



Host preferences of aphidophagous hoverflies from field distribution of their larvae

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Abstract

The patterns of occurrences among aphid colonies of the larvae of two species of highly polyphagous predatory hoverflies, *Episyrphus balteatus* (de Geer) and *Syrphus ribesii* (L.) (Diptera: Syrphidae), were assessed in three areas (Nottingham, Cardiff (UK) and the Czech Republic); in the last two sites, larvae of other syrphid species were also identified. The two syrphid species showed considerable diet overlap, their larvae using many of the same aphids as food, but with significant exceptions. Together with information from the literature, even for these very generalist species there was a consistent pattern of preference among aphid species. Most other species showed restricted preferences. Larvae were more frequent on developed aphid colonies than on colonies that were younger or had almost disappeared.

Keywords: food specificity, niche breadth, predatory insects, aphids, Syrphidae.

Introduction

Predators are often assumed to be generalists, despite plenty of evidence to the contrary (Tauber & Tauber 1987; Bristowe 1988; Hodek 1993). Although the larvae of some insect predators are relatively mobile, many are not, and thus depend on female oviposition preferences for prey choice. Even where larvae are mobile and can make their own choices to a greater or lesser extent, the suitability of the first few prey items can often be critical in determining survival (e.g. Schmutterer 1972). Jaenike (1978) concluded that a female should oviposit in response to a particular food item early in her search if (1) this item is very suitable for her larvae, (2) the probability of finding an alternative is low, (3) the egg load is high or (4) alternative food items are unpredictable in space or time. Competitor density is a further factor influencing preference (e.g. in galling aphids: Whitham, 1978, 1980). Overall, a female's decisions should reflect the subsequent welfare of her progeny, and there is substantial individual variation in this among females (see Thompson 1988; Courtney & Kibota 1990; Price 1997; Schoonhoven *et al.* 1998). The field distribution of eggs will therefore reflect the sum of the responses of individual females.

Here, we measure the field distribution of hoverfly larvae among colonies of the more common aphid prey, and especially those of two very common hoverflies (Diptera: Syrphidae), *Episyrphus balteatus* (DeGeer) and *Syrphus ribesii* (L.). These syrphid species are normally labelled as generalists in their prey choice. We have previously shown that females prefer to oviposit in response to certain aphid species (Sadeghi & Gilbert 2000a), and that their preferences alter in magnitude but not in rank order with female age and host deprivation (Sadeghi & Gilbert 2000b). Some individual females of *E. balteatus* differ from others in their preferences, entailing life-historical trade-offs in performance (Sadeghi & Gilbert 1999), despite an overall lack of relationship between preference and performance in this species (Sadeghi & Gilbert 2000c): there appears to be a weak preference-performance correlation in *S. ribesii* (Sadeghi & Gilbert 2000c).

Like many species of coccinellid (Hodek 1993), the larvae of many predatory syrphids are in fact specialised (summarised in Laska 1978; Rotheray & Gilbert 1989; Gilbert 1990;

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Rotheray 1993; Gilbert *et al.* 1994). Furthermore, although the two hoverfly species studied here have been reported from colonies of more than 100 aphid species in the world (F. Gilbert, unpublished), there are in fact rather few quantitative or even qualitative data in the literature on the relative abundance and distribution of aphid colonies and their syrphid predators. The few data that do exist show that while *E. balteatus* and *S. ribesii* larvae feed on a huge variety of aphid species, even within a single habitat (e.g. Mizuno *et al.* 1997), there are clear indications of host preferences. *E. balteatus* is recorded as being more generalized than *S. ribesii* (e.g. Ninomyia 1957), but more usually the two species occur in different prey colonies within one habitat (Wnuk 1972, 1979; Malinowska 1979; Wnuk & Medvey 1986; Mizuno *et al.* 1997). Salveter (1998) studied the agricultural environment and showed that *E. balteatus* was the dominant predator in aphid colonies on wheat, but *Syrphus* spp. dominated in the herb aphid colonies surrounding wheat fields. In Poland *E. balteatus* was dominant in crop habitats, but *S. vitripennis* was dominant in aphid colonies on fruit trees and *S. ribesii* sub-dominant on both (Malinowska 1979). Even among different aphids on a single hostplant, there are strong indications of selectivity (e.g. Wnuk 1972).

Here we investigate whether larval distribution suggests that females discriminate against certain aphid species. Data from widely separate sites in the UK and Europe are used to check for consistency in the patterns of prey choice.

Materials & Methods

This study was carried out principally in the UK at Nottingham (1° 10' W, 52° 58' N). For comparison, we took advantage of two further data sets which were less systematically collected, but were more comprehensive in their species coverage. These were from Cardiff (3° 13' W, 51° 30' N) and the Czech Republic (Olomouc and vicinity: 17° 15' E, 49° 38' N). Nomenclature follows Laska *et al.* (2013).

Data from Nottingham, UK

From early May until late October 1996, a weekly sampling programme of aphid colonies and associated larvae of certain syrphid predators was carried out, following different routes through the study site on each occasion. Sampling was normally during the morning hours. This part of the study formed the background to other detailed laboratory studies (Sadeghi & Gilbert 1999, 2000a-c) and hence for pragmatic reasons was never intended to be exhaustive; sample sizes were therefore rather small. Syrphid larvae that were hiding well away from the aphid colonies were probably not sampled using the methods we adopted.

The site of field sampling was the Nottingham University campus, a large area of about 90 ha with a vegetation consisting mainly of grasslands and a few areas of woodland. The grassland sites are dominated by perennial ryegrass (*Lolium perenne*) with swards of white clover (*Trifolium repens*), and daisy (*Bellis perennis*). Numerous other plants are also present, such as greater plantain (*Plantago major*), together with scattered trees of silver birch (*Betula pendula*), beech (*Fagus sylvaticus*), and horse-chestnut (*Aesculus hippocastaneum*). The woodland areas are dominated by sycamore (*Acer pseudoplatanus*), and common ash (*Fraxinus excelsior*): other species present include beech (*Fagus sylvaticus*), oak (*Quercus robur*), elder (*Sambucus nigra*), and common alder (*Alnus glutinosa*). The ground flora of the woods contains mainly ivy (*Hedera helix*) and bramble/blackberry (*Rubus* spp), together with other ground flora such as dock (*Rumex obtusifolius*), lords and ladies (*Arum maculatum*), thistle (*Cirsium vulgare*), and nettle (*Urtica dioica*). Plant names used here are from Mabberley (1997) and Clapham *et al.* (1968).

When an aphid infestation was discovered, a more intensive search was initiated and from every five aphid-infested leaves/stems discovered, the fifth was removed into a plastic

bag. A single sampling unit consisted of up to 50 aphid-infested leaves (for sycamore, beech, elm, apple, and blackberry) or ten 20-cm aphid-infested stems (for other plants: willow-herb, nettle, hogweed, dock, rose, and elder), depending upon availability. Once a sample had been taken from an aphid species, no further colonies of that species were sampled during that week. The size of sampled aphid colonies was recorded on a three-point scale (1 = < 5; 2 = 5-40, 3 = > 40) to give a rough idea of colony size: other features affecting prey usage (ease of capture, defensive behaviour, etc) were not recorded on logistical grounds. To estimate the overall relative availabilities of the different aphids, the colony sizes of all samples were summed for each aphid species.

Aphid species	Plant species	Name used in text for aphid	Index of aphid availability ¹	Number of larvae	
				<i>Episyrphus balteatus</i>	<i>Syrphus ribesii</i>
<i>Aphis fabae</i>	<i>Rumex obtusifolius</i>	Dock	23	3	3
<i>Aphis grossulariae</i>	<i>Epilobium hirsutum</i>	Willow-herb	16	22	2
<i>Aphis pomi</i>	<i>Malus domestica</i>	Apple	13	3	3
<i>Aphis ruborum</i>	<i>Rubus fruticosus</i>	Blackberry	21	1	3
<i>Aphis sambuci</i>	<i>Sambucus nigra</i>	Elder	39	5	3
<i>Cavariella</i> sp.	<i>Heracleum sphondylium</i>	Hogweed	21	16	25
<i>Drepanosiphum plantanoidis</i>	<i>Acer pseudoplatanus</i>	Sycamore	30	4	28
<i>Macrosiphum rosae</i>	<i>Rosa</i> sp.	Rose	35	9	4
<i>Microlophium carnosum</i>	<i>Urtica dioica</i>	Nettle	25	2	13
<i>Phyllaphis fagi</i>	<i>Fagus sylvatica</i>	Beech	21	0	2
<i>Schizoneura ulmi</i>	<i>Ulmus</i> sp.	Elm	16	6	3

¹The sum of recorded abundance scores over of all sampling days.

Table 1: List of plants and associated aphid species sampled during May-October 1996 at the Nottingham University Campus

The bags containing aphid colonies (Table 1) were brought to the laboratory. After a day, the contents of each sample bag were searched carefully using a binocular microscope, and the type and number of each syrphid species recorded, and the aphid identified (Table 1) using Rotheray (1989) and Blackman & Eastop (1994). This method of sampling syrphid larvae is effective for all larvae within the colonies themselves, since they become obvious on the inside of the plastic after being held overnight. The focus of this part of the study was only on the two species considered here; aphids not used by these species, and other syrphid species on these (Table 1) and other plants in the field, were not identified because of the effort required to rear them. Identification of adults used Gilbert (1993) and Stubbs & Falk (1996).

Using the methods advocated in Ludwig & Reynolds (1988), we calculated the ecological niche breadth for each species (an index of the variety of resources used), and the niche overlap, the similarity between these two syrphids in their use of prey aphid species.

Data from Cardiff, UK

Throughout the growing season (May–August) of 1977-78, various sites in and around Cardiff were visited regularly. Standard paths were followed, and plants inspected for the presence of aphid colonies: samples of aphid-infested plants were collected into polythene bags, and any syrphid larva present was reared to the point where identification was possible using larval or adult characters. Here only the total numbers of larvae found in all the colonies of each aphid species are reported: the composition of predatory larvae at individual aphid colonies, which gives a true estimate of competitor density, is not reported here. As in most sites in the UK, aphid availability fell into two main phenological periods, in spring (May-June) and summer (July-August), separated by a distinct gap when aphids were scarce. We therefore separate

these two periods in the data. Systematic sampling was not carried out, and the size of the aphid colonies was not assessed, since the major aim was to rear all species of syrphid and to record their incidence in the different aphid colonies.

Data from the Czech Republic

As part of a long-term programme of research on syrphid larvae (e.g. Dusek & Laska 1974, Laska 1984), from 1955 to 1962, during the main part of the season (May-August), colonies of aphids were sampled haphazardly for the presence of syrphid larvae: no regular systematic sampling was carried out, and aphid density was not recorded, because the focus of the study was again the collection of as many syrphid species as possible, and merely to record their incidence in the various aphid colonies. Each sample consisted of picked infested leaves (usually 40) or stems (usually 10) brought into the laboratory to search intensively for syrphid larvae; all larvae were identified to genus and reared, but a number were parasitized or died and thus could not be identified to species. Sampling sites were in or near Praha, Roudnice, Jičín, Nová Paka, Žlunice, Olomouc, Čánka, and Nový Budžov. Because each sample consisted of different numbers of aphid colonies, the mean numbers of larvae per 100 colonies are reported..

Results

1. Nottingham

a) Phenology of syrphid larvae throughout the season. The seasonal activity of larvae of the two syrphids on aphids of 11 plant species at the Nottingham University campus throughout the growth season 1996 is shown in Tables 2 and 3. In this study, *E. balteatus* larvae were collected from all aphid colonies except beech aphid (Table 2) but their relative abundances were different among different aphids. In the first 2 months of the sampling programme, this syrphid larva was seen only in colonies of rose and sycamore aphids, but in low numbers. Most larval records occurred in July and August; in July, the larvae were collected from aphids on elder, elm, rose, blackberry, nettle, willow-herb, and hogweed, and in August two new aphids (apple and dock) were added to the list of hosts of this syrphid. Peak abundances were on willow-herb aphids in July and hogweed aphids in August. No *E. balteatus* larvae were collected from any aphid in September or October.

Syrphus ribesii larvae were collected from all the studied aphid species (Table 3). The abundance of larvae was highest in June, early July, September, and early October; virtually no records occurred in late July or August for this species. The abundance of larvae on aphid colonies of sycamore, hogweed, and then nettle was greater than on other aphids, reaching a maximum on hogweed aphids in early July.

b) Availability of aphids during sampling period.

The aphid availability and the mean size index of the aphid colonies are shown in Table 4. In availability and seasonal occurrence, the studied aphids could be divided into two groups. The first group includes those aphids present nearly all season on their hosts: sycamore, nettle, rose, blackberry, and dock aphids. Sycamore aphid was found throughout the season on sycamore trees, but only in spring, late summer, and early autumn were they used as prey for syrphid larvae. We concentrated upon *Drepanosiphum* colonies because these were by far the commonest aphids on sycamore: other species were uncommon, and syrphid larvae did not appear to feed on them. During early summer, the winged adult aphids almost exclusively present at that time appeared difficult for syrphid larvae to capture. The other aphids of this group were present all season on sampled plants, with low numbers during summer months (Table 4).

Table 2: The mean number (\pm SE, range, number of samples) and seasonal occurrence of larval stages of *Episyrphus balteatus* (DeGeer) per sampled aphid colony on different plants at the Nottingham University campus. Data include colonies with zero larvae; the "-" symbol indicates that no aphid colonies were found during that month.

Month	Aphid										
	Sycamore	Beech	Elm	Elder	Apple	Rose	Blackberry	Dock	Hogweed	Nettle	Willow-herb
May	0.2 \pm 0.2 (0-1, 5)	0	0	0	- (0-1, 5)	0.2 \pm 0.2	0	-	-	0	-
June	0.8 \pm 0.5 (0-2, 4)	0	0	0	0 (0-2, 4)	1.0 \pm 0.4	0	0	0	0	-
July	-	0	1.5 \pm 1.0 (0-4, 4)	0.5 \pm 0.3 (0-1, 4)	0	0.5 \pm 0.3 (0-1, 4)	0.3 \pm 0.3 (0-1, 4)	0	0.5 \pm 0.3 (0-1, 4)	0.5 \pm 0.3 (0-1,4)	2.8 \pm 0.3 (2-3, 4)
August	-	-	-	0.6 \pm 0.6 (0-3, 5)	0.6 \pm 0.4 (0-2, 5)	0.4 \pm 0.2 (0-1, 5)	0	0.6 \pm 0.4 (0-2, 5)	2.8 \pm 0.3 (2-4, 5)	0	2.2 \pm 0.4 (1-3, 5)
September	0	-	-	-	-	0	0	0	-	0	0
October	0	-	-	-	-	0	0	0	-	0	-

Table 3: The mean number (\pm SE, range, number of samples) and seasonal occurrence of the larval stages of *Syrphus ribesii* per sampled aphid colony on different plants at the Nottingham University campus. Data include colonies with zero larvae.

Month	Aphid										
	Sycamore	Beech	Elm	Elder	Apple	Rose	Blackberry	Dock	Hogweed	Nettle	Willow-herb
May	1.6 \pm 0.8 (0-4, 5)	0	0	0.4 \pm 0.4 (0-2, 5)	-	0	0	-	-	0	-
June	2.5 \pm 0.9 (0-4, 4)	0.5 \pm 0.5 (0-2, 4)	0.8 \pm 0.8 (0-3, 4)	0.3 \pm 0.3 (0-1, 4)	0.3 \pm 0.3 (0-1, 4)	0.8 \pm 0.5 (0-2, 4)	0.8 \pm 0.5 (0-2, 4)	0	1.3 \pm 0.8 (0-3, 4)	0.8 \pm 0.5 (0-2, 4)	-
July	-	0	0	0	0	0	0	0	5.0 \pm 1.8 (0-8, 4)	0	0.5 \pm 0.3 (0-1, 4)
August	-	-	-	0	0	0	0	0	0	0	0
September	1.5 \pm 0.9 (0-3, 4)	-	-	-	-	0	0	0.3 \pm 0.3 (0-1, 4)	-	1.3 \pm 0.8 (0-3, 4)	0
October	1.3 \pm 0.7 (0-2, 3)	-	-	-	-	0.3 \pm 0.3 (0-1, 3)	0	0.7 \pm 0.7 (0-2, 3)	-	1.7 \pm 1.2 (0-4, 3)	-

Table 4: Mean size (\pm SE, range, number of samples) of aphid colonies of sampled plants through the season at the Nottingham University campus. Colony size is scored on a three-point scale, where 1 = < 5 aphids, 2 = 5-40 aphids, 3 = > 40 aphids in the colony.

Month	Aphid										
	Sycamore	Beech	Elder	Elm	Apple	Rose	Blackberry	Dock	Hogweed	Nettle	Willow-herb
May	2.0 \pm 0.4 (1-3, 5)	1.0 \pm 0.3 (0-2, 5)	0.8 \pm 0.4 (0-2, 5)	0.6 \pm 0.4 (0-2, 5)	0	1.6 \pm 0.2 (1-2, 5)	1.0 \pm 0.3 (0-2, 5)	0	0	0.8 \pm 0.2 (0-1, 5)	0
June	2.3 \pm 0.5 (1-3, 4)	2.5 \pm 0.3 (2-3, 4)	2.5 \pm 0.3 (2-3, 4)	2.0 \pm 0.0 (2-2, 4)	0.3 \pm 0.3 (0-1, 4)	2.3 \pm 0.3 (2-3, 4)	1.0 \pm 0.4 (0-2, 4)	0.5 \pm 0.3 (0-1, 4)	0.8 \pm 0.3 (0-1, 4)	1.3 \pm 0.3 (1-2, 4)	0
July	0	1.5 \pm 0.3 (1-2, 4)	3.0 \pm 0.0 (3-3, 4)	1.3 \pm 0.3 (1-2, 4)	1.5 \pm 0.3 (1-2, 4)	1.8 \pm 0.3 (1-2, 4)	1.5 \pm 0.3 (1-2, 4)	2.0 \pm 0.4 (1-3, 4)	1.8 \pm 0.3 (1-2, 4)	1.8 \pm 0.3 (1-2, 4)	2.3 \pm 0.5 (1-3, 4)
August	0	0	1.6 \pm 0.2 (1-2, 5)	0	1.2 \pm 0.4 (0-2, 5)	0.4 \pm 0.2 (0-1, 5)	0.4 \pm 0.2 (0-1, 5)	1.2 \pm 0.2 (1-2, 5)	2.2 \pm 0.4 (1-3, 5)	0.8 \pm 0.2 (0-1, 5)	1.2 \pm 0.2 (1-2, 5)
September	1.3 \pm 0.8 (0-3, 4)	0	0	0	0	1.0 \pm 0.4 (0-2, 4)	0.3 \pm 0.3 (0-1, 4)	1.0 \pm 0.0 (1-1, 4)	0	0.5 \pm 0.3 (0-1, 4)	0.5 \pm 0.3 (0-1, 4)
October	2.0 \pm 0.6 (1-3, 3)	0	0	0	0	1.7 \pm 0.3 (1-2, 3)	1.0 \pm 0.0 (1-1, 3)	1.0 \pm 0.0 (1-1, 3)	0	1.0 \pm 0.0 (1-1, 3)	0

Table 5: Syrphid larvae recorded from aphid colonies sampled in habitats around Cardiff (UK) during 1977-78

Aphid	Host-plant	<i>Syrphus ribesii</i>	<i>Episyrphus balteatus</i>	<i>Baccha elongata</i>	<i>Dasyrphus albostrigatus</i>	<i>Epistrophe eligans</i>	<i>Eupeodes corollae</i>	<i>Eupeodes luniger</i>	<i>Melangyna cincta</i>	<i>Melangyna umbellatarum</i>	<i>Melanostoma scalare</i>	<i>Meliscavea auricollis</i>	<i>Pipiza</i> sp.	<i>Platycheirus albimanus</i>	<i>Platycheirus manicatus</i>	<i>Platycheirus peltatus</i>	<i>Platycheirus scutatus</i>	<i>Scaeva pyrastris</i>	<i>Sphaerophoria menthasstri</i>	<i>Sphaerophoria scripta</i>	<i>Syrphus vitripennis</i>
Spring	<i>Aphis grossulariae</i> Kalténbach	<i>Ribes uva-crispa</i> L.	5	0	0	0	5	0	0	0	0	0	0	0	0	0	2	0	0	0	0
	<i>Aphis sambuci</i> L.	<i>Sambucus nigra</i> L.	11	0	0	0	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Brachycaudus</i> sp.	<i>Silene dioica</i> Clairv.	75	0	1	2	6	6	25	0	0	1	0	2	1	0	45	0	2	0	0
	<i>Drepanosiphum platanoidis</i> (Schrank)	<i>Acer pseudoplatanus</i> L.	53	0	0	5	5	0	0	0	0	0	0	0	0	0	0	0	0	0	2
	<i>Eucallipterus tiliae</i> (L.)	<i>Tilia europaea</i> L.	7	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Hyalopterus pruni</i> (Geoff.)	<i>Prunus</i> sp.	4	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Macrosiphonella sanborni</i> (Gillette)	<i>Aster</i> sp.	8	0	0	0	1	2	11	0	0	0	0	0	0	0	1	0	0	0	0
	<i>Macrosiphum rosae</i> (L.)	<i>Centranthus rubur</i> L.	13	1	0	0	0	0	4	0	0	0	0	1	0	0	6	0	1	0	0
	<i>Macrosiphum rosae</i> (L.)	<i>Rosa</i> sp.	12	0	2	0	0	0	3	0	0	0	0	0	0	0	5	0	0	0	0
	<i>Microlophium carnosum</i> (Buckton)	<i>Urtica dioica</i> L.	201	1	0	0	3	7	57	0	0	0	0	0	0	0	19	0	0	0	0
	<i>Myzocallis coryli</i> (Goeze)	<i>Corylus avellana</i> L.	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	<i>Phyllaphis fagi</i> (L.)	<i>Fagus sylvatica</i> L.	0	0	0	0	0	0	33	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Sitobion fragariae</i> (Walker)	<i>Agrostis stolonifera</i> L.	22	0	6	0	11	0	10	0	0	0	0	2	0	0	0	0	0	0	0
	<i>Sitobion fragariae</i> (Walker)	<i>Rubus</i> sp.	14	0	0	0	0	1	9	0	0	0	0	0	0	0	5	0	0	0	1
Summer	<i>Aphis epilobii</i> Kalténbach	<i>Epilobium hirsutum</i> L.	9	10	0	0	0	0	4	0	0	0	0	0	0	0	11	3	0	3	0
	<i>Aphis fabae</i> Scopoli	<i>Artemisia vulgaris</i> L.	57	4	1	0	0	0	12	0	0	0	2	0	0	0	15	0	0	2	0
	<i>Aphis fabae</i> Scopoli	<i>Rumex acetosa</i> L.	13	9	1	0	0	0	0	0	0	0	3	0	0	0	3	0	0	1	0
	<i>Aphis fabae</i> Scopoli	<i>Vicia faba</i> L.	42	1	0	0	0	4	15	0	0	0	0	0	0	0	5	3	0	26	0
	<i>Aphis fabae cirsiacanthoidis</i> Scopoli	<i>Cirsium vulgare</i> Ten.	7	18	0	0	0	0	7	0	0	0	0	0	0	0	3	5	0	0	0
	<i>Brevicoryne brassicae</i> (L.)	<i>Brassica oleracea</i> L.	51	19	0	0	0	0	23	0	0	2	0	3	5	1	76	1	0	17	0
	<i>Cavariella</i> sp.	<i>Heracleum sphondylium</i> L./ <i>Pastinaca sativa</i> L.	965	314	18	0	0	0	119	0	69	2	1	8	0	0	196	71	0	51	0
	<i>Drepanosiphum platanoidis</i> (Schrank)	<i>Acer pseudoplatanus</i> L.	90	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	13
	<i>Hyalopterus pruni</i> (Geoff.)	<i>Phragmites communis</i> Trin.	26	37	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Hyperomyzus lactucae</i> (L.)	<i>Sonchus oleraceus</i> L.	4	3	8	0	0	0	2	0	0	0	0	0	0	0	19	3	0	2	0
	<i>Microlophium carnosum</i> (Buckton)	<i>Urtica dioica</i> L.	36	16	0	0	0	0	8	0	0	0	0	0	0	0	3	10	0	0	0
	<i>Tuberculatus (Tuberculooides) annulatus</i> (Hartig)	<i>Quercus robur</i> L.	20	13	0	0	1	1	0	13	0	0	0	0	0	0	0	0	0	0	1

Figures represent the total number of larvae recorded during the sampling periods of "spring" (May-June) and "summer" (July-August)

Table 6: Mean numbers of syrphid larvae per 100 'colonies'³ collected from various sites in the Czech Republic¹ between 1955 and 1962. Sampling was haphazard in time, and hence not all years are represented in the data.

Aphid species	Plant species	N ²	Number of larvae ³								
			<i>Episyrphus balteatus</i>	<i>Syrphus</i> spp. ⁴	<i>Eupeodes (Metasyrphus) spp.</i> ⁵	<i>Scaeva pyrastris</i>	<i>Epistrophe</i> spp. ⁶	<i>Sphaerophoria</i> spp. ⁷	<i>Meligramma triangulifera</i>	<i>Platycheirus</i> spp. ⁸	<i>Pipiza</i> spp. ⁸
<i>Aphis fabae</i>	<i>Beta vulgaris</i>	14	3.9 ± 1.7	7.5 ± 1.8	4.1 ± 1.3	4.3 ± 1.4	1.1 ± 0.9	0.9 ± 0.6	0.2 ± 0.2	0	0
<i>Aphis fabae</i>	<i>Euonymus europaeus</i>	30	7.3 ± 1.8	4.3 ± 1.3	3.9 ± 1.5	0.3 ± 0.1	5.9 ± 2.9	0	0.3 ± 0.1	0	0
<i>Aphis fabae</i>	<i>Cirsium arvense</i>	13	15.0 ± 5.9	12.7 ± 6.0	4.2 ± 2.7	3.5 ± 2.1	9.6 ± 6.8	3.1 ± 1.3	0	0.8 ± 0.5	0
<i>Aphis sambuci</i>	<i>Sambucus nigra</i>	8	0	21.3 ± 12.0	0.3 ± 0.3	0.6 ± 0.4	2.8 ± 0.9	0	0.4 ± 0.3	0	0
<i>Brachycaudus helichrysi/cardui</i>	<i>Prunus domestica</i>	6	4.3 ± 4.3	57.1 ± 41.0	0	0	12.9 ± 7.1	0	0	0	25.7 ± 17.7
<i>Brevicoryne brassicae</i> ⁹	<i>Brassica oleracea</i>	20	6.8 ± 4.8	10.0 ± 7.5	7.1 ± 4.0	1.1 ± 0.7	0	82.4 ± 19.4	0	4.7 ± 2.1	0
<i>Hyalopterus pruni</i>	<i>Prunus domestica</i>	7	4.3 ± 4.3	82.9 ± 31.3	1.4 ± 1.4	0	5.7 ± 5.7	0	0.3 ± 0.3	0	0
<i>Myzus cerasi</i>	<i>Prunus avium</i>	13	2.1 ± 1.7	26.3 ± 12.0	4.4 ± 2.2	1.0 ± 0.5	7.9 ± 2.2	0	0.3 ± 0.2	0	1.7 ± 1.4
<i>Phyllaphis fagi</i>	<i>Fagus sylvaticus</i>	5	0	7.5 ± 4.5	1.5 ± 1.5	0	0	0	0	0	0
<i>Rhopalosiphum padi</i>	<i>Prunus padus</i>	18	6.4 ± 2.4	12.4 ± 3.4	1.8 ± 0.8	0	0	0	0.4 ± 0.2	0	1.3 ± 0.5
<i>Uroleucon cichorii</i>	<i>Crepis biennis</i>	20	4.1 ± 1.8	4.8 ± 1.5	0	7.3 ± 1.9	0.1 ± 0.1	8.0 ± 2.4	0	1.5 ± 1.5	0
<i>Uroleucon cichorii</i>	<i>Cichorium intybus</i>	8	1.3 ± 0.9	0	1.3 ± 1.3	5.6 ± 3.6	0	2.8 ± 1.5	0	0.9 ± 0.7	0

¹ Sites were in or near Praha, Roudnice, Jičín, Nová Paka, Žlunice, Olomouc, Čánka, and Nový Budžov.² N = number of samples; one sample = 40 infested leaves or 10 infested stems, or 10 infested plants (*Brassica*).³ Per 100 colonies [one colony = one infested leaf or shoot or plant (*Brassica*)]. In addition, *Platycheirus ambiguus* was found virtually exclusively on *Brachycaudus helichrysi/cardui* colonies (72.9 ± 21.0 per 100) on *Prunus domestica*; *Fagisyrphus cinctus* was only found in colonies (14.5 ± 6.9) of *Phyllaphis fagi* on *Fagus sylvaticus*; *Epistropheella euchroma* only in colonies (4.8 ± 2.6) of *Myzus cerasi* on *Prunus avium*; and *Paragus* spp. only (5.0 ± 4.2) in *Aphis fabae* on *Cirsium arvense*.⁴ Of those reared to adult, there were 79 *Syrphus ribesii*, 72 *S.torvus* and 112 *S.vitripennis*.⁵ Mostly *Eupeodes (Metasyrphus) corollae* and *luniger*.⁶ Mostly *Epistrophe nitidicollis*, except on *Aphis fabae* on *Euonymus europaeus*, where they were dominated by *Epistrophe eligans*.⁷ Mostly *Sphaerophoria scripta*.⁸ Not identified to species.⁹ Data collected 1967-69, published in Laska (1984).

Table 7: The results of measuring niche breadth and niche overlap for the two aphidophagous hoverflies, for data collected from three different geographical regions. Calculations follow Ludwig & Reynolds (1988).

Source of data	Location	Syrphid species	Niche breadth	Specific overlap ¹	General overlap ²
Sadeghi	Nottingham, U.K.	1 <i>Episyrphus balteatus</i>	5.41	0.41***	0.84***
		2 <i>Syrphus ribesii</i>	4.80	0.54***	
Laska	Olomouc, Czech Republic	1 <i>Episyrphus balteatus</i>	6.02	0.44***	0.88***
		2 <i>Syrphus ribesii</i>	4.77	0.77***	
Rotheray	Cardiff, U.K.: all season	1 <i>Episyrphus balteatus</i>	1.98	0.62***	0.92***
		2 <i>Syrphus ribesii</i>	3.06	1.00	
	: summer only	1 <i>Episyrphus balteatus</i>	1.84	0.80***	0.96***
		2 <i>Syrphus ribesii</i>	1.96	0.75***	

¹ Overlap in the resource used by the species of the row on the resources used by the other species. The significance (***) = $p < 0.001$ gives the probability that the utilisation curve of one species could have been drawn from the other's utilisation (see Ludwig & Reynolds 1988).

² Overlap of either species on common resources; the significance (***) = $p < 0.001$ gives the probability that the utilisation curve of both species could have been drawn from a common utilisation spectrum (see Ludwig & Reynolds 1988).

Table 8 The four most- and least-preferred aphid prey of *Episyrphus balteatus* and *Syrphus ribesii*, as assessed from field distribution in three areas.

Hoverfly		Nottingham	Cardiff	Czech Republic
<i>Episyrphus balteatus</i>	Most	<i>Aphis grossulariae</i> on willow-herb <i>Cavariella</i> on hogweed <i>Macrosiphum</i> on rose (<i>Schizoneura</i> on elm)	<i>Cavariella</i> on hogweed <i>Hyalopterus</i> on reed <i>Brevicoryne</i> on cabbage <i>Aphis fabae</i> on thistle	<i>Aphis fabae</i> on thistle <i>Aphis fabae</i> on spindle <i>Brevicoryne</i> on cabbage <i>Rhopalosiphum</i> on bird-cherry
	Least	<i>Phyllaphis</i> on beech <i>Aphis ruborum</i> on blackberry <i>Microlophium</i> on nettle <i>Aphis pomi</i> on apple	<i>Aphis fabae</i> on bean <i>Drepanosiphum</i> on sycamore <i>Hyperomyzus</i> on milk-thistle <i>Aphis fabae</i> on mugwort	<i>Phyllaphis</i> on beech <i>Aphis sambuci</i> on elder <i>Uroleucon</i> on cichory <i>Myzus cerasi</i> on wild cherry
<i>Syrphus ribesii</i>	Most	<i>Drepanosiphum</i> on sycamore <i>Cavariella</i> on hogweed <i>Microlophium</i> on nettle (<i>Macrosiphum</i> on rose)	<i>Cavariella</i> on hogweed <i>Microlophium</i> on nettle <i>Drepanosiphum</i> on sycamore <i>Brachycaudus</i> on campion	<i>Hyalopterus</i> on plum <i>Brachycaudus</i> on plum <i>Myzus</i> on wild cherry <i>Aphis sambuci</i> on elder
	Least	<i>Phyllaphis</i> on beech <i>Aphis grossulariae</i> on willow-herb (dock, apple, blackberry, elder, elm aphids)	<i>Phyllaphis</i> on beech <i>Myzocallis</i> on hazel <i>Hyalopterus</i> on <i>Prunus</i> <i>Hyperomyzus</i> on milk-thistle	<i>Uroleucon</i> on cichory <i>Aphis fabae</i> on spindle <i>Uroleucon</i> on hawksbeard <i>Aphis fabae</i> on beet

The second group of aphids is those present for just a short period on particular hosts. In this group some species are autoecious, but their activity is limited to 2-3 months only. For example, apple aphid appeared in June, forming colonies at the tips of young shoots, and disappeared at the end of July. The majority of this group is polyphagous, however, and some migrate between alternative hosts. In this study, elder aphid had colonies on the young shoots of elder during the early season, but towards the end of August the colonies disappeared, probably due to the activity of its predators (ladybirds as well as syrphid larvae) or migration to other host plants. Beech and elm aphids were available during May-July but then also disappeared. The other two aphids of this group were hogweed and willow-herb. Hogweed aphids appeared in June and were active until the end of August, synchronised with the flowering period of hogweed. Willow-herb aphid appeared relatively late in summer, when the colonies of other aphids were going into decline.

c) Frequency of larvae in relation to size of aphid colony

For both syrphid species, the number of larvae was significantly greater in larger aphid colonies ($F_{2,316} = 3.73$, $P < 0.05$), but there were no overall differences between the syrphid species ($F_{1,316} = 0.75$, NS), nor in their gross responses to colony sizes ($F_{2,316} = 0.07$, NS). For individual aphids, these relationships do not hold. For example, although elder aphid had the largest colonies in July, the proportion of *E. balteatus* larvae was small. There was a positive relationship between size of colonies of willow-herb or hogweed aphids and the number of larvae of *E. balteatus*.

In case of *S. ribesii*, in early summer (May-June) beech, elder, sycamore, rose, and elm aphids had larger colonies than the other sampled aphids, but only sycamore aphid had greater numbers of larvae. In early July, elder aphids had the largest colonies whereas hogweed had the greatest number of larvae.

2. Cardiff

As at Nottingham, *S. ribesii* larvae were most abundant on hogweed, nettle, and sycamore aphids, with the addition of campion (*Silene*) aphids in spring, and *E. balteatus* larvae were most abundant on hogweed aphids (Table 5). Unlike Nottingham, *E. balteatus* larvae were not particularly abundant on willow-herb aphids. There are two main features of the data. The first is the obvious difference between spring and summer aphids as the resource-base for the larvae of predatory hoverflies: there is a resource-poor separation between these periods in early July. The second feature is the astonishingly high numbers of larvae on hogweed aphids; while this may have been a year in which gravid females synchronised particularly well with the availability of this aphid, clearly this aphid is a key resource.

3. Czech Republic

In this site (Table 6), *Syrphus* spp. were commonest on the aphids of *Prunus domestica*, whereas *E. balteatus* larvae were commonest on *Aphis fabae* on *Cirsium arvense*. *Syrphus* larvae were completely absent from *Uroleucon* aphids on *Cichorium*, as were *E. balteatus* larvae from aphids on *Fagus* and *Sambucus*. It is a pity that records for *S. ribesii* and *S. vitripennis* were not differentiated (although most were said to be *S. ribesii*), because there are probably strong niche differences between these congeners among tree aphids (cf. Wnuk 1972).

Comparisons between the two species

The results of analysing data collected from three different areas, in terms of niche breadth of each syrphid and the extent of similarity or overlap of these species in utilising common host prey are shown in Table 7. As seen in both Nottingham and the Czech Republic, niche breadth of *E. balteatus* was greater than for *S. ribesii*, and equal in Cardiff during the summer. The

absence of *E. balteatus* in the spring leads to a greater niche breadth overall for *S. ribesii* in the intensively sampled Cardiff site. The two species showed considerable diet overlap, their larvae using many of the same aphids as food. The extent of the specific overlap (i.e. the probability that the utilization curve of one species could have been drawn from the other's utilisation) by *S. ribesii* onto *E. balteatus* was greater than the overlap of *E. balteatus* onto *S. ribesii*. Overall, the most-preferred and least-preferred aphids in study sites are shown in Table 8.

Discussion

There are obvious problems in estimating the oviposition preferences of gravid females from the field distribution of the eggs or larvae. The availability and intrinsic suitability of the food, differential mortality, as well as factors intrinsic to the forager, all influence the final outcome. Thompson (1988) stated that host preferences cannot be determined in the field from simple counts of the proportion of eggs (here larvae) on each host, because of oviposition by more than one female and variation in the abundance and availability of hosts. Rotheray (1989) noted that “female syrphids searching for colonies to lay their eggs may only find the most abundant aphids, missing rarer but equally suitable species. Also, there may be suitable aphids which do not occur within the geographical region [in which the search is done]”. In part, these difficulties represent the normal problems encountered when measuring the niche of any species: it is rarely possible to determine the availability of a resource as perceived by a forager, and other variables (e.g. age and egg load) also influence whether eggs are actually laid. Wiklund (1975) gave a dramatic example of a case where the field distribution of eggs of swallowtail butterflies seemed to bear little or no relation to the subsequent survival of the larvae: females selected plants where their larvae would inevitably die, and ignored plants that supported high larval survival. Despite these difficulties, field distribution should still give a strong hint of the average preferences of a population of gravid females.

Gravid syrphid females obviously select among plants for oviposition sites. Chandler (1968a-c) thought that a major distinction among syrphid species was between those orientating towards plant-related stimuli (*phytozetic* species) and those orienting towards aphid-related stimuli (*aphidozetic* species). While probably not a useful classification, it does highlight the fact that females probably orientate towards plants first, then aphids. Other factors must also play an important role. The larger number of larvae, in particular of *E. balteatus*, on hogweed or willow-herb aphids in Nottingham data could be the result of a number of factors: the larger colonies of these aphids compared with the size of colonies of other aphids at the time, a better synchrony in the activity of the syrphid females with the occurrence of the aphids on these host-plants, or the attractiveness of hogweed to adult females as a source of food during the flowering period (Schneider 1969). Ideas about how to augment the role of syrphids in the biological control of aphids depend largely on the last of these effects (Ruppert 1993; Hickman & Wratten 1996; Salveter 1998).

Females also select among aphids within plants. Most studies including this one concern aphids that are each studied only associated with one plant species. There are a few studies of several aphid species on one plant, where the selectivity of gravid female syrphids is more obvious: Wnuk & Medvey's (1986) sampling from redcurrant bushes, and Wnuk's (1972) samples from apple trees. In the latter case, two of the three commonest syrphids were completely absent from colonies of *Aphis pomi*, but all three were present in colonies of *Dysaphis plantaginea* on the same trees.

We found evidence that females oviposit selectively among aphid colonies in relation to their size (cf. Dixon 1959; Chandler 1968b; Ito & Iwao 1977, Iwao 1979; Sanders 1979; Wnuk 1979; Guest 1984; Budenberg & Powell 1992). Comparing the frequency of larvae at

sampled aphid species with the size of aphid colonies during the sampling season, the abundance of larvae on developed aphid colonies is higher than on colonies that are either young or almost disappeared, suggesting a tendency for both syrphids to oviposit in a density-dependent manner, preferring large aphid colonies to small ones. In fact, syrphid oviposition is more subtle than this, because females differentiate among colony stages as an index of future colony size: Kan (1988) showed that *E. balteatus* females respond specifically to young aphids rather than winged adults, thus avoiding old colonies that might disappear before the larvae have completed development. Dixon (1959) found that the number of eggs and adults of syrphid *Eupeodes (Metasyrphus) luniger* on broom decreased toward the end of the flowering period, possibly for the same reason.

In the UK, there are two major periods of aphid availability, in spring and late summer, with a distinct gap between them in resource availability for aphid predators (Rotheray 1989; Gilbert 1993). Only very few *E. balteatus* larvae were collected in the first two months of sampling, probably derived from adult females that have overwintered successfully in the UK. The majority of adults come from the continent to the UK in late spring (Rotheray 1989; Gilbert 1993), producing the peak in abundance of larvae in July-August. In contrast, *S. ribesii* overwinters in the U.K. (Hart & Bale 1997) and is therefore present in numbers to exploit the spring peak of aphids; this generates the wider niche breadth seen in the very detailed Cardiff data. From these data, during the summer aphid peak, *E. balteatus* is usually slightly more specialised than *S. ribesii*, but because the latter larvae are also present during the spring aphid peak, the niche breadth over the whole year is broader in *S. ribesii*.

It is not surprising that there are differences in niche breadth among geographically separated populations. Many factors are known to influence niche breadth, including activities of natural enemies, competitors, resource availability, etc. (see Putman & Wratten 1984). Despite this, after allowing for differences in the plants that were sampled, there are obvious similarities in the preferences of each species (Table 8). For *E. balteatus*, hogweed, thistle, and cabbage aphids were preferred over the other aphids. *S. ribesii* prefer sycamore, hogweed, then nettle aphids. In the Nottingham area, for the sampled aphids, these preferences are modified into willow-herb, hogweed, and rose aphids for *E. balteatus*.

Estimating oviposition choices from the field distribution of immature stages clearly involves many possible errors, including sampling and differential mortality. In this context it is interesting that oviposition preferences measured directly by experiment (Sadeghi & Gilbert 2000a) were not correlated with field distribution in either species (Sadeghi & Gilbert 2000c). Despite identifying hogweed aphids as a major prey resource for *E. balteatus*, gravid females had a relatively low oviposition preference for this aphid (Sadeghi & Gilbert 2000a).

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