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Flower constancy in the hoverflies *Episyrphus balteatus* (Degeer) and *Syrphus ribesii* (L.) (Syrphidae)

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The causes and consequences of flower constancy have been the focus of many studies, but almost all have examined the foraging behavior of bumblebees, honeybees, or butterflies. We test whether constancy occurs in an overlooked group of pollinators, the syrphid flies. Foraging sequences of wild flies of two species, *Episyrphus balteatus* and *Syrphus ribesii*, were examined when visiting flowers in seminatural plant communities and in artificial arrays of two color morphs of *Lobularia maritima* planted at a range of frequencies. Both species exhibited marked floral constancy when foraging in the mixed-plant community. Because all groups of pollinating insect so far examined exhibit constancy at least under some circumstances, we suggest that this is the predominant strategy used by pollinators and that there is probably a common explanation. Neither syrphid species exhibited constancy to different color morphs within a plant species, in contrast to previously published studies of Hymenoptera foraging among polymorphic flowers, which all describe positive frequency-dependent selection. Possible explanations for this discrepancy are discussed. We argue that constancy in these syrphids is unlikely to result from learning constraints on handling ability, currently the most widely accepted explanation for flower constancy, because they forage primarily for pollen which is easily located in most flowers they visit. *Key words:* color morph, foraging, handling time, hoverflies, interference, pollination, search image, Syrphidae. *[Behav Ecol 9:213–219 (1998)]*

The phenomenon of flower constancy (a learned fidelity to particular plant species that previously provided a reward) has long been known (Darwin, 1876) and has been the focus of numerous studies (e.g., Barth, 1985; Waser, 1986). Attention to date has focused almost exclusively on Hymenoptera, particularly honeybees and bumblebees. Foraging behavior of other pollinator groups has received comparatively little attention. In butterflies, constancy has been identified in all three species studied to date (Goulson and Cory, 1993; Goulson et al., 1997a,b; Lewis, 1989), and circumstantial evidence from analysis of gut contents in pollen-feeding beetles suggests that they may also exhibit constancy (De Los Mozos Pascual and Domingo, 1991). The causes of flower constancy have long been debated (e.g., Barth, 1985; Goulson et al., 1997b; Oster and Heinrich, 1976; Real, 1981; Waser, 1986; Woodward and Laverty, 1992), but whatever the cause it has far reaching implications for the reproductive ecology of plants (Grant, 1993; Goulson, 1994; Goulson and Jerrim, 1997; Kunin, 1993; Levin, 1978).

Syrphids are frequent visitors to and pollinators of a diverse range of plant species (e.g., Affre et al., 1995; Arruda and Sazima, 1996; Conner and Rush, 1996; Kampny, 1995; Kato, 1996; Olesen and Warncke, 1989; Parmenter, 1956; Pollard, 1971; Sugiura, 1996). There is evidence that they may also effect pollination in reputedly anemophilous flowers (Leereveld, 1982, 1984). However, in comparison with bees and butterflies, there have been few studies of the patterns of foraging behavior of adult syrphids (but see Gilbert, 1981, 1983; Stanton, 1987). No previous work has explicity attempted to assess whether syrphids exhibit flower constancy, although evidence from a study of competition for pollination services between *Saxifraga reflexa* and *S. tricuspidata* suggests that they might (McGuire and Armbruster, 1991). The paucity of studies of syrphid foraging behavior probably reflects the small size and rapid flight of most species, which make them difficult to follow when foraging. However, with patience, short foraging sequences can be recorded. We assessed whether two species of syrphid, *Erisyrphus balteatus* and *Syrphus ribesii*, exhibit flower constancy. Most studies of floral constancy have used artificial arrays of (often artificial) flowers because this simplifies interpretation of foraging patterns (Smithson and Macnair, in press; Stanton, 1987; Wells and Wells, 1983; 1986; Wells et al.; 1992). However, floral constancy can be distinguished in foraging sequences of insects visiting natural distributions of flowers provided that the sequence of all flowers passed by during flight (not just those visited by the insect) are recorded (Goulson et al., 1997a; Lewis, 1989). We examined foraging behavior of wild flies among seminatural plant communities and within artificial arrays of two color morphs of *Lobularia maritima* (Alyssum) (Cruciferae).

METHODS

Foraging sequences among seminatural distributions of plant species

Wild hoverflies were observed while foraging among plant species at the Hawthorns Wildlife Centre, Southampton, UK, during June and July 1995. The gardens of the Wildlife Centre are planted with native flora to simulate a range of natural communities on a small scale, including heathland, scrub, pond, and marsh areas. The area thus provides a high diversity of flowering plants and attracts an abundance of hoverflies.

Experimental methods followed an established technique (Goulson et al., 1997a; Lewis, 1989) developed by Mackay (1985) for studying oviposition behavior in butterflies. We followed individual hoverflies while they foraged, maintaining a distance of at least 2 m to avoid disturbance, and using num-

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Table 1

Preference indices for the flowering plants visited for nectar or pollen by two syrphid species

Key	Species	Family	*E. balteatus* preference index	*S. ribesii* preference index
1	*Pulicaria dysenterica*	Compositae	1.68	1.38
2	*Eupatorium cannabinum*	Compositae	1.03	0.44
3	*Centaurea nigra*	Compositae	0.89	1.48
4	*Echium vulgare*	Boraginaceae	1.54	0.00
5	*Crepis capillaris*	Compositae	1.23	0.51
6	*Epilobium hirsutum*	Onagraceae	0.51	0.63
7	*Rumex crispus*	Polygonaceae	0.31	0.00
8	*Achillea millefolium*	Compositae	0.90	0.00
9	*Lythrum salicornia*	Lythraceae	0.49	0.00
10	*Dipsacus fullonum*	Dipsacaceae	0.46	1.10
11	*Plantago lanceolata*	Plantaginaceae	2.04	0.00
12	*Senecio jacobaea*	Compositae	0.00	1.39
13	*Mentha aquatica*	Labiatae	0.00	0.96
14	*Lapsana communis*	Compositae	0.00	2.55
15	*Lathyrus latifolius*	Leguminosae	—	2.04
16	*Ranunculus repens*	Ranunculaceae	—	2.55

Based on observation of visits to 253 and 261 inflorescences for *E. balteatus* and *S. ribesii*, respectively. Preference = (proportion of inflorescences visited)/(proportion of inflorescences encountered).

bered canes to mark the path. Recording was terminated when the fly was lost or when it encountered a conspecific. We reconstructed flight paths with the aid of the numbered canes. Inflorescences which came within 5 cm of the flight path (as estimated by the observer) were considered to have been encountered (i.e,. detected) by the fly and were recorded in sequence. We recorded 81 foraging sequences (41 for *E. balteatus* and 40 for *S. ribesii*). Visits were scored only if the fly was seen to probe the inflorescence for nectar or pollen; rarely flies would perch on a flower but not attempt to feed, and these events were scored as encounters. A single visit was recorded regardless of the number of flowers probed on an inflorescence. To minimize repeated observations on the same fly, observations were alternated between the two species. Given the large fly population present, it is unlikely that many individuals were followed more than once. We did not record sex because it could not always be distinguished without close examination, which might have disrupted natural behavior.

We estimated the probability of a fly visiting a particular inflorescence which it encountered (the visit likelihood) using GLIM (McCullagh and Nelder, 1989) with binomial errors following Goulson et al. (1997). Factors included in the model were syrphid species, the plant species encountered, and whether this was the same species as that last visited by the insect (plus all two- and three-way interactions). Factors that did not contribute significantly to the model were removed in a stepwise manner. The error structure was substantiated during analysis. Means for each individual fly/plant species combination were used to avoid pseudoreplication.

Foraging sequences among color morphs of *L. maritima*

Arrays of varying frequencies of container-grown white and purple morphs of *L. maritima* (varieties Carpet of snow and Oriental night, respectively) were planted on 5 July 1995 in the University Experimental Garden at Chilworth, near Southampton. *L. maritima* is a widely cultivated annual which is naturalized in southern UK. It has small flowers (corolla depth approximately 2.5 mm) of typical shape for the Cruciferae, with up to 24 flowers open at any point in time on each inflorescence. Numbers of purple and white plants in each array were 12:0, 12:3, 12:6, 12:12, 6:12, 3:12 and 0:12, giving ratios of 1:0, 4:1, 2:1, 1:1, 1:2, 1:4, and 0:1. Within an array, plants were randomly allocated to positions on a 5×5 grid with 15 cm (minimum) between plants. Each frequency was replicated 3 times, and the 21 arrays allocated randomly to a 7×3 grid with 3 m between arrays (single color morph arrays were included, as the arrays were used for a number of different experiments, but they are not considered further here).

Once established and in flower, the plants attracted an abundance of hoverflies and other insects. We recorded the number of flowers per plant for a random sample of 30 plants of each color on 21 July. The foraging behavior of *E. balteatus* and *S. ribesii* within arrays was observed on sunny days between 19 July and 14 August 1995, with all observations made between 1000 h and 1700 h. We watched individual flies while foraging and recorded the sequence of movements between plants within an array onto audio tapes for subsequent analysis. Each sequence ended when the fly departed from the array or ceased to feed. To avoid pseudoreplication, we condensed foraging sequence data for each fly into two figures, the proportion of the plants visited that had white flowers, and the proportion of movements between plants that involved a movement between plants of different flower color. These proportions were compared with expected frequencies of visits to and switches between color morphs assuming random movement (no color preference or history effect). Proportions were arcsine transformed and compared to expected values using a *t* test. For example, 44 individual *E. balteatus* were recorded foraging among arrays of 12 white and 12 purple-flowered plants. The mean proportion of white-flowered plants visited was tested against the expected value of 0.5, and the mean proportion of movements between plants of different color was calculated against an expected value of 0.52 (when a fly departs from a particular plant it has a choice of 23 plants to fly to, of which 12 are of a different color).

RESULTS

Foraging sequences among plant species

The two most abundant syrphid species, *E. balteatus* and *S. ribesii*, were each observed to visit 11 different species of flow-

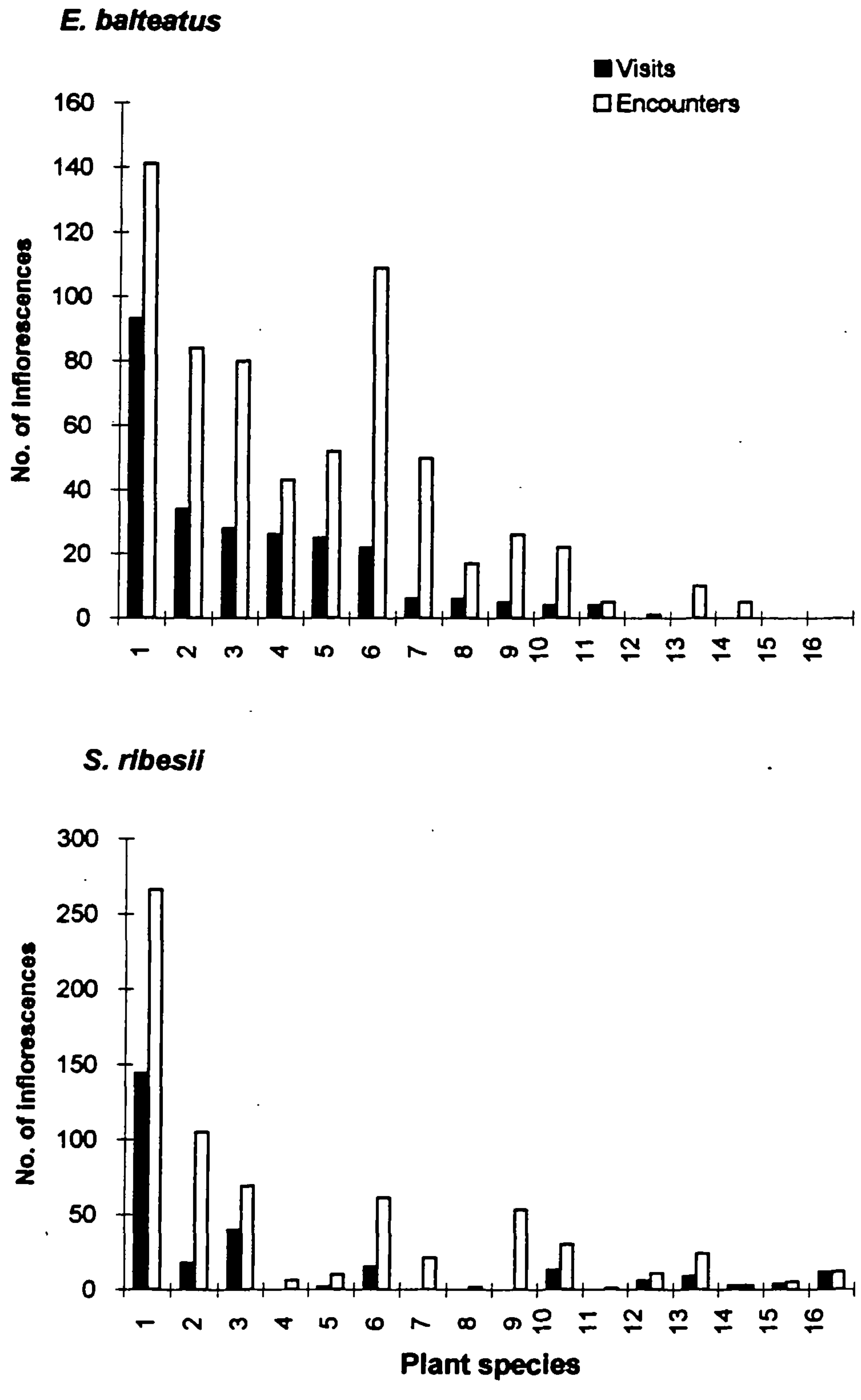

Figure 1
The distribution of visits and encounters (flew within 5 cm when foraging) of inflorescences of the plant species visited by *E. balteatus* and *S. ribesii* for pollen or nectar, based on 41 foraging sequences for *E. balteatus* and 40 for *S. ribesii*, in total composed of 256 visits to inflorescences of the 645 inflorescences encountered during flight for *E. balteatus* and 266 visits of 678 inflorescences encountered for *S. ribesii*. The encounters category includes inflorescencess which were visited and those which were rejected. Plant species are given in Table 1.

ering plant for nectar or pollen (not all the same species; Table 1). In total 81 foraging runs were recorded (41 for *E. balteatus* and 40 for *S. ribesii*), composed of 256 visits to inflorescences of the 645 inflorescences encountered during flight for *E. balteatus* and 266 visits of 678 inflorescences encountered for *S. ribesii*. The mean (and range) of visits per foraging run were 6.2 (3–14) and 6.7 (3–14) for *E. balteatus* and *S. ribesii*, respectively. The distribution of visits and encounters among the plant species gives an indication of both the relative abundance of inflorescences of the different species of flowering plant and their attractiveness to each syrphid species (Figure 1). These data can be used to calculate a preference index for each plant species (Table 1). A substantial portion of the diet of both species consisted of Compositae (74% and 82% of visits by *E. balteatus* and *S. ribesii*, respectively), particularly the three species *Pulicaria dysenterica, Eu-*

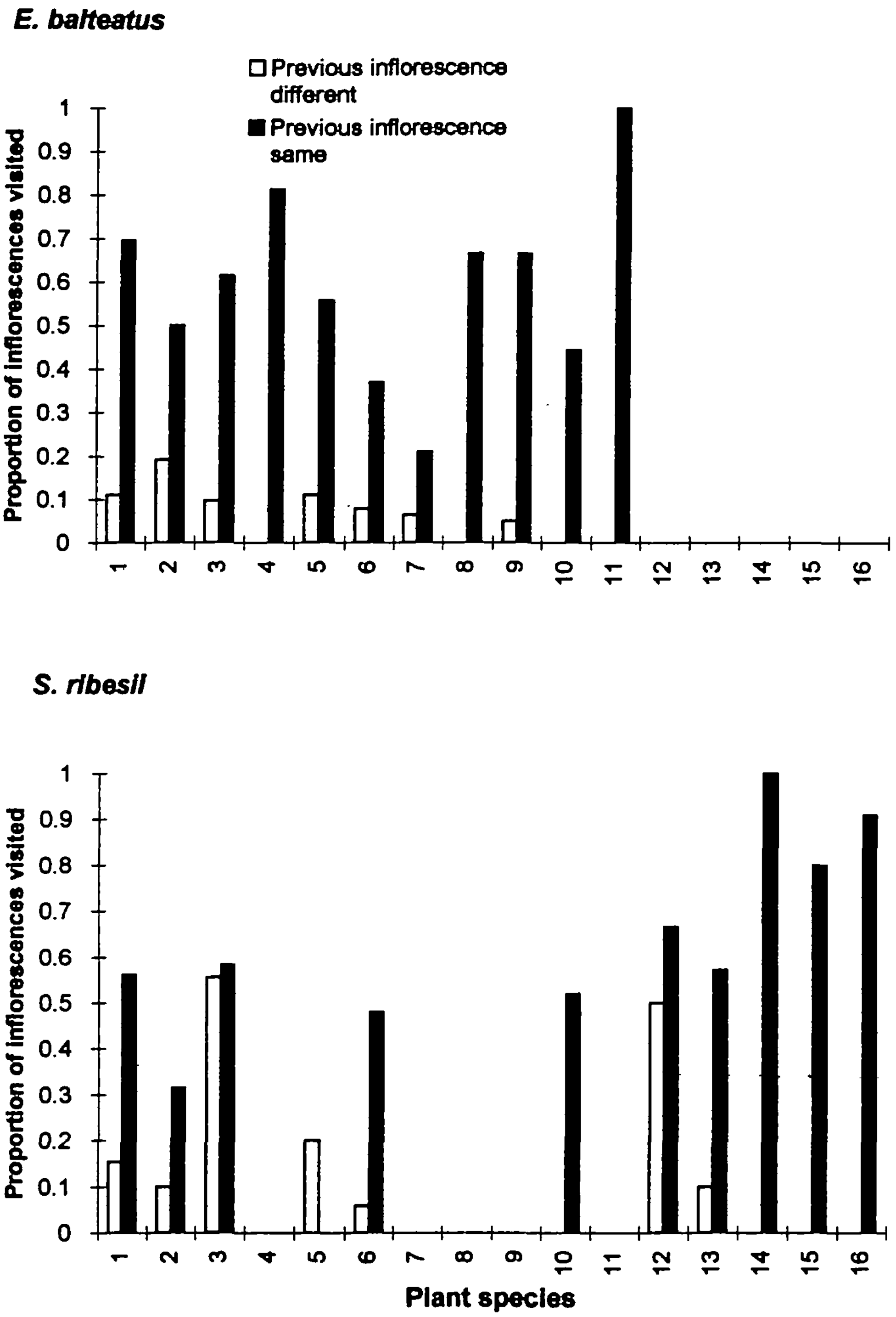

Figure 2
Visit likelihoods (probabilities) following an encounter for each of the 16 plant species visited by *E. balteatus* and *S. ribesii*. Likelihoods calculated using GLIM with binomial errors and using a mean for each individual fly to avoid pseudoreplication.

patorium cannabinum, and *Centaurea nigra*. These three species were also among the most frequently encountered (Figure 1).

The visit likelihood (the probability of a fly visiting a particular inflorescence which it encounters) differed between syrphid species ($\chi^2_1 = 4.05, p < .05$), with *E. balteatus* visiting a slightly higher proportion of the inflorescences encountered than *S. ribesii* (26.2% and 25.7%, respectively). It must be remembered that this proportion will depend on the distance (5 cm) chosen for inclusion of inflorescences as having been encountered by the foraging fly. This distance was arbitrarily chosen as representing a conservative estimate of the distance at which syrphids can detect flowers, and choice of a larger distance would reduce the proportion of visits to encounters.

There was a strong effect of plant species upon the visit likelihood ($\chi^2_{15} = 54.9$, $p < .001$), again indicating preferences for particular species (Figure 2). No syrphid species×plant species interaction was apparent ($\chi^2_{15} = 13.8$, ns), indicating that differences in plant preferences of the two species (Table 1) were not statistically significant. However, it is worth noting that there was a weak negative relationship between preference indices for the two species (Pearson product-moment correlation coefficient = −0.441, ns). There was

Table 2

Proportions of visits by species of syrphids to white flowered *Alyssum* in mixed arrays of white and purple flowered plants

Proportion of white flowered plants in array	*E. balteatus*		*S. ribesii*	
	Mean	*t* (df)	Mean	*t* (df)
0.8	0.81	0.36 (6)	0.85	0.67 (8)
0.667	0.53	0.19 (15)	0.71	0.37 (19)
0.5	0.45	0.02 (11)	0.55	0.34 (32)
0.333	0.21	0.36 (2)	0.22	0.53 (10)
0.2	0	—	0.31	0.36 (8)

Numbers of white and purple plants in each array were 12:0, 12:3, 12:6, 12:12, 6:12, 3:12 and 0:12, giving ratios of 1:0, 4:1, 2:1, 1:1, 1:2, 1:4 and 0:1. Figures given are means for three replicates. None of the values for *t* approach statistical significance.

also a strong "history effect" (*sensu* Lewis, 1989) in that the visit likelihood was far higher when the inflorescence encountered was of the same species as that last visited (i.e., the flies exhibited flower constancy; χ^2_1 = 200.9, $p < .001$; Figure 2). If inflorescence distributions are clumped (which is generally the case), then a fly is most likely to encounter and therefore to visit the same species as that which it visited last, but this would not result in a history effect. The calculation is based on the proportion of visits to encounters, so that a history effect will only occur if the insect visits a higher (or lower) proportion of inflorescences of the species it last fed on than of inflorescences of a different species.

There was no interaction between history effects and syrphid species (χ^2_1 = 1.17, ns), suggesting that both syrphid species respond in the same way to prior experience (they are both more likely to visit inflorescences if they are of the species that they last visited). There was a significant interaction between plant species and history effect (χ^2_{13} = 36.3, $p < .005$), indicating that the hoverflies responded differently to prior experience of different plant species (Figure 2).

Foraging sequences among color morphs of *L. maritima*

The two color morphs did not differ in the number of flowers produced per plant, although there was great variation between individual plants (means±SE, 242±32 and 229±41 for white and purple morphs, respectively, $F_{1,58}$ = 0.42, ns). Overall, 647 plants were visited within arrays, 230 by *E. balteatus* and 417 by *S. ribesii*. All flies fed on pollen rather than on nectar. Neither species exhibited a preference for a particular color morph; the proportion of white-flowered plants visited did not differ from the proportion present for any of the five frequencies at which they were presented (Table 2). The frequency of switches between color morphs did not differ from that which would be expected from a pattern of random foraging within arrays (Table 3).

DISCUSSION

Honeybees, bumblebees, butterflies, and (probably) beetles exhibit floral constancy (Barth, 1985; De Los Mozos Pascual and Domingo, 1991; Goulson and Cory, 1993; Goulson et al., 1997a; Lewis, 1989; Waser, 1986). Our data demonstrate that when foraging among wild flowers, two species of Syrphidae exhibit a significant degree of constancy to plant species previously visited. This is the first time that flower constancy has been convincingly demonstrated in Diptera and adds to the evidence suggesting that flower constancy is a general phenomenon among insects that forage for nectar or pollen.

It seems probable that the floral constancy observed in diverse pollinators has a common cause. The favored explanation for flower constancy is that it results from memory constraints (Darwin's interference hypothesis; Darwin, 1876; Dukas and Real, 1993; Lewis, 1986; Lewis and Lipani, 1990). Laboratory and field studies have found a small reduction in handling time associated with constancy (Laverty, 1994b; Lewis, 1986; Woodward and Laverty, 1992). Hence constancy may increase foraging efficiency. However, data for bumblebees suggest that switching between flower species only incurs a handling time penalty when the flowers have a complex structure; switching between simple flowers occurs frequently and incurs no penalty (Laverty, 1994a,b; Woodward and Laverty, 1992). Also, bumblebees may be able to retain handling skills for at least two plant species (Gegear and Laverty, 1995). Most of the smaller syrphid species (including those studied here) have short probosces and tend to visit shallow and simple flowers (relative to honeybees or bumblebees; e.g., Gilbert, 1981). These two species feed predominantly on pollen rather than nectar (Gilbert, 1981), as pollen is generally more easily located because it is usually presented at, or outside of, the mouth of the corolla. Thus it is likely that switching between plant species incurs little increase in handling time.

Levin (1978) suggested an alternative to Darwin's interference hypothesis, proposing that constancy may result from formation of a search image for flowers of plant species that previously provided a reward. Studies of bumblebees have recently provided some experimental support for this idea (Wilson and Stine, 1996). However, if this were true for syrphids,

Table 3

Proportion of between-plant movements for *Alyssum* of different color morphs in mixed arrays

Proportion of white flowered plants in array	Expected frequency of movement between colors	*E. balteatus*		*S. ribesii*	
		Observed mean	*t* (df)	Observed mean	*t* (df)
0.8	0.34	0.52	0.53 (6)	0.06	1.52 (8)
0.667	0.47	0.51	0.25 (15)	0.53	0.34 (19)
0.5	0.52	0.61	0.44 (11)	0.49	0.10 (32)
0.333	0.47	0.31	0.33 (2)	0.58	0.45 (10)
0.2	0.34	0	—	0.43	0.36 (8)

Overall 647 plants were visited within arrays, 230 by *E. balteatus* and 417 by *S. ribesii*. Expected values were calculated for random foraging (without an innate color preference or learned constancy); *t* tests used arcsine-transformed proportions for each insect. None of the values for *t* approach statistical significance.

we might expect constancy in mixed arrays of flowers of the same species (and hence of the same structure) but differing in color: this did not occur in our study. This concurs with the only previous study that tested for constancy of syrphids when foraging among arrays of polymorphic flowers (of wild radish, *Raphanus sativus*) (Stanton, 1987). However, studies of other pollinating insects visiting flowers that were polymorphic for shape, color, or size have found positive frequency-dependent selection (disproportionate visitation of the commonest morph) (Cresswell and Galen, 1991; Epperson and Clegg, 1987; Levin, 1970, 1972; Waser and Price, 1981, 1983). The absence of such an effect in syrphids is puzzling. Previous studies have found that the syrphid *Eristalis tenax* has an innate preference for yellow flowers and preferentially visits yellow-flowered morphs of the radish *Raphanus raphanistrum* (Kay, 1976; Lunau, 1993; Lunau and Wacht, 1994). It is possible that the white and purple color morphs of *L. maritima* are not readily distinguished by the photoreceptors of *E. balteatus* and *S. ribesii*. This seems unlikely given the marked contrast between color morphs to human vision, but until the spectral reflection of color morphs and spectral sensitivity of these syrphid species (particularly of ultrviolet frequencies) is quantified it cannot be ruled out. Suitable methods are described by Lunau (1993).

Despite widespread support for Darwin's interference hypothesis (Heinrich et al., 1977; Lewis, 1986, 1993; Waser, 1986), at present it has not been convincingly demonstrated that this hypothesis explains floral constancy in any group of insects collecting nectar from flowers. Our identification of constancy in pollen-feeding syrphids casts further doubt on its ability to explain forager behavior. Quantification of handling times and handling errors following switching between flower species versus constancy has not been attempted in pollen-feeding syrphids and should indicate whether the handling efficiency is affected by past experiences. Even a small decrease in handling time associated with constancy may increase time available for other activities (e.g., searching for mates or oviposition sites) (Goulson et al., 1997a). If switching is not associated with a handling penalty, then we must reexamine alternative explanations for floral constancy (e.g., Barth, 1985; Dukas and Real, 1993; Levin, 1972; Proctor and Yeo, 1976; Real, 1981).

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