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Floral display size in comfrey, *Symphytum officinale* L. (Boraginaceae): relationships with visitation by three bumblebee species and subsequent seed set

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Abstract The fecundity of insect-pollinated plants may not be linearly related to the number of flowers produced, since floral display will influence pollinator foraging patterns. We may expect more visits to plants with more flowers, but do these large plants receive more or fewer visits per flower than small plants? Do all pollinator species respond in the same way? We would also expect foragers to move less between plants when the number of flowers per plant are large, which may reduce cross-pollination compared to plants with few flowers. We examine the relationships between numbers of inflorescence per plant, bumblebee foraging behaviour and seed set in comfrey, *Symphytum officinale*, a self-incompatible perennial herb. Bumblebee species differed in their response to the size of floral display. More individuals of *Bombus pratorum* and the nectar-robbing *B. terrestris* were attracted to plants with larger floral displays, but *B. pascuorum* exhibited no increase in recruitment according to display size. Once attracted, all bee species visited more inflorescences per plant on plants with more inflorescences. Overall the visitation rate per inflorescence and seed set per flower was independent of the number of inflorescences per plant. Variation in seed set was not explained by the numbers of bumblebees attracted or by the number of inflorescences they visited for any bee species. However, the mean seed set per flower (1.18) was far below the maximum possible (4 per flower). We suggest that in this system seed set is not limited by pollination but by other factors, possibly nutritional resources.

Key words *Bombus* spp. · Foraging · Comfrey · Floral display · Seed set

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Introduction

Provision of a floral reward (nectar or pollen) encourages foragers to visit flowers and distribute pollen. However, rewards are patchy in time and space due to, among other factors, the distribution and varying size of individual plants, patterns of flowering phenology, nectar production and depletion of rewards by other insects (Real and Rathcke 1988; Cresswell 1990; Waser and Mitchell 1990). These factors are likely to influence the pattern of movement within and among individual plants and among plant species adopted by pollinators, which will in turn determine the reproductive success of the plants (Levin 1978). Depending on the foraging strategy used, plants may compete with other species for visitation of insect pollinators or incur improper pollen transfer, with the importance of these two processes determined by relative densities of plant species and the degree of similarity in floral morphology (Waser 1978; Feinsinger 1978; Kunin 1993). However, conspecifics may have facilitative effects through increased visitation and by acting as sources of pollen (Levin 1972; Jennersten and Nilsson 1993; Kunin 1993).

One factor likely to be a major determinant of the pattern of pollinator movement within and between plants is the number of flowers produced per plant. Zoophilous plants face an evolutionary dilemma: they must attract large numbers of insects to maximise outcrossing in pollination but at the same time must then encourage these pollinators to depart swiftly rather than foraging for long periods on one plant. The latter will result in self-pollination (geitonogamy) in self-fertile species or pollen wastage and stigma clogging in self-incompatible species (Klinkhamer and de Jong 1993; Robertson and Macnair 1995). A large number of flowers is likely to attract more pollinators to a plant, but will it attract more pollinators per flower? Will a large number of flowers encourage pollinators to stay longer on one plant? What are the effects of flower number on seed set? Studies of the effects of variation in numbers of flowers per plant on visitation rate and seed set have produced differing results. Plants with a larger floral display have been shown to attract more pollinators per flower or to achieve higher rates of pollen deposition or removal (e.g. Cruzan 1988; Klinkhamer et al. 1989; Andersson 1991; Dudash 1991; Ohara and Higashi 1994). However, other studies have found no effect of numbers of flowers per plant on individual success of flowers (e.g. Chaplin and Walker 1982; Geber 1985; Wolfe 1987; Piper and Waite 1988; Bullock et al. 1989; Campbell 1989; Robertson and Macnair 1995), while Andersson (1988) found a negative relationship between seed set per flower and number of flowers per plant.

We attempt to quantify the relationships between floral display, pollinator visitation and plant fecundity in comfrey, *Symphytum officinale* L. *S. officinale* is a perennial herb found throughout southern England, predominantly in damp habitats especially beside rivers. It is self-incompatible (J.C. Stout, unpublished work). Each plant supports a variable number of inflorescences (3–177 in this study), each with up to 25 tubular flowers, with approximately 2–6 open at any one time. The flowers appear in a range of colours from white through to dark mauve and pink (to human vision), and are open mainly from May to July. The main insect pollinators are bumblebees, which feed on the nectar produced in nectaries at the base of the flowers. Short-tongued species are excluded from direct access, but *Bombus terrestris* and *B. lucorum* bite a hole in the base of the corolla and "rob" the nectar. These robbing holes are subsequently used by other individuals of the same and different species (authors, personal observations). Nectar robbing may have important implications for the reproductive success of the plant since robbers are unlikely to be effective pollinators (Roubik 1982; Inouye 1983). Longer-tongued bee species (e.g. *B. pascuorum*) visit *S. officinale* flowers in the conventional manner to obtain nectar.

Materials and methods

Field-work was carried out during June and July 1996 at the Itchen Valley Country Park (near Southampton, Hampshire) in southern England. Four sites within the park were studied, each with a varying number of *S. officinale* plants (17, 30, 56 and 48 in sites 1, 2, 3 and 4 respectively). All four sites were visited by a guild of five species of bumblebee (*B. terrestris*, *B. lucorum*, *B. lapidarius*, *B. pascuorum* and *B. pratorum*). However, it is not possible to distinguish reliably between the morphologically very similar workers of *B. terrestris* and *B. lucorum* without capturing them, so these two species were grouped and are henceforth described as *B. terrestris*.

Visitation rates and duration

Bumblebee foraging was recorded during 5-min observations of each plant. Three figures were recorded for each bee species: the number of bees attracted, the number of inflorescences visited per bee, and the total number of inflorescences visited per five minutes. This was repeated at all four sites observing 16, 28, 23 and 22 plants in sites 1, 2, 3 and 4 respectively ($n = 89$) on each of 5 days. The number of inflorescences on every plant at each site was recorded (including those not observed for bee visitation rates). The number and proximity of neighbouring plants (within 1 m) and the number of inflorescences they supported was also determined.

Nectar measurements

To examine whether standing rewards of nectar varied with plant size, nectar volume was measured in 25 plants at site 4 within 1 h (1030–1130 hours) on 4 July. Five flowers were sampled for each plant. Nectar was extracted using a drawn-out glass microcapillary tube, and the drop of nectar blotted onto filter paper (Whatman No. 1). A calibration curve was constructed using known volumes of sucrose solution pipetted onto filter paper. The resulting regression line fitted through the origin (area = 2.675 × volume, $r^2 = 98\%$) was then used to convert the diameter of each circle on the filter paper into a volume (see Goulson et al., in press).

Seed set

The number of seeds set by each flower was counted for all 59 plants from which data for pollinator visitation rate were available and which had not been destroyed by trampling or grazing (16 at site 1, 24 at site 2 and 19 at site 3). Flowers set a maximum of four seeds, so that the number of seeds set out of a potential maximum could be assessed. All flower heads were removed from each plant and seeds counted in the laboratory. Timing of assessment of seed set in *S. officinale* is not crucial since fallen seeds leave distinctive scars within the calyx, so that even after many of the seeds have dropped the number of seeds set per flower can be assessed accurately. Seed set at site 4 was not measured as the plants in this site were destroyed by grazing before seed set.

Analysis

Analyses were confined to the three most abundant bee species, *B. terrestris*, *B. pratorum* and *B. pascuorum* (numbers of *B. lapidarius* were too low for detailed examination to be informative). For each bee species the three classes of bee visitation data were analysed separately:

A. Numbers of bee visits per plant per 5 min
B. Numbers of inflorescence visited per bee
C. Total number of inflorescences visited by all bees

All analyses used the mean value across all time points for each plant to avoid psuedoreplication ($n = 89$). Numbers of bees (A) were analysed using Poisson errors in GLIM (McCullagh and Nelder 1989) according to site, total number of inflorescences on each plant and numbers of inflorescences visited by other bee species (C) (plus pairwise and three-way interactions). The error structure was substantiated during analysis. Factors which did not contribute significantly to the model were removed in a stepwise manner.

Numbers of inflorescence visited per bee (B) approximated to a normal distribution without transformation. In this analysis numbers of individual bees (of each species) were included as factors.

The total number of inflorescences visited by bees of each species (C) approximated to a normal distribution after a square root transformation, and were similarly analysed. The total number of inflorescences visited per five minutes was also analysed as a proportion of the number of inflorescences on the plant, using normal errors following an arcsine transformation.

The proportion of seeds set per plant (seeds set/4 × number of flowers) was analysed in GLIM with binomial errors for effects of site, number of inflorescences per plant, number of inflorescences on neighbouring plants, prior visitation rates by each of the three bumblebee species (both numbers of bees (A) and numbers of inflorescence visited by all individuals (C), and all pairwise interactions. William's procedure (Collett 1991) was used since the data were overdispersed (Crawley 1993).

Results

Numbers of bees attracted

In total 892 bumblebee visits were recorded to the 89 study plants. None of the bees observed were collecting pollen (pollen collection was only observed earlier in the season before this study commenced). *B. terrestris* were exclusively nectar robbers. *B. pascuorum* and *B. pratorum* generally fed in the conventional way, although small numbers were seen to utilize holes made by nectar robbers. *B. terrestris* was the most common visitor (totals observed: 498 *B. terrestris*, 226 *B. pratorum*, 170 *B. pascuorum* and 8 *B. lapidarius*). Analysis was confined to the first three of these species since numbers of *B. lapidarius* were low. A summary of factors which were significantly related to numbers of bee visits of each species is given in Table 1. The only factor which affected numbers of all three bee species was site, with marked differences between sites. The number of bee visits to each plant varied significantly with the number of inflorescences supported by the plant for *B. terrestris* and *B. pratorum*, but not for *B. pascuorum* (Table 1, Fig. 1). *B. terrestris* exhibited a steady increase in numbers of bee visits according to inflorescence number, with on average one bee attracted in 5 min for every 15–20 inflorescences (Fig. 1). Conversely *B. pratorum* exhibited an apparent preference for plants of intermediate size, with highest numbers of bee visits to plants with 21–30 inflorescences (Fig. 1). *B. pascuorum* exhibited no clear preference according to size (Fig. 1).

Table 1 Factors significantly affecting bee (*Bombus* spp.) visitation rates to *Symphytum officinale* plants. For each bee species three separate analyses were carried out, using number of bees, number of flowers visited per bee, and total number of inflorescences visited. The following factors were examined: number of inflorescences per plant, number of inflorescences on other plants within 1 m, site, colour morph and colour morph frequency within the site, plus all pairwise and three-way interactions. Factors not shown below did not contribute significantly to the model

	B. terrestris	B. pratorum	B. pascuorum
No. of bees attracted/5 min	No. inflor. $\chi^2_1 = 7.65$** Site $\chi^2_3 = 26.9$**	No. inflor. $\chi^2_1 = 8.97$** Site $\chi^2_3 = 93.5$**	Site $\chi^2_3 = 18.8$**
No. inflorescences visited/bee	No. inflor. $F_{1,64} = 15.4$** Site $F_{3,64} = 4.1$*	No. inflor. $F_{1,18} = 10.8$** No. *B. pratorum* $F_{1,48} = 5.27$*	–
Mean no. inflorescences visited/ 5 min (total for all bees of each species)	No. inflor. $F_{1,84} = 10.6$** Site $F_{3,84} = 6.46$**	No. inflor. $F_{1,83} = 4.30$* Site $F_{3,83} = 19.0$** No. inflor. visited by *B. pascuorum* $F_{1,83} = 4.67$*	No. inflor. visited by *B. pratorum* $F_{1,87} = 16.8$**

* $P < 0.05$, ** $P < 0.01$

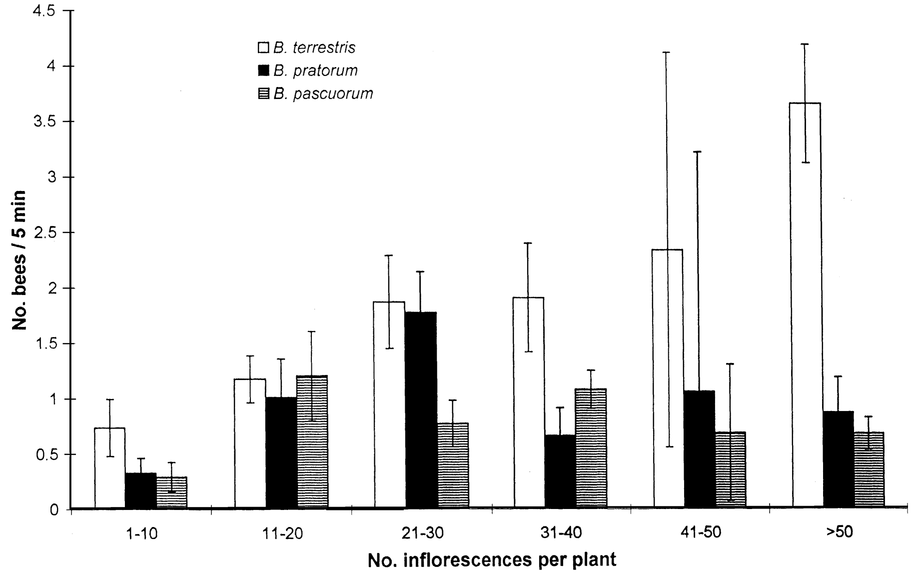

Fig. 1 Number of bees (*Bombus* spp.) visiting each plant of comfrey (*Symphytum officinale*) per 5 min according to number of inflorescences per plant for the three commonest bee species. A single mean per bee species was calculated for each of 89 plants using at least three 5-min observation periods (treating plants as replicates), and then a mean and standard error calculated for each size class

The number of inflorescences on neighbouring flowers (within 1 m) and numbers of inflorescence visited by other bee species did not affect numbers of bees attracted for any of the three species.

Number of inflorescences visited per bee

As with numbers of bees attracted, all three species visited more inflorescences on plants with more inflorescences, although this relationship was not significant for *B. pascuorum* (Table 1, Fig. 2). Estimates of the slope of this relationship (±SE) are 0.07 ± 0.02, 0.07 ± 0.02 and 0.06 ± 0.03 for *B. terrestris*, *B. pratorum* and *B. pascuorum*, respectively.

For *B. terrestris* the number of inflorescences visited per bee varied between sites, with more inflorescences visited per plant at site 2 than elsewhere (means ± SE; 7.2 ± 1.4, 11.5 ± 1.2, 5.4 ± 0.7 and 6.0 ± 0.7 for sites 1–4, respectively) (Table 1). Individual *B. pratorum* visited more inflorescences on plants which exhibited a high recruitment of *B. pratorum* in terms of numbers of bees.

Total numbers of inflorescences visited per plant

The number of inflorescences visited per plant by all individual bees of a species is given by the number of bees multiplied by the number of inflorescences visited per bee. As with numbers of bees attracted, *B. terrestris* and *B. pratorum* visited significantly more inflorescences on larger plants (Table 1). While this relationship is marked for *B. terrestris*, the pattern is less clear for *B. pratorum* with an apparent decline in visitation to the

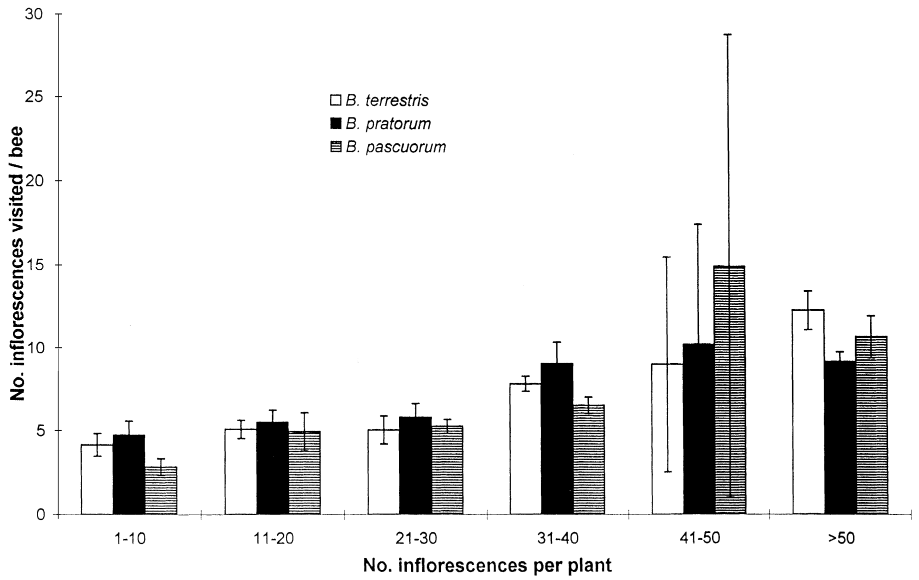

Fig. 2 Number of inflorescences visited per bee according to number of inflorescences per plant for the three commonest bee species. Sample sizes were 76, 50 and 59 for *B. terrestris*, *B. pratorum* and *B. pascuorum*, respectively. A single mean per bee species was calculated for each plant, and a mean and standard error calculated for each size class

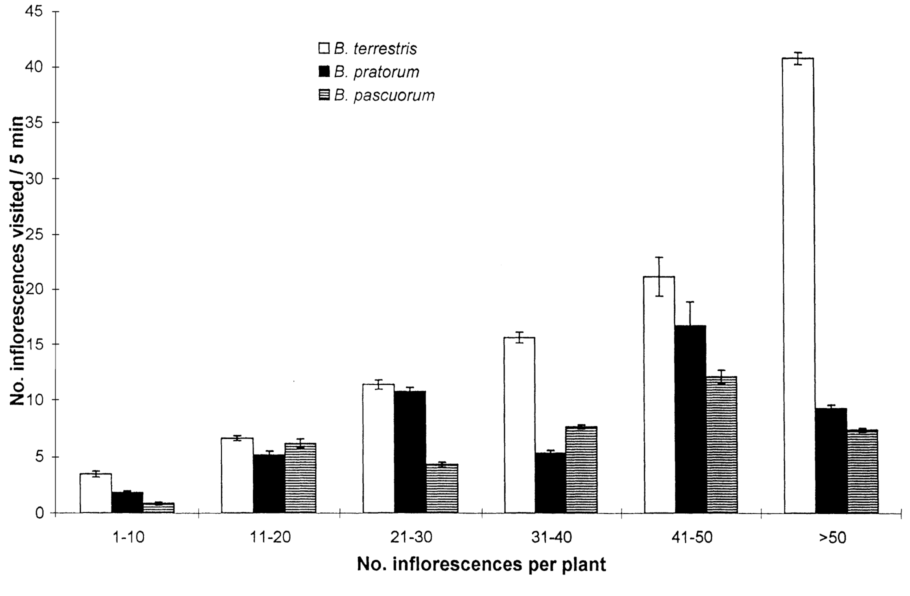

Fig. 3 Total number of inflorescences per plant visited by all individual bees of each species per 5 min (mean ± SE, $n = 89$)

very largest plants (Fig. 3). There was a positive relationship between the numbers of inflorescences visited by *B. pratorum* and *B. pascuorum*; this was the only factor which explained a significant proportion of the variation in numbers of inflorescence visited by *B. pascuorum*. The product-moment correlation coefficient for the numbers of inflorescences per plant visited by these two species was 0.44. Even when numbers of visits by *B. pratorum* are excluded from the analysis, there was no significant relationship between the number of inflorescences per plant and the number of inflorescences visited by *B. pascuorum* ($F_{3,85}$ = 2.62, n.s.) (Fig. 3).

The proportion of inflorescences per plant visited in five minutes showed no relationship to any of the factors measured for *B. pascuorum*, and only varied according to site for the other two species ($F_{3,81} = 9.24$, $P < 0.01$ and $F_{3,85} = 28.3$, $P < 0.01$ for *B. terrestris* and *B. pratorum*, respectively). In particular it was independent of inflorescence number for all three bee species ($F_{1,78} = 0.05$, $F_{1,78} = 0.15$ and $F_{1,78} = 1.22$ for *B. terrestris*, *B. pratorum* and *B. pascuorum*, respectively).

Nectar volume measurements

The mean nectar volume per flower was 0.26 ± 0.03 μl (± SE), with a maximum of 1.83 μl in one flower; 28% of flowers contained no nectar when sampled. When these flowers are excluded, the mean volume per flower was 0.36 ± 0.03 μl. There was no significant difference in standing crop of nectar according to the number of inflorescences on the plant ($F_{1,119} = 0.024$).

Seed set

The proportion of seeds set differed between sites ($\chi^{22} = 24.4$, $P<0.01$), with highest seed set at site three and lowest at site one (means ± SE; 0.24 ± 0.024, 0.27 ± 0.017, 0.37 ± 0.027 for sites 1–3, respectively). Variation between sites accounted for 25.4% of the variation in seed set between plants. There were no significant interactions between factors, and none of the following contributed significantly to the model: number of inflorescences on the plant, number of inflorescences on neighbouring plants, the visitation rate of any bumblebee species, or the visitation rate of all bumblebee species combined. Overall the mean seed set was 1.18 seeds per flower, of a maximum possible of 4.

Discussion

Distributions of bee species

The three bee species differed markedly in their patterns of abundance and responses to variation in floral display. Numbers of each bee species visiting *S. officinale* plants varied greatly among sites within the study area. This may result from the proximity of nests of each species to each site. Bumblebees in Colorado exhibit powerful interspecific competition and competitive exclusion (Inouye 1978; Pyke 1982), but Ranta and Vepsäläinen (1981) found little evidence for competition among bumblebees in northern Europe and attribute coexistence of up to 11 species to spatio-temporal heterogeneity in nest distribution and floral resources.

Effects of plant size on bee recruitment

Response to variation in plant size differed between species, with *B. terrestris* the only species to show a clear increase in recruitment to large plants (Fig. 1) (this relationship is also significant but less marked for *B. pratorum*). The lack of any clear response in *B. pascuorum* but with highest recruitment to intermediate sized plants is both counter-intuitive and contrary to the findings of previous studies on other systems (Heinrich 1979; Schaffer and Schaffer 1979). The differences in the response of bumblebee species to variation in floral display are intriguing, since at a superficial level the three species appear to forage in a similar manner. In a previous study of pollinator recruitment, Dreisig (1995) combined data for *B. terrestris*, *B. hortorum* and *B. pascuorum* following the assumption that they all behaved in the same manner. From our data it appears that it may not be valid to treat bumblebee species as a behaviourally homogeneous group with regard to the foraging strategies that they adopt. Our data for *B. terrestris* must thus be treated with caution since the individuals observed may in fact have belonged to two species which are indistinguishable in the field (*B. terrestris* and *B. lucorum*).

Both theoretical argument and empirical data suggest that the presence of neighbouring conspecifics may have facilitative effects on pollinator recruitment (Rathcke 1983; Kunin 1993). However, we found that the number of inflorescences on neighbouring plants (within 1 m) had no effects on bee recruitment, although perhaps the scale used may have been too small. As bees are highly mobile, it may be that the number of inflorescences per site would be a more appropriate scale on which to examine overall recruitment to the area.

Effects of plant size on number of inflorescences visited per bee

The number of inflorescences visited on each plant by individual bees exhibited an increase in response to plant size in all three bee species (although the increase was not significant in *B. pascuorum*). However, the relationship does not appear to be either linear or proportional for any species. The number of inflorescences visited per bee increases very little across the range of 1–30 inflorescences per plant, with rather small increases above 31 inflorescences. These data suggest that individual bees visit a smaller proportion of the inflorescences on a plant as the number available increases. Departure from a plant is likely to occur when it becomes hard to locate unvisited inflorescences or as a response to visiting unrewarding inflorescences (Cresswell 1990; Kadmon and Shmida 1992). The frequency of empty flowers is high (28%). Observation of bumblebees suggests that their foraging behaviour consists of bouts of visits to groups of adjacent inflorescences interspersed by occasional longer flights of >0.5 m. On small plants these longer flights are bound to result in departure from the plant, whereas on large plants (which may be >1 m in diameter) several bouts of foraging interspersed with longer flights can occur within one plant. This may in part explain the observation that numbers of inflorescence visited per plant by each bee only increases substantially on large plants carrying more than 30 inflorescences.

For a self-incompatible plant, a shallow response to increasing size may be beneficial since prolonged foraging within large plants will result in pollen wastage, stigma clogging and/or ovule loss (Hessing 1988; Waser and Price 1991; de Jong et al. 1992). We did not quantify patterns of pollen deposition, but studies on other systems have found that the majority of pollen is deposited quickly. For example for *B. terrestris* foraging on *Brassica napus* the pollen picked up from a particular flower is mostly deposited on the first 4 flowers visited subsequently (Cresswell 1994; Cresswell et al. 1995). There is probably a small optimum number of flowers per plant beyond which cross-pollination does not increase but the bee continues to deplete nectar reserves. The high frequency of empty flowers may thus benefit the plants by promoting departure after only a few visits.

Effects of plant size on total numbers of inflorescences visited per plant

For *B. terrestris* and *B. pratorum*, the total number of inflorescences visited increases on larger plants (since these species both exhibit higher recruitment to large plants and visit more inflorescence per bee on larger plants). However, for all three bee species the proportion of inflorescences visited did not change significantly across the range of size of floral displays present. This is in accordance with previous work and suggests that bees' foraging strategies may approximate to an ideal free distribution with inflorescences on all plants visited at approximately equal rates resulting from the multiplicative effects of small increases in recruitment to large plants and small increases in numbers of inflorescence visited per bee.

The numbers of visits to inflorescences by *B. pascuorum* and *B. pratorum* appear to be positively correlated. Perhaps factors such as position or mean reward per inflorescence make particular plants more attractive to both species. Further research is required to explain this association.

Seed set

The relative importance of pollen versus resource limitation in determining seed set remains contentious (e.g. Stevenson 1981; Bierzychudek 1981; Wilson et al. 1994) but a recent review suggests that pollen limitation may be most common (Burd 1994). Our data show that seed set was not significantly affected by either bee recruitment or total numbers of visits per plant for any bee species. This suggests that pollinator abundance is not limiting seed set. However, seed set per flower was low, with an overall mean of 1.18 seeds per flower from a maximum of four. Since bees were very rarely observed to switch between *S. officinale* and other flowers, this reduction is unlikely to be due to improper pollen transfer (Rathcke 1983), so we tentatively conclude that seed set in this system may be limited by resources other than pollination.

In summary, the effects of floral display size on pollinator recruitment and their duration of stay within plants are complex, but in this study did not appear to determine seed set. Marked differences in the response of different bee species to variation in plant size require further investigation since they have no obvious explanation; experimental manipulation of floral display size may be informative. The causes of low seed set in this system despite an apparent abundance of pollinators may also prove to be a fruitful area for further study.

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