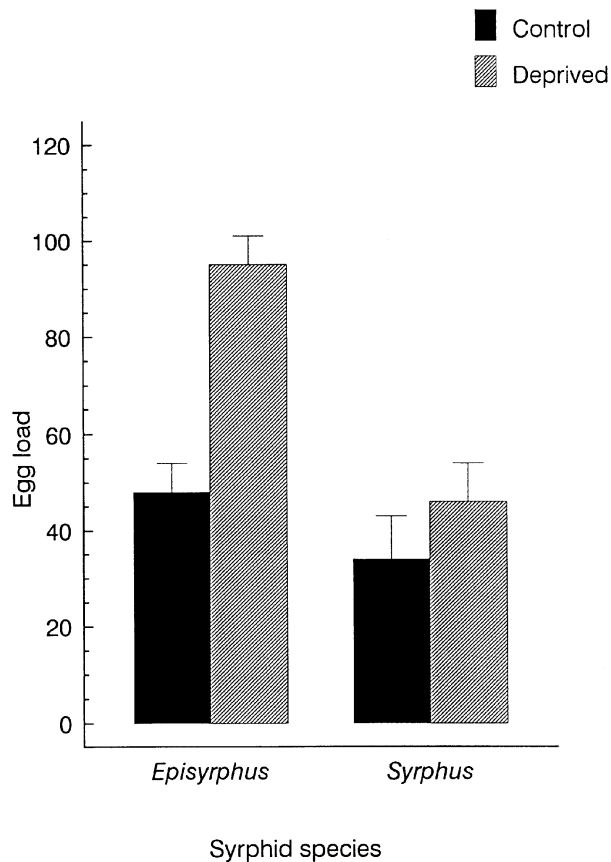


Fig. 1. The effect of being deprived of oviposition stimuli (aphid prey) on total egg load in two predatory species of hoverfly, *Episyrphus balteatus* and *Syrphus ribesii*. The two species had significantly different egg loads ($F_{1,103}=74.4$, $P<0.001$), there was a significant effect of deprivation ($F_{1,103}=72.3$, $P<0.001$), and these factors also interact ($F_{1,103}=20.7$, $P<0.001$). In the experiment, length of deprivation was also a factor (with four levels) but this had no significant main effect ($F_{3,103}=1.6$, NS) and no interaction with species ($F_{3,103}=0.4$, NS) or deprivation ($F_{3,103}=1.5$, NS); there was no species \times deprivation \times length interaction ($F_{3,103}=0.1$, NS).

more strongly in response to being deprived of aphid hosts for oviposition (Fig. 1). Egg load more than doubled in *E. balteatus* in response to host deprivation whereas it increased by only about 30%, if at all, in *S. ribesii*. There was no effect of the length of deprivation on egg load (see legend to Fig. 1); the increase in the egg loads of *E. balteatus* females happened very rapidly in response to short-term deprivation, not increasing with time.

Similarly, the proportion of the egg load remaining unlaidd after the test differed between the two species, and was affected by the deprivation treatment but not by the length of deprivation (Fig. 2a). There was a complication, however, in that the egg-load covariate affected each species differently, being related negatively to the proportion unlaidd in *E. balteatus* but positively to the proportion unlaidd in *S. ribesii* (Fig. 2b,c). Thus deprivation and the consequent higher egg loads led to a greater proportion of the egg load being laid in *E. balteatus*, but egg load (but not deprivation) led to a lower proportion being laid in *S. ribesii*. After allowing for this, there was no effect of the length of deprivation or of any of the possible interactions among species, deprivation, and length (see legend to Fig. 2).

The proportion of the egg load oviposited in response to any one of the aphids was complicated to interpret initially because of a significant five-way interaction among species \times aphid \times deprivation \times days \times order ($F_{12,213}=2.18$, $P<0.01$), however the effect of different aphids was numerically dominant in terms of sums of squares. Interpretation was improved by analysing each species separately, thus avoiding all the interactions that included species. In *S. ribesii*, the covariate ($F_{1,47}=8.4$, $P<0.01$, slope = -0.052 ± 0.018) and aphid ($F_{2,47}=23.6$, $P<0.001$) were the only significant effects. In contrast, in *E. balteatus*, although there was no effect of the covariate, there were many more other significant effects: of aphid ($F_{2,167}=31.3$, $P<0.001$), deprivation ($F_{1,167}=8.0$, $P<0.01$), order ($F_{2,167}=10.3$, $P<0.001$), aphid \times days ($F_{6,167}=3.4$, $P<0.01$), deprivation \times order ($F_{2,167}=4.3$, $P<0.05$), and days \times order ($F_{6,167}=3.1$, $P<0.01$).

Both species laid the greatest proportion of their eggs on pea aphids and the lowest on nettle aphids (Fig. 3), with *S. ribesii* showing greater discrimination than *E. balteatus* (a significant species \times aphid interaction in the initial five-way ANOVA: $F_{2,213}=3.14$, $P<0.05$). Most individual females also followed this pattern of preference (75% of *E. balteatus*, 60% of *S. ribesii*) but there were individual females with completely different rank preferences (one female *E. balteatus* laid most of its eggs on nettle aphids).

The deprivation treatment overall increased the proportion of eggs laid on all aphids in *E. balteatus* (Fig. 4a) but not in *S. ribesii* (Fig. 4b), relative to the control; although not significant, there is a suggestion of greater discrimination among aphids by deprived female *S. ribesii*. The rank order of preference, however, remained unchanged. With time, however, the preferences converge in *E. balteatus*: the older the female, the less the discrimination among aphids (Fig. 5a,b), but deprivation does not affect this. In *S. ribesii*, neither length of deprivation nor age had any effect on discrimination among the three aphids (Fig. 5c,d).

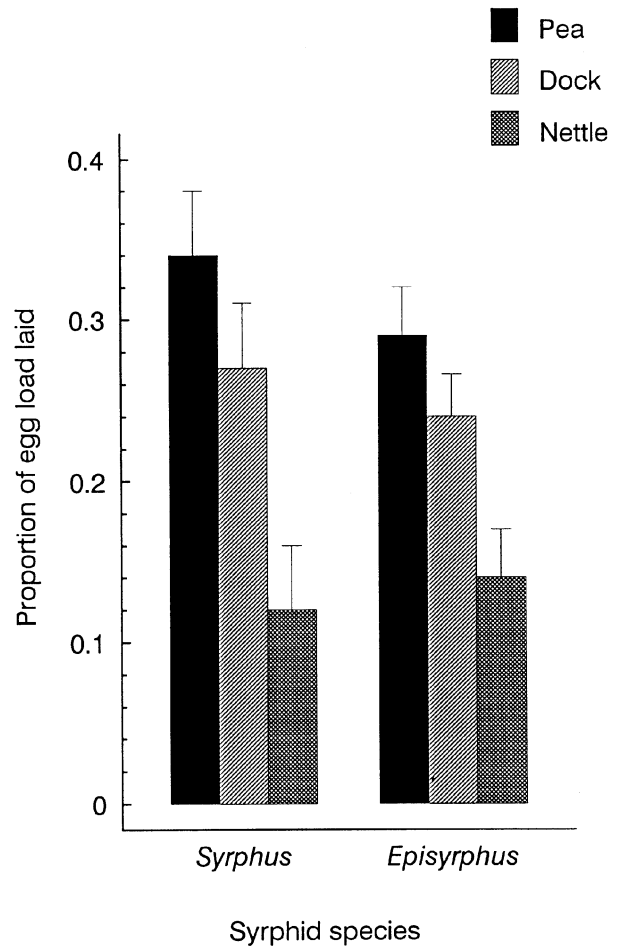
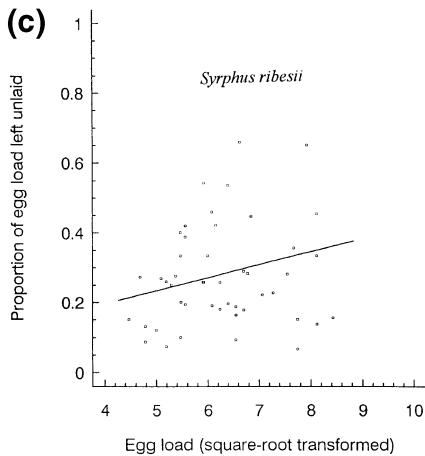
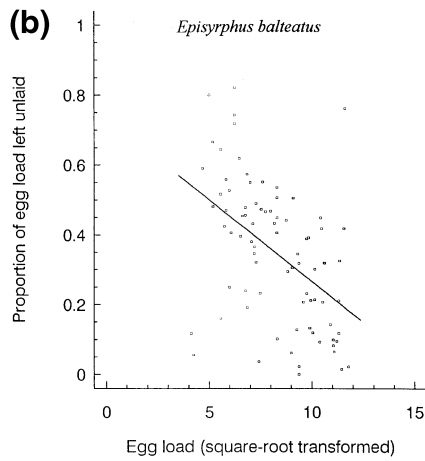
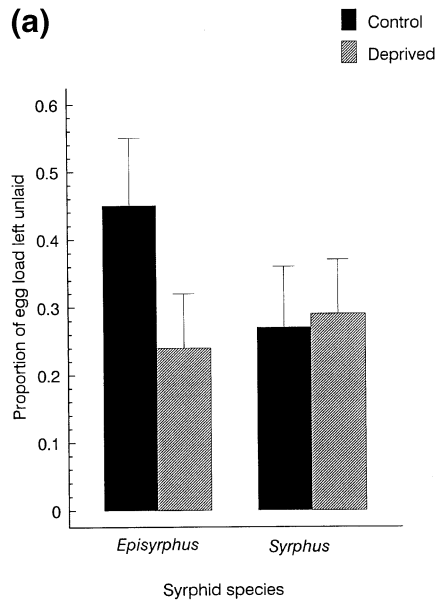


Fig. 3. The proportion of the total egg load laid in response to aphids by females of each hoverfly species to the three aphid species offered. Note the statistically significant interaction ($F_{2,213} = 3.14$, $P < 0.05$), with *Syrphus ribesii* showing more discrimination than *Episyrphus balteatus*.

Fig. 2. Influences on the proportion of eggs remaining unladen after offering three species of aphid as oviposition stimuli: (a) the effect of deprivation of hosts on *Episyrphus balteatus* and *Syrphus ribesii*; (b) the negative effect of total egg load in *E. balteatus*; (c) the positive effect of total egg load in *S. ribesii*. In an ANCOVA fitted by GLIM4, egg load (square-root transformed) was nonsignificant overall ($F_{1,102} = 0.03$, NS) but this hid an interaction between egg load and species ($F_{1,102} = 4.71$, $P < 0.05$). Allowing for this covariate interaction, the two species differed ($F_{1,102} = 15.26$, $P < 0.001$), and there was an effect of deprivation ($F_{1,102} = 5.12$, $P < 0.05$), but these were the only significant effects (length of deprivation and all its interactions, $F_{3,102} < 2.39$, NS). (a) Plots the species \times deprivation interaction, which, despite appearances, is nonsignificant after allowing for the species-covariate interaction ($F_{1,102} = 2.31$, NS).

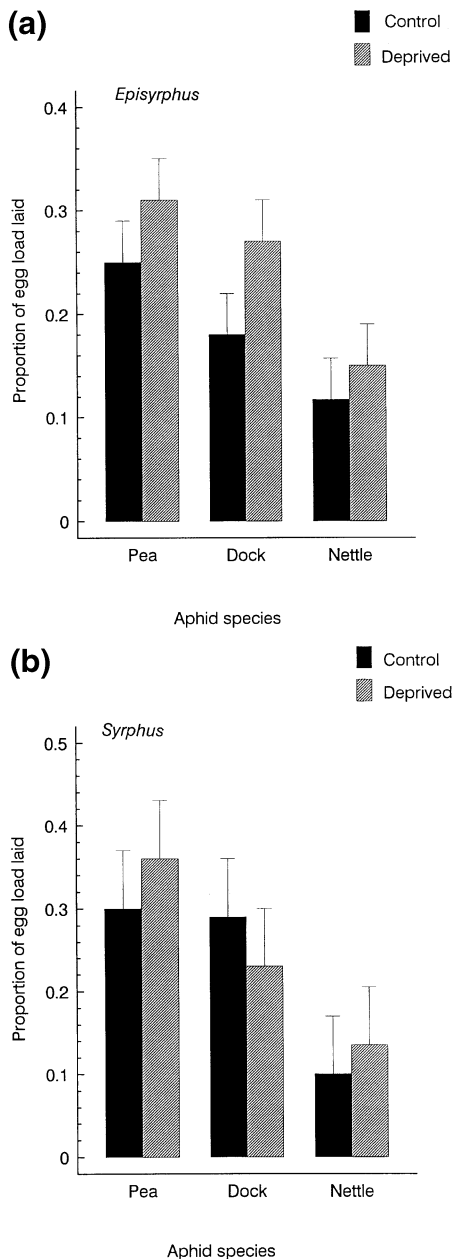


Fig. 4. The overall effects of host deprivation on aphid choice by ovipositing hoverflies in (a) *Episyrphus balteatus* and (b) *Syrphus ribesii*.

There were strong order effects in *E. balteatus*, with a greater proportion of eggs being laid on the first aphid to be presented (Fig. 6a); deprivation increased this effect (Fig. 6b), as did the length of deprivation (Fig. 6c). All these effects were absent in *S. ribesii*.

Discussion

As in previous experiments (Sadeghi & Gilbert, 1999, 2000), the results of oviposition preference tests showed that both

syrphid species are consistent in the preference order of hosts, preferring pea aphid, followed by dock aphid, with nettle the least preferred aphid. As females aged, their discrimination among aphids decreased but, as in previous experiments (Sadeghi & Gilbert, 2000), this effect was much stronger in *E. balteatus* than in *S. ribesii*; however, the rank-order of these aphids to both syrphids did not change throughout the experiments. These results are consistent with the predictions of the hierarchy threshold model (Courtney *et al.*, 1989): that ageing will lower the acceptability threshold and reveal more of the rank order of host acceptability; that the rank-order hierarchy will not change with age; and that increasing egg load will not alter the rank-order hierarchy but will result in a broader diet by including more of the lower-ranking host species. The reason why ageing or greater egg loads should increase diet breadth is probably connected with the risk of decreased fitness due to being too selective (Fitt, 1986; Courtney *et al.*, 1989; Minkenberg *et al.*, 1992).

In experiments using host deprivation as a treatment, experience with hosts has been noted as a common confounding variable with egg load (see Minkenberg *et al.*, 1992). In the experiments reported here, however, it seems unlikely that host preferences were influenced by conditioning during pre-test exposure to aphids because all the test aphids were offered during the pre-test period. It is possible that pea aphid was the most preferred aphid because of some sort of conditioning during the previous generation in culture.

There are some reports that gravid syrphids are able to withhold mature eggs for a long time (e.g. Dixon, 1959; Kan, 1988). The experiments reported here revealed the same for *S. ribesii* as well as *E. balteatus*. Females do not waste their mature eggs when facing a shortage of hosts or when there is no suitable aphid, and this 'may serve to further increase the advantage of the 'buy-future' tactics of the female' (Kan, 1988).

Egg load is well known to influence host choice in herbivorous (Minkenberg *et al.*, 1992) and parasitoid (Jervis & Copland, 1996) insects, and is incorporated into several models of host choice (Courtney *et al.*, 1989; Mangel, 1989). Age and egg load can be correlated in a resource-poor environment, but the present experimental design separates the two factors. There is an intriguing difference between the two species in their responses. While egg load does not increase with age or length of deprivation, there is an immediate effect on total egg load of short-term deprivation in *E. balteatus* but no effect in *S. ribesii*. In *S. ribesii*, aphid-related cues are overwhelmingly important in determining the proportion of the egg load laid in response to any one aphid colony, with no other detectable effects except current egg load (with the proviso that sample sizes were smaller for this species because it is much more difficult to culture, and hence the tests are less powerful). In *E. balteatus*, while aphid-related cues are still the most important factor, various other factors influence the outcome: the occurrence of deprivation, the order of presentation, and their interaction; the interaction between aphid species and female age, and between presentation order and female age. The way these operate seems logical:

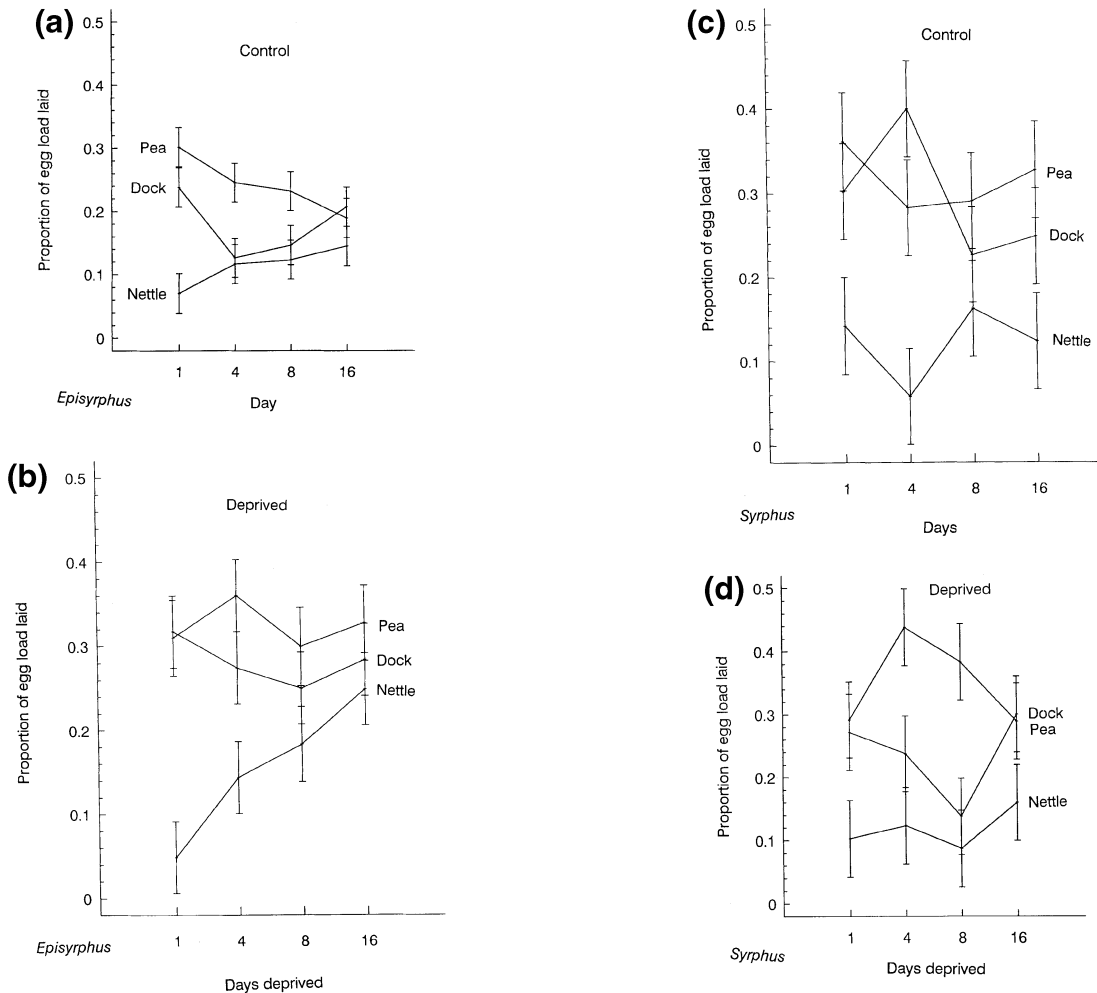


Fig. 5. The impact of the length of host deprivation on aphid preference in (a,b) *Episyrphus balteatus* and (c,d) *Syrphus ribesii*. In the control groups (a,c), females had continuous access to aphids until the day of test; in the deprived groups (b,d), females had no access to aphids.

deprivation and age increase the proportion of the egg load laid on the aphid that is encountered first, and age leads to a lower degree of discrimination among aphids. Why should these species differ in this way? It may be, of course, that the increased number of replicates of *E. balteatus* has led to more effects being found to be significant. Alternatively there may be a biological rather than a statistical explanation. Most of the *E. balteatus* in the U.K. are migrants whereas most *S. ribesii* are residents (although this species is also a frequent migrant). Female migrants, mated but not gravid, arrive early in the growing season in the U.K. at a time when aphid populations are just getting started. They must feed and mature their eggs before oviposition, and there is a large premium on being the first to exploit the growing aphid resource. The ability to accumulate eggs ready for ovipositional opportunities might be a distinct advantage. Accumulating eggs in the ovaries can be seen in females in the field through the stretched semi-transparent cuticle between the tergites and

sternites, and one of the most obvious species to do this is *Eupeodes corollae*, the other major migrant in Europe (Gilbert, 1993).

Egg resorption might reduce egg load under certain situations of oviposition or food deprivation. There was no sign of resorption during the dissection of females at the end of each assay in these experiments, although field-caught adults of certain aphidophages syrphids, but not others, frequently have degenerating eggs in their ovaries: the relevant species are dominated by the genera *Pipiza*, *Melanostoma*, *Platycheirus*, and *Baccha* (Gilbert, 1981), the most plesiomorphic of all the aphidophagous (Rotheray & Gilbert, 1989, 1999). The transition from *Baccha* to *Episyrphus* in the phylogenetic tree is close but entails large changes in larval morphology almost certainly associated with becoming specialised to feed only on aphids (Rotheray & Gilbert, 1989; Gilbert, 1990; Rotheray, 1993; Gilbert *et al.*, 1994). This transition may also be associated with better regulation of ovariole productivity.

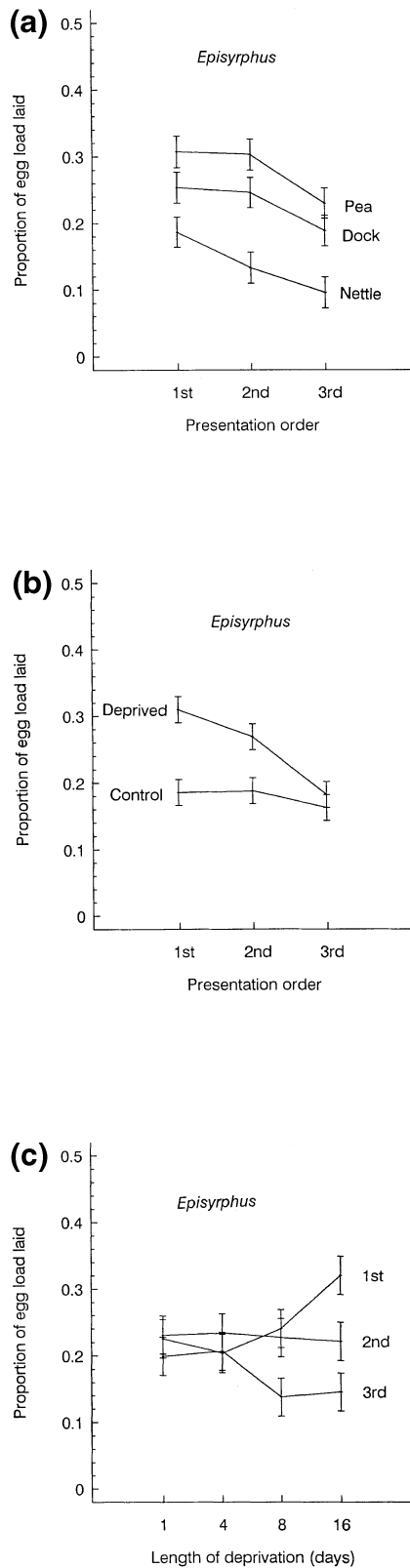


Fig. 6. The effect of presentation order on the proportion of the total egg load laid by female *Episyrphus balteatus*, interacting with (a) aphid species, (b) deprivation treatment, (c) length of deprivation.

These results suggest that the absence of aphids probably retards egg maturation in ovipositing females of both *E. balteatus* and *S. ribesii*, better regulated in the latter species. Other flies [e.g. the generalist *Dacus tryoni* Frogg (Fitt, 1986) or the specialist onion fly *Delia antiqua* (Harris & Miller, 1988)] show no regulation of egg maturation in the absence of their hosts. Harris and Miller (1988) suggested that increasing egg load in laboratory cultures may be due to the more nutritious diet that females receive compared with the field situation. This is questionable in the present case: syrphid females were given bee-collected pollen, which is probably not as good as fresh pollen from flowers.

Over and above the actual results of these experiments, it is clear that insect predators respond to factors such as egg load and host deprivation in ways similar to phytophagous or parasitoid insects. There is no reason why they should be treated differently in theoretical considerations of foraging behaviour or host specialisation.

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