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The influence of relative plant density and floral morphological complexity on the behaviour of bumblebees

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Abstract We assessed the combined effects of varying the relative density and the relative floral morphological complexity of plant species on the behaviour of their bumblebee pollinators. Three species of bumblebee (*Bombus pascuorum*, *B. terrestris* and *B. hortorum*) were observed foraging on experimental arrays consisting of pair-wise combinations of four plant species: *Borago officinalis*, *Phacelia tanacetifolia* (both with simple flowers), *Antirrhinum majus* and *Linaria vulgaris* (both with complex flowers). Plant arrangements consisted of either two simple-flower species, a simple with a complex species or two complex species. The number of plants in each array was constant, while the frequency of each species was manipulated so that it was either rare, equal or common compared with its competitor. Contrary to predictions, rare plants were actually at an advantage in terms of the number of bees attracted per plant. However, rare plants were at a disadvantage in terms of pollen wastage because foragers more often went to a flower of another species after visiting a rare plant. The behaviour of bees on each plant species was further affected by plant floral complexity and the identity of the other species in the array. The three bumblebee species were markedly different in their foraging behaviour and in their responses to varying floral density and complexity. Each species preferred particular flower species. The results are discussed with reference to resource partitioning among bumblebee species.

Key words *Bombus* spp. · Foraging · Pollination · Resource utilisation · Visitation rates

Introduction

The effect of plant density on the behaviour of pollinators has been studied in natural plant populations (Allison 1990; Goulson et al. 1998), experimental arrays (Feinsinger et al. 1991; Kunin 1993, 1997; Karron et al. 1995) and using theoretical models (Rathcke 1983; Goulson 1994; Kunin and Iwasa 1996). It is believed that the efficiency of pollination of one plant species may vary according to the relative density of sympatric species which share the same pollinators (Levin and Anderson 1970; Inouye 1978; Feinsinger et al. 1991). Rathcke (1983) proposed that plants which occur at low densities receive low pollinator visitation. Furthermore, as plant density increases so does pollinator visitation up to a maximum level after which pollinators are saturated and visitation per plant decreases. Hence dense patches of plants attract many pollinators to the patch, but individual plants compete for pollinator visitation and so receive fewer visitors per plant than plants at lower densities. At very low density, plants are visited rarely and when they are, the pollen they receive is more likely to be heterospecific (Kunin 1993; Goulson 1994). Intraspecific competition between common plants causes a reduction in the 'quantity' of pollinators, whilst very rare plants receive poor-'quality' visits and rare plants also suffer from a decline in pollinator 'quantity' because of interspecific competition (Kunin and Iwasa 1996).

Pollinators tend to maximise their foraging efficiency by using more flowers per plant when plants are scarce compared to when they are common (Heinrich 1979a; Klinkhamer and de Jong 1993). This will cause increased within-plant pollen transfer in rare plants and may reduce fitness in obligate outcrossers (de Jong et al. 1993). Rare plants are therefore predicted to be at a disadvantage, and also their relative success in attracting pollinators is lowest when foragers are flower constant (Kunin 1993). Most pollinators exhibit some degree of floral constancy – foragers tend to visit flowers of one species overlooking other rewarding plant species

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(Grant 1950; Heinrich et al. 1977; De Los Mozos Pascual and Domingo 1991; Goulson et al. 1997).

Bumblebees (*Bombus* spp. Latreille, Hymenoptera, Apidae) are less conservative than other pollinators. They generally include several flower species in their foraging strategy and may visit rare plants during foraging bouts (Heinrich 1976a, 1979b). Bumblebees do not incur any loss of efficiency when switching among several species provided these species are relatively simple to handle (Lavery 1980). However, bumblebees tend not to switch between species if the handling skills required to extract rewards are too complex (Lavery 1980, 1994a; Gegear and Lavery 1995). A greater period of learning is required to locate and extract rewards from complex flowers, and handling times are generally greater on complex compared with simple flowers (Lavery 1994b).

Thus, the relative floral complexity of plant species in a mixed array may have profound effects on pollinator behaviour. The complexity of flowers may affect whether pollinators become specialists displaying flower constancy, or whether they visit more than one species as generalists. In the field experiments performed by Kunin (1993, 1997), simple flower species were chosen to manipulate pollinators to become generalists, specialists or mixed-strategy foragers in arrays with differing plant densities. Although these studies did not use complex flowers, the effects of floral complexity were considered in computer simulations carried out by Kunin and Iwasa (1996). They found that an increase in floral complexity was generally disadvantageous to plants regardless of density as it penalizes pollinators with increased handling times. To our knowledge there are currently no experimental data to support this theory.

Several species of bumblebee are common in southern England (Goulson et al. 1998) and they vary slightly in morphology (Alford 1975). Body size, head width and tongue length limit which species of bumblebee forage on which species of flower (Barrow and Pickard 1985). Partitioning of resources between different species of forager according to body morphology may affect visitation to flowers with different complexities and this too may be affected by floral density. Three species were observed in this study: *Bombus pascuorum* (Scopoli), a medium-sized bee with an average tongue length of 8.6 mm; *B. terrestris* (L.), a large bee with a relatively short tongue (averaging 8.2 mm) and large mandibles which it uses to make holes in flower corollas to rob nectar (Prys Jones and Corbet 1991), and *B. hortorum* (L.), a large bee with a long tongue of approximately 13.5 mm (Alford 1975; Prys Jones and Corbet 1991).

Here we investigate the importance of each of the following factors and their interactions on pollinator behaviour in experimental arrays:

- (a) plant species and floral complexity
- (b) relative plant density
- (c) floral complexity of the competing plant species (the other species in the array)
- (d) species of bumblebee.

Specifically, we test the following hypotheses:

- (1) Rare plants are at a disadvantage because (a) they attract fewer bees per plant per minute, (b) bees visit a higher proportion of the flowers available on rare plants, hence increasing geitonogamous (within-plant) pollen transfer and (c) rare plants are likely to suffer from high pollen wastage as pollinators are likely to depart to flowers of other species.
- (2) Floral morphological complexity affects bumblebee behaviour and different bumblebee species show preferences for specific plant types. This may result in resource partitioning.

Materials and methods

Study species

Four species of plant were chosen for this study on the basis of flower morphology, flowering phenology, attractiveness to bumblebees and ease of manipulation: *Borago officinalis* L. (Boraginaceae), *Phacelia tanacetifolia* Benth. (Hydrophyllaceae), *Antirrhinum majus* L. and *Linaria vulgaris* Mill. (both Scrophulariaceae). *B. officinalis* and *P. tanacetifolia* were designated 'simple' flower species due to their actinomorphic open flower structure. *A. majus* and *L. vulgaris* were designated 'complex' since both are zygomorphic, with closed corollas which have to be pushed open by foragers to access the nectaries. Nectar is concealed within a long spur at the base of the corolla in *L. vulgaris* flowers (Barrow and Pickard 1985).

Experimental arrays

Experimental plants were grown in 14-cm-diameter pots. Thirty-six plants were arranged in a triangular patch with approximately 25 cm between plants in the research gardens at the University of Southampton Research Centre at Chilworth (Hampshire, UK). Plant arrangements consisted of three different relative frequencies of two plant species, each plant species being 'common' (33 plants), 'equal' (18 plants) or 'rare' (3 plants) (Table 1). The combinations of flower species used were:

- (a) a simple and a complex species (*B. officinalis* and *A. majus*)
- (b) two simple species (*B. officinalis* and *P. tanacetifolia*)
- (c) two complex species (*A. majus* and *L. vulgaris*).

There were thus a total of nine different treatments (three frequencies \times three species combinations). As far as we could

Table 1 The plant arrangements used in this study

| | | | | Number of observation periods |
|---|---------|----------------------------|----------------------------------|-------------------------------|
| 1 | 3A:33B | 3 <i>Antirrhinum majus</i> | 33 <i>Borago officinalis</i> | 7 |
| 2 | 18A:18B | 18 <i>A. majus</i> | 18 <i>B. officinalis</i> | 7 |
| 3 | 33A:3B | 33 <i>A. majus</i> | 3 <i>B. officinalis</i> | 7 |
| 4 | 3B:33P | 3 <i>B. officinalis</i> | 33 <i>Phacelia tanacetifolia</i> | 6 |
| 5 | 18B:18P | 18 <i>B. officinalis</i> | 18 <i>P. tanacetifolia</i> | 8 |
| 6 | 33B:3P | 33 <i>B. officinalis</i> | 3 <i>P. tanacetifolia</i> | 5 |
| 7 | 3A:33L | 3 <i>A. majus</i> | 33 <i>Linaria vulgaris</i> | 5 |
| 8 | 18A:18L | 18 <i>A. majus</i> | 18 <i>L. vulgaris</i> | 7 |
| 9 | 33A:3L | 33 <i>A. majus</i> | 3 <i>L. vulgaris</i> | 5 |

establish, there were no other plants of these species within 500 m of the study site. Plants were randomly positioned within the patch and the sequence of plant arrangements on successive days was also random. The arrangement of plants in the patch was changed at 1200 hours each day. Observations of bumblebee visitation patterns were made between 0800–1200 hours and 1500–1900 hours on all dry days between 24 June and 15 August 1997 (56 observation periods in total, temperature range 18–28°C). The number and length of observation periods completed for each plant arrangement was variable, depending on the weather and the number of suitable plants available.

Of the three species of wild bumblebees observed foraging on the experimental patch (*B. pascuorum*, *B. terrestris* and *B. hortorum*), *B. pascuorum* was the most abundant. Each individual bumblebee observed foraging in the experimental array was marked on the dorsal surface of the thorax with acrylic paint (light blue, dark blue, light green, dark green, red, pink, white, light brown, orange, yellow) in different patterns to enable recognition of individuals. This was necessary to prevent pseudoreplication in behavioural analysis (Hurlbert 1984). We observed every bee that entered the plot and used those data to calculate visit rates per plant, but considered only the initial foraging bout of each individual to calculate the proportion of flowers visited and the proportion of departures to the same plant species (see data analysis below). Bumblebees were followed from their arrival at the patch and all flowers visited and movements between plants were recorded onto a dictaphone and later transcribed.

Data analysis

The total number of plants of each species visited in each observation period was divided by the total number of plants of that species available. This gave a single value of the mean number of visits per plant for each observation period. This value was then divided by the length of the observation period to give mean visits per plant per minute. These figures were analysed with Poisson errors in GLIM (Crawley 1993) according to plant species, plant species abundance, competitor plant species and bumblebee species (plus all interactions). This error structure was substantiated during analysis. Since we were using Poisson errors, critical values were compared with chi-squared values (Crawley 1993). Factors which did not contribute significantly to the model were removed in a stepwise manner.

For each individual bumblebee, the average number of flowers visited per plant was calculated for each plant species visited. This average was then analysed as a proportion of the average number of flowers available on those plants (using only the plants actually visited by the individual bee). Data were log-transformed to approximate a normal distribution and were then analysed with normal errors in GLIM as above.

The number of times a bumblebee departed from a flower and visited a flower of the same species and the total number of departures from flowers for each individual bumblebee were calculated. The proportion of departures to flowers of the same species was analysed with binomial errors with a logit link in GLIM as above. Since the ratio of the residual deviance to the residual degrees of freedom was lower than 1.5, the test statistics given are chi-squared values.

Results

A total of 225 *B. pascuorum*, 34 *B. terrestris* and 53 *B. hortorum* individuals were observed.

Visit rate per plant

Three two-way interactions and all the individual factors had a significant effect on the number of visits per plant

per minute (Table 2). The plant species received significantly different numbers of visits per plant, with *B. officinalis* plants receiving most visits (visits per plant per hour for *B. officinalis* = 0.33, *A. majus* = 0.19, *P. tanacetifolia* = 0.15 and *L. vulgaris* = 0.17). Plant abundance also influenced visitation: rare plants received significantly more visits per plant than more abundant ones (visits per plant per hour for rare plants = 0.31, equal = 0.20, common = 0.17). The identity of the competing species also influenced visitation: plants which had *P. tanacetifolia* as the competitor received the most visits (visits per plant when *P. tanacetifolia* is competitor = 0.30, while the corresponding values with the other three species as competing species were 0.13, 0.28 and 0.28 for *B. officinalis*, *A. majus* and *L. vulgaris*, respectively). However, the single factor which explained most variation in the number of visits per plant per minute was the species of bumblebee. There were more *B. pascuorum* attracted per plant per hour than the other two bee species (visits per plant per hour by *B. pascuorum* = 0.48, *B. terrestris* = 0.09 and *B. hortorum* = 0.11).

There was a significant interaction between the species of bee and the three factors plant species, plant abundance and competitor species (Table 2). Different bee species preferred different plant species (Fig. 1): *B. pascuorum* and *B. terrestris* made most visits to *B. officinalis*, while *B. hortorum* visited *A. majus* more often than the other plant species. Each bee species was also affected differently by plant density (Fig. 2), *B. pascuorum* and *B. hortorum* made more visits (per plant) to rare plants, whilst *B. terrestris* made more visits to plants when they were in equal abundance to their

Table 2 Factors affecting the number of visits per plant per minute

| Factor | df | χ^2 |
|------------------------------------------------|----|----------|
| Plant species | 2 | 9.4** |
| Plant species abundance | 2 | 10.3** |
| Competitor plant species | 2 | 9.7** |
| Bumblebee species | 2 | 107.2*** |
| Plant species and bumblebee species | 4 | 43.7*** |
| Competitor plant species and bumblebee species | 4 | 39.4*** |
| Plant abundance and bumblebee species | 4 | 39.4*** |

** $P < 0.01$; *** $P < 0.001$

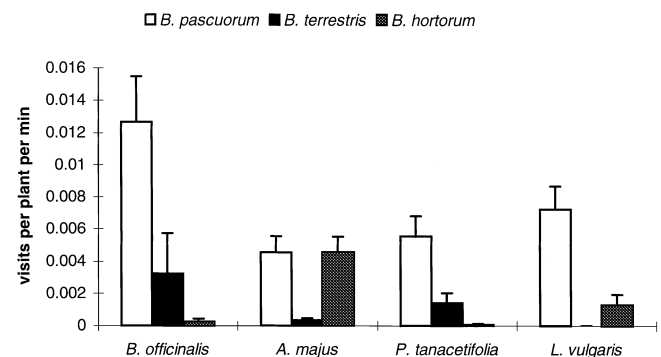


Fig. 1 The mean number of bees of each *Bombus* species attracted to each plant species per plant per minute (+SE)

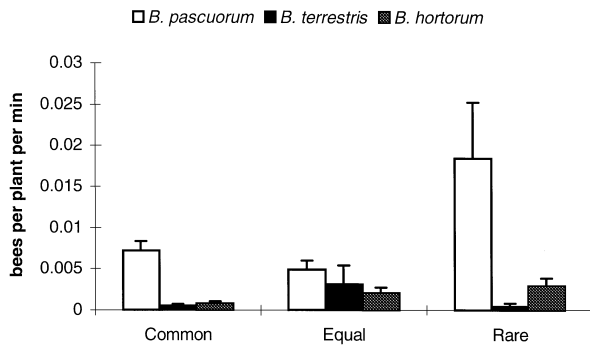


Fig. 2 The mean number of bees of each species visiting each plant per minute according to plant abundance (+SE)

competitors. Different bee species were also affected by the identity of the competing plant species. Simple *B. officinalis* plants received more *B. pascuorum* visits when in an array with the other simple species *P. tanacetifolia*, but received more *B. terrestris* visits when in an array with the complex species *A. majus* (Fig. 3a). *A. majus* received similar numbers of visits from *B. terrestris* and *B. hortorum* regardless of the competitor,

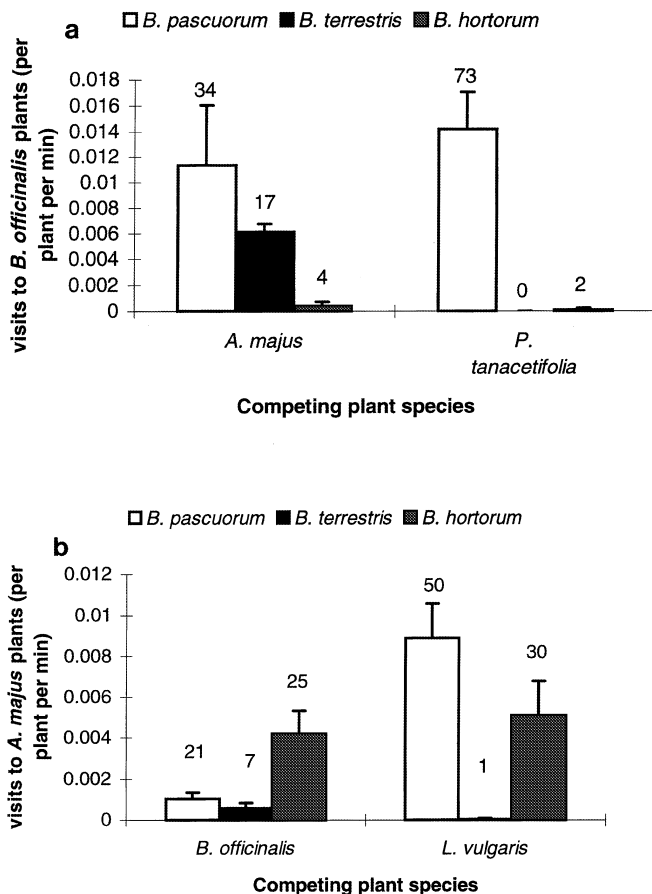


Fig. 3 The mean number of visits by bees of each species per plant to simple (a) and complex (b) plants (per plant per minute) according to the competing plant species (+SE). Numbers above bars represent sample sizes

but received more visits from *B. pascuorum* when with the other complex species *L. vulgaris* (Fig. 3b).

Proportion of flowers visited per plant

Each plant species had different numbers of flowers open at any one time. *B. officinalis* had an average of 4.6 flowers open per plant, *A. majus* 12.2, *P. tanacetifolia* 12.8 and *L. vulgaris* 19.9. Only plant species and competitor species had a significant influence on the proportion of flowers visited per plant (plant species: $F_{2,312} = 24.75$, $P < 0.001$ and competitor plant species; $F_{2,312} = 3.78$, $P < 0.05$). The proportion of flowers visited per plant was highest on *P. tanacetifolia* (proportion of flowers visited per plant on *P. tanacetifolia* = 0.77, *B. officinalis* = 0.50, *A. majus* = 0.25 and *L. vulgaris* = 0.20). The proportion of flowers visited per plant on *B. officinalis* was higher when these plants were in an array with the other simple plant species *P. tanacetifolia* than with the complex species *A. majus* (Table 3). However the proportion of flowers visited per *A. majus* plant was the same regardless of the competitor.

Proportion of departures to flowers of the same species

Two two-way interactions and all the individual factors had a significant effect on the proportion of departures to flowers of the same species (Table 4). The proportion of departures to conspecific flowers was significantly different for each plant species (proportion of departures to flowers of the same species: *B. officinalis* = 0.93, *A. majus* = 0.89, *P. tanacetifolia* = 0.82 and *L. vulgaris* = 0.75) and at each abundance (proportion of departures to conspecifics: rare plants = 0.77,

Table 3 The average proportion of flowers visited per plant on each plant species in each plant array

| Simple/complex | <i>B. officinalis</i> | <i>A. majus</i> |
|-----------------|-----------------------|-------------------------|
| | 0.465 | 0.242 |
| Simple/simple | <i>B. officinalis</i> | <i>P. tanacetifolia</i> |
| | 0.602 | 0.397 |
| Complex/complex | <i>A. majus</i> | <i>L. vulgaris</i> |
| | 0.255 | 0.175 |

Table 4 Factors affecting the proportion of departures to flowers of the same species

| Factor | df | χ^2 |
|------------------------------------------------|----|----------|
| Plant species | 2 | 23.4*** |
| Plant species abundance | 2 | 26.0*** |
| Competitor plant species | 2 | 15.7*** |
| Bumblebee species | 2 | 7.7* |
| Plant species and bumblebee species | 3 | 9.8* |
| Competitor plant species and bumblebee species | 3 | 9.5* |

* $P < 0.05$; *** $P < 0.001$

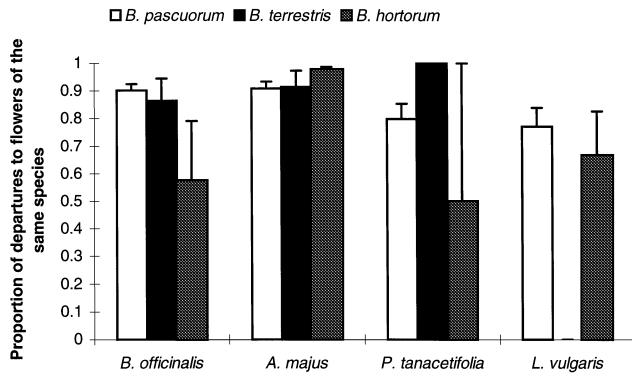


Fig. 4 The mean proportion of departures to conspecific flowers by bumblebees of each species on plants of each species (+SE)

equal = 0.85 and common = 0.95). Competing species also affected the proportion of departures to conspecifics: bees made more departures to conspecifics when *L. vulgaris* was the competing species. Since *A. majus* was the only species to occur in an array with *L. vulgaris*, most departures to conspecifics occurred on *A. majus* when it was with the other complex species *L. vulgaris* (proportion of departures when *L. vulgaris* was the competing species = 0.92, while the corresponding values with the other three species as competitor are 0.88, 0.86 and 0.85 for *B. officinalis*, *A. majus* and *P. tanacetifolia*, respectively).

Each bee species behaved in a significantly different manner: *B. pascuorum* individuals visited consecutive flowers of the same species on average less than the other two bee species (proportion of departures to flowers of the same species by *B. pascuorum* = 0.87, *B. terrestris* = 0.91 and *B. hortorum* = 0.90). Furthermore, each bumblebee species behaved differently according to plant species visited (Fig. 4) and competing plant species. Generally, departures to conspecifics increased when plants were with species dissimilar in terms of floral complexity. For example, *B. pascuorum* departed to conspecifics of *B. officinalis* more often when this plant was in an array with the complex species *A. majus* than when it was in an array with the simple species *P. tanacetifolia* (Fig. 5a). In addition, the proportion of departures by *B. pascuorum* from the complex species *A. majus* to flowers of the same species was higher when *A. majus* was with the simple species *B. officinalis* compared to when it was in an array with the complex species *L. vulgaris* (Fig. 5b).

Discussion

Bumblebee species, plant abundance, plant species and competing species all had an effect on the number of visits per plant and the proportion of departures to flowers of the same species. Plant species and competing species influenced the number of flowers visited per plant. Bumblebee species was also an important inter-

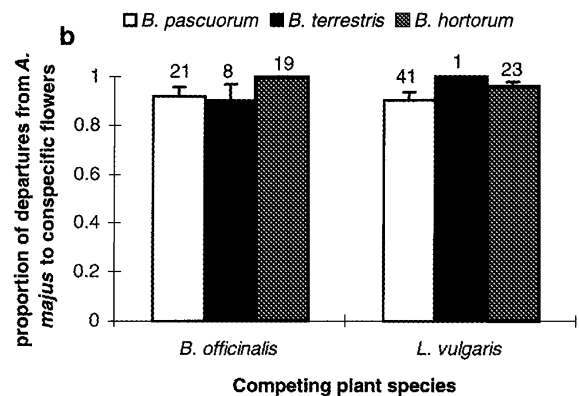
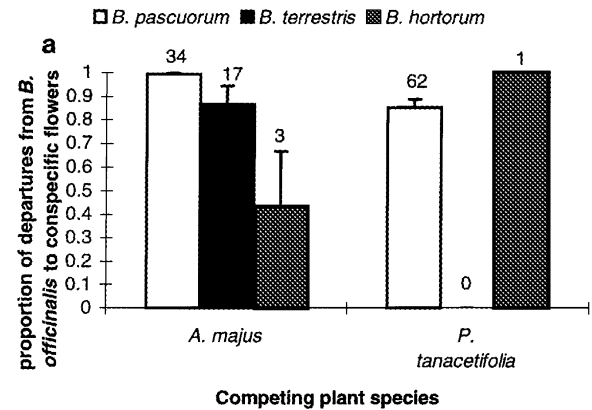


Fig. 5 The mean proportion of departures to conspecific flowers by bumblebees of each species on simple plant species (a) and complex plant species (b) according to the competing plant species (+SE). Numbers above bars represent sample sizes

active factor influencing visitation per plant and the probability of departure to conspecifics. Contrary to the predictions made by Kunin and Iwasa (1996), there were no interactions between the complexity of a flower species and its abundance on the attraction and behaviour of bumblebees.

Bee species

Bumblebee species differed markedly in visitation rates and flower constancy. There were significant interactions with plant species, plant abundance and competitor species which affected visitation and constancy. The three bumblebee species behaved differently towards the four plant species. *B. pascuorum* individuals have a medium-length tongue and a small body size and generally visit a wider range of flower species, and this may account for the fact that this was the only species which regularly visited all four plant species. *B. terrestris* on the other hand is a short-tongued bee more suited to the short open corollas of *B. officinalis* and *P. tanacetifolia*. *B. terrestris* was occasionally seen to visit *A. majus*,

where it inserted its whole body into the flower corolla. However, this bumblebee species could not reach the nectar in the long spur of *L. vulgaris* and was never seen to visit this plant species during observational periods. *B. hortorum* individuals have the longest tongues of any common bumblebees in Britain, and are clearly suited to collecting nectar from *L. vulgaris*. *B. hortorum* was rarely seen visiting the simple flowers of *B. officinalis* and *P. tanacetifolia*, although when this bee species did visit the simple plants, it preferred *B. officinalis* over *P. tanacetifolia*. *B. hortorum* regularly visited *A. majus* and *L. vulgaris*. It is possible that *B. hortorum* with its very long tongue is less efficient than the shorter-tongued species when foraging on simple open flowers and so is displaced. This has been shown for long-tongued bumblebees (*B. appositus*) in North America (Graham and Jones 1996). Alternatively, *B. hortorum* may have had no need to visit *B. officinalis* and *P. tanacetifolia* because it could exploit flowers with a longer corolla which the short-tongued bees could not use.

Interspecific variation in resource use among bee species which differ in tongue length has been shown in bumblebee species in North America (Heinrich 1976b; Inouye 1978; Pyke 1982; Graham and Jones 1996) and Scandinavia (Ranta and Vepsäläinen 1981; Ranta et al. 1981). There seems to be a similar pattern of interspecific variation in the three species of our study, although we also found considerable overlap. Bumblebee species have been shown to utilise different plant species in the UK (Brian 1951, 1957; Fussell and Corbet 1993). In addition to the influence of tongue length on flower choice, it has been suggested that preferences may be due to physiological differences between bumblebee species (Newsholme et al. 1972; Prys-Jones 1986). Bumblebees need to maintain a high body temperature (Heinrich 1975), and this is partly achieved through the energy-releasing biochemical cycle that generates heat in the flight muscles without muscle contraction. The activity of fructose biphosphatase, an enzyme in this biochemical cycle, differs between bumblebee species (Prys-Jones and Corbet 1991). Bumblebees with high enzyme activity readily generate heat without contraction of the flight muscles and thus need to fly less frequently to maintain a high body temperature. *B. terrestris* individuals have a relatively high level of enzyme activity and can afford to spend little time flying, and forage on flowers which are clumped on an inflorescence (Prys-Jones 1986). *B. hortorum* have a low enzyme activity and fly between flowers more often in order to maintain a high body temperature. *B. pascuorum* have an enzyme activity lower than *B. terrestris*, but higher than *B. hortorum*. The flowers of *P. tanacetifolia* are clumped on inflorescences and were visited mostly by *B. terrestris* and *B. pascuorum* individuals which were rarely observed to fly between flowers on the same inflorescence. However *B. hortorum* rarely visited these clumped flowers and preferred those of the other species, requiring the bees to fly from one to another.

As well as enzyme activity, physiological differences among species in terms of carbohydrate requirements may cause species-specific flower choice. Flowers upon which bees forage generally produce nectar with higher sugar concentrations than flowers which other pollinators visit (Cruden et al. 1983), and there may also be differences in flower choice according to sugar concentration at the species level. Another difference in flower choice among bumblebee species may be attributed to whether bees are more inclined to collect pollen or nectar or both. *B. pascuorum* and *B. hortorum* individuals are more likely to collect both pollen and nectar when both are available than are *B. terrestris* individuals (Brian 1957). Differences in pollen and nectar yields of each of the plants studied may have affected the number and species of bees attracted. The collection of pollen and/or nectar was not easy to distinguish, except on *B. officinalis* when the bumblebees were seen to 'buzz' for pollen (King 1993). Hence, the collection of nectar and/or pollen by each individual was not recorded in this study.

Plant abundance

Overall rare plants were at an advantage in terms of pollinator visitation, but were at a disadvantage in terms of pollen wastage to heterospecific plants because bees more often visit a heterospecific flower after a flower of a rare species. This would result in more pollen being wasted on heterospecific flowers as most pollen is likely to be deposited on the first few flowers visited (Cresswell et al. 1995). Previous investigations into flower choice by bumblebees have found that bees preferentially visit common flower types (Real 1990; Smithson 1995). Common plants received fewer visits per minute possibly because individual plants are in competition with each other for pollinator visitation, even though a large array of a single species of plants can attract, support and share pollinators by a process of facilitation (Levin and Andersson 1970; Rathcke 1983).

Plant species and floral complexity

Different species received different levels of pollinator visitation, the proportion of flowers visited per plant were different and pollinator constancy varied among plant species. In contradiction to Kunin and Iwasa (1996) who predicted that complex plants were always at a disadvantage, we found that although complex plants received fewer pollinator visits per plant than one of the simple species, *B. officinalis*, they received more visits per plant than the other simple species, *P. tanacetifolia*. Complex plants were also at an advantage in terms of outcrossing because pollinators visited a smaller proportion of flowers per plant than they did on simple plants. However, the complex species had more flowers

per plant and this may have influenced this result. In terms of the proportion of departures to conspecific flowers, bees were more flower constant when foraging on complex *A. majus* than all the other species, and least flower constant when foraging on the other complex species *L. vulgaris*. Low floral constancy on *L. vulgaris* is contrary to expectation because, according to accepted theories, once a bee has learnt the handling skills for a complex plant it is more likely to remain constant (Laverty 1994a). The low floral constancy on *L. vulgaris* requires further investigation.

Different levels of rewards (both nectar and pollen) in different plant species may also affect visitation rates, the number of flowers pollinators visit and whether foragers then depart to a flower of the same species or not (Goulson et al. 1997). Rewards may differ between simple and complex flowers which may also affect their relative success. Kunin and Iwasa (1996) showed in their model that the disadvantages of complexity disappeared when rewards were augmented in rare plants. Preliminary investigations into nectar levels in the flowers used in this study suggested that nectar rewards did not differ greatly between the four species (J.C Stout, unpublished data).

Competing plant species

There were significant effects of the competitor on pollinator visitation, proportion of flowers visited per plant and constancy. Plants received a higher level of pollinator visitation in arrays with similar plant species. For example *B. officinalis* attracted a higher number of pollinators when in an array with another simple plant species and *A. majus* received more visits per plant when in an array with another complex plant species. Similar plant species therefore facilitated each other's pollinator visitation. This agrees with the predictions of Bobisud and Neuhaus (1975) that flowering plants which occur with similar plants are at an advantage in terms of pollinator visitation over plants which occur with dissimilar plants. When *B. officinalis* and *A. majus*, which have flowers of very different shapes, were in a mixed array, they competed for visitation. The simple species *B. officinalis* attracted more pollinators.

However, bees were more flower constant when plants were in arrays with dissimilar species. When plants were with similar species their pollinators moved between flower species more often. This trend was especially obvious when arrays consisted of two simple plant species. The decline in flower constancy displayed by foragers when plants are with similar species may be more detrimental to plants by reducing seed set than the decline in pollinator visitation when plants are with dissimilar species (Kunin 1993). Thus, while plants receive increased pollinator visitation when they occur with similar-flowered plants, they may receive more heterospecific pollen.

Conclusions

The effects of differences in floral morphology and changes in plant density on the behaviour of bumblebees are complex. Bumblebee species exhibited distinct behavioural patterns on each plant species and were affected by plant abundance in different ways. Grouping bumblebee species together for analysis may be misleading, as bumblebee species forage in different and distinct manners. Rare plants which are usually considered to be at a great disadvantage may not always be so badly off in terms of pollinator visitation. They may, however, be at a disadvantage in terms of pollen removal to heterospecifics and deposition of heterospecific pollen. Indeed, preliminary studies of pollen grains on stigmas of plants in these arrays suggested that rare plants do receive a higher proportion of heterospecific pollen (J.C. Stout, unpublished data). The mechanisms underlying the complex behavioural patterns observed here remain unresolved and require further investigation. Are differences in behaviour due to physiological constraints or to differences in resource quality among flower species or are they due to competition? We are currently working on the effects of the exclusion of (potentially) competing bee species on foraging behaviour to test whether the patterns described here were in part due to interspecific competition between bees.

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