

Foraging bumblebees avoid flowers already visited by conspecifics or by other bumblebee species

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Abstract. Honey bees, *Apis mellifera*, use short-lived repellent scent marks to distinguish and reject flowers that have recently been visited by themselves or by siblings, and so save time that would otherwise be spent in probing empty flowers. Conversely, both honey bees and bumblebees, *Bombus* spp., can mark rewarding flowers with scent marks that promote probing by conspecifics. We examined detection of recently visited flowers in a mixed community of bumblebees foraging on comfrey, *Symphytum officinale*, in southern England. When foraging among inflorescences on a plant, three abundant species of *Bombus* probed fewer inflorescences more than once than would be expected from random foraging. Bees frequently encountered inflorescences but departed without probing them for nectar. Examination of the incidence of such rejections in the two most common species, *B. terrestris* and *B. pascuorum*, revealed that the low incidence of multiple probing visits was due to two factors: bees both foraged systematically and selectively rejected inflorescences that they had previously visited. When presented with inflorescences of known history, bees selectively rejected those that had been recently visited by themselves or by conspecifics compared with randomly selected inflorescences. They were also able to distinguish inflorescences that had been visited by other *Bombus* species. Bees were unable to distinguish and reject inflorescences from which the nectar had been removed artificially. We conclude that these *Bombus* species are probably using scent marks left by previous visitors. The significance of deposition and detection of interspecific scent marks for competitive interactions between species is discussed.

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Honey bees, *Apis mellifera*, and bumblebees, *Bombus* spp., have become a popular vehicle for examining the assumptions and predictions of foraging models and the interplay between learning, memory constraints and foraging efficiency in a complex and unpredictable environment (e.g. Heinrich 1979; Wells & Wells 1986; Cresswell 1990; Wells et al. 1992; Dukas & Real 1993a, b, c; Dreisig 1995; Menzel & Muller 1996). Both honey bees and bumblebees learn quickly, and can use scent, colour, shape or a combination of all three to identify flower species that previously provided a reward; they also learn handling skills appropriate to flower structures, so that foraging efficiency increases with age and with experience (Koltermann 1969; Menzel & Erber 1978; Laverty

1980; Barth 1985; Laverty & Plowright 1988; Giurfa & Núñez 1992a; Menzel et al. 1993; Laverty 1994a, b).

There is considerable evidence that both bumblebees and honey bees can distinguish between rewarding and non-rewarding flowers of the same species without sampling the reward available. They may hover in front of a flower, sometimes briefly touching the corolla, and then depart without probing into the flower structure. These rejected flowers contain, on average, less nectar than flowers that are probed (Heinrich 1979; Corbet et al. 1984; Wetherwax 1986; Kato 1988; Duffield et al. 1993). Several mechanisms may be in operation. Bees can assess pollen content of open flowers visually (Zimmerman 1982), and may be able to determine the nectar content of some flower species in the same way (Thorpe et al. 1975, 1976; Kevan 1976). They may also be able to assess nectar volumes from the scent of the nectar itself or of fermentation

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products from yeasts in the nectar (Crane 1975; Heinrich 1979; Williams et al. 1981), or from humidity gradients surrounding the flower (Corbet et al. 1979). Although these possibilities have not been excluded, there is mounting evidence that a primary cue to whether bees probe or reject flowers is given by scent marking left by the same insect or by conspecifics on previous visits (Cameron 1981; Free & Williams 1983; Marden 1984; Kato 1988; Schmitt & Bertsch 1990; Giurfa 1993). Such markings are postulated to increase foraging efficiency by reducing time spent handling unrewarding flowers (Kato 1988; Schmitt & Bertsch 1990).

It appears that both attractant and repellent scent marks may be in operation. Honey bees leave short-lived repellent marks on recently visited flowers which deter both themselves and individuals from the same colony from probing recently emptied flowers, and thus promote systematic foraging (Núñez 1967; Wetherwax 1986; Giurfa & Núñez 1992b; Giurfa 1993; Giurfa et al. 1994). There is little convincing evidence for use of repellent scent marks by bumblebees (see Schmitt & Bertsch 1990). Conversely, both honey bees and bumblebees can leave scent marks on rewarding flowers that are attractive to themselves and to conspecifics, and thus concentrate subsequent foraging bouts on rewarding flowers only (Ferguson & Free 1979; Kato 1988; Schmitt & Bertsch 1990). In bumblebees the chemical cue is secreted from the tarsi (Schmitt et al. 1991).

Guilds of sympatric bumblebee species with similar habitat requirements are common throughout the temperate zones of the northern hemisphere, stimulating classic studies of competition in Colorado (Inouye 1978; Pyke 1982). In southern Britain various combinations of five or more species can frequently be observed foraging together (D. Goulson, personal observation). Although there are differences between species in tongue length and corresponding differences in flower preferences (Brian 1957; Hobbs et al. 1961; Hobbs 1962; Medler 1962; Prys-Jones & Corbet 1987), many nectar and pollen-rich plants are visited simultaneously by several bee species. Also, several of the abundant species in this region (particularly *Bombus terrestris* (L.), *B. lucorum* (L.) and *B. lapidarius* (L.)) all have tongues of similar length (Alford 1975; Prys-Jones & Corbet 1987). To our knowledge no study has examined whether scent marking occurs in such guilds, and

whether bumblebees can detect scent marks left by other species within the guild.

We examined foraging behaviour of bumblebee species on a shared nectar resource. We assessed whether bumblebees were systematic in their searching of inflorescences on a single plant, and whether the observed pattern of foraging within the inflorescences on a plant was due to non-random searching or remote detection of inflorescences that had already been visited. We then tested whether bees were able to discriminate flowers that they, and conspecifics, had recently visited from those that they had not. Finally, for the two most abundant species, *B. terrestris* and *B. pascuorum* Scopoli, we tested whether each species can detect flowers that have been previously visited by an individual of the other species.

We studied bees foraging on comfrey, *Symphytum officinale* L. (Boraginaceae). This is a nectar-rich herbaceous perennial native to the U.K., and usually found in damp places particularly near rivers and streams (Clapham et al. 1987). At the study site, the dominant visitors were the bumblebees *B. terrestris* and *B. pascuorum*, with smaller numbers of *B. pratorum* (L.) and *B. lapidarius* (we cannot be certain that some workers identified as *B. terrestris* were not *B. lucorum*, since the two can be indistinguishable even after dissection). All species were primary or secondary nectar robbers; the vast majority of open flowers had been perforated close to the nectary. Of the four species of bee, only *B. terrestris* is known to make such holes (Prys-Jones & Corbet 1987), but all four species used them for nectar extraction.

METHODS

We conducted experiments in June and July 1996 in grass and shrub land near the River Itchen in the Itchen Valley Country Park, Southampton, Hampshire, and used only worker bees since queens and drones were scarce.

Foraging Pattern

To determine if bumblebee visits to inflorescences were random (or whether bees avoided visiting inflorescences they had previously visited on the same foraging bout), we recorded the pattern of visits to the inflorescences on a plant by

a single bee, from the bee's arrival on the plant to its departure. *Symphytum officinale* plants support a variable number of inflorescences (8–177 in this study). Each inflorescence is made up of approximately 20 flowers, with up to six open at any one time (usually one or two). Visits to individual flowers within an inflorescence could not be accurately recorded without disturbing the bee. We marked the route of each bee on a map of the inflorescences on each plant and noted any inflorescences that were visited more than once. We recorded a visit only if the bee landed and probed for nectar (either from the top of a flower, or by feeding from a hole at the base of the flower), thus excluding instances in which a bee approached an inflorescence but departed without probing for nectar (rejections). A preliminary study of 50 individual bees of three species (28 *B. terrestris*, 15 *B. pascuorum* and 7 *B. pratorum*) revealed strong evidence for non-random visits of inflorescences on a plant (i.e. avoidance of previously visited inflorescences: see Results).

This pattern could be due to a systematic search pattern, an ability to remember which inflorescences had recently been visited, or an ability to sense and reject inflorescences that had recently been visited (e.g. by scent). In an attempt to determine the mechanism involved, we repeated the study, concentrating on the two most abundant species, *B. terrestris* (30 individuals) and *B. pascuorum* (35 individuals) and recording both visits to and rejection of inflorescences separately. A rejection was defined as an approach to within 1 cm of an inflorescence followed by departure without probing.

We analysed the data by comparing the numbers of visits to each inflorescence (0, 1 or >1) with the expectation for a Poisson distribution of random visits. The mean of this distribution was taken to be the total number of visits by each bee to each plant divided by the number of inflorescences available on the plant. For example if a bee made 30 visits to a plant carrying 67 inflorescences (mean visits per inflorescence=0.45), we expect 19.2 inflorescences to be visited once only, and 5.0 to be visited more than once. We compared the observed and expected number of multiple visits to the same inflorescence using Wilcoxon's signed-ranks test.

We followed a similar procedure for foraging patterns where both visits and rejections were

recorded; the probability of each event was calculated, and expected frequencies obtained by assuming that visits to inflorescences and rejection of inflorescences were independent events (essentially a null hypothesis). We then used Wilcoxon's signed-ranks tests to compare the observed and expected frequencies of multiple encounters (using a single observed value for each individual bee), and to compare the expected and observed frequencies of rejection of inflorescences that had previously been visited.

Discrimination of Recently Visited Inflorescences

To assess whether bumblebees are able to discriminate between inflorescences that had been recently visited by themselves, conspecifics or other *Bombus* species compared with randomly selected inflorescences, we performed a series of trials in which naturally foraging bees were presented with inflorescences and their response recorded. We picked the inflorescence under test together with a short stem, and held it in the anticipated flight path of a bee. Since bees tend to move between adjacent inflorescences we held the test inflorescence next to another being probed for nectar by the chosen bee so that it was encountered by the bee as soon as it moved on. Recordings were not made if the bee departed from the previous inflorescence in a direction such that it did not encounter the inflorescence under test. Once encountered, bees either probed the inflorescence or rejected it. We carried out five experiments concurrently as follows: (1) presentation of randomly selected inflorescences to *B. terrestris* (107 trials) and to *B. pascuorum* (54 trials; the recent history of visits to these inflorescences was unknown); (2) presentation to *B. terrestris* of an inflorescence that had been visited by the same individual within the previous 2 min (91 trials); (3) presentation to *B. terrestris* of an inflorescence that had been visited by a conspecific within the previous 2 min (89 trials); (4) presentation to *B. terrestris* of an inflorescence that had been visited by *B. pascuorum* within the previous 2 min (90 trials); (5) presentation to *B. pascuorum* of an inflorescence that had been visited by *B. terrestris* within the previous 2 min (81 trials). Two minutes was chosen as the maximum time between visits because it provided sufficient time in which to locate another bee and carry out a trial.

Manipulation of Nectar Volume

To determine if bumblebees can detect nectar levels in flowers directly (i.e. not using scent marks), but without probing the flower, we manipulated nectar levels in inflorescences before presenting them to bees as above. We first covered inflorescences with fine netting for 1 h to exclude visiting insects. This period allowed nectar to accumulate and we assumed that it gave time for any short-acting scent marks to dissipate. Subsequently we removed the inflorescences and either presented them immediately to foraging bees or first removed the nectar before presentation. We removed nectar using a drawn-out glass capillary tube inserted in the nectary of each flower (with this procedure we cannot be certain that all nectar was removed). This was repeated for 56 inflorescences presented to *B. terrestris* (26 without nectar and 30 with nectar) and for 58 inflorescences presented to *B. pascuorum* (33 without nectar and 25 with nectar).

We cannot rule out the possibility that some individual bees were assessed on more than one occasion. Since the local population of all three species was large, however, we suggest that this was a rare event. To minimize the likelihood of repeated presentations to the same individuals, observations were alternated between species and were taken at a range of different sites within the study area. Each inflorescence was used only once.

RESULTS

Foraging Pattern

The preliminary study of the foraging pattern of 50 individual bees of *B. terrestris*, *B. pascuorum* and *B. pratorum* suggests that mechanisms are in operation to reduce multiple visits to the same inflorescence. Every one of the 28 *B. terrestris*, 15 *B. pascuorum* and 7 *B. pratorum* studied visited fewer inflorescences more than once than would be expected from a pattern of random foraging (Wilcoxon signed-ranks test: $T=0$, $N=28$, $P<0.001$; $T=0$, $N=15$, $P<0.001$; $T=0$, $N=7$, $P<0.05$, respectively).

Examination of the incidence of rejection of inflorescences by a further 65 bees of the two most common species (30 *B. terrestris* and 35 *B. pascuorum*) demonstrates that the low incidence

of repeated probing visits to the same inflorescence was because the incidence of rejection of inflorescences that bees had already visited was higher than expected (compared with a pattern of random acceptance/rejection of flowers; Wilcoxon signed-ranks test based on observed and expected values for individual bees: $T=12$, $N=30$, $P<0.001$ and $T=22$, $N=35$, $P<0.001$ for *B. terrestris* and *B. pascuorum*, respectively). No bee was observed to reject an inflorescence on first encountering it and to accept it on a later encounter. Overall, *B. terrestris* rejected 15 of 19 inflorescences when encountering them for the second time compared with only 21 of 156 rejections on the first encounter. The corresponding figures for *B. pascuorum* are 14/22 and 56/190, respectively.

There was also evidence for systematic searching of the plants resulting in a low incidence of multiple encounters (visits and rejections combined) compared with the expected value for a strategy of random foraging (Wilcoxon signed-ranks test: $T=86$, $N=30$, $P<0.005$ and $T=57$, $N=35$, $P<0.001$ for *B. terrestris* and *B. pascuorum*, respectively).

It is notable that the proportion of inflorescences visited on each plant (of the total number available) was low (23, 30 and 16% for *B. terrestris*, *B. pascuorum* and *B. pratorum*, respectively).

Discrimination of Recently Visited Inflorescences

Bees rejected 29% (*B. terrestris*) and 33% (*B. pascuorum*) of randomly selected inflorescences, the remaining inflorescences being probed for nectar. It is important to note that these inflorescences might have been visited recently by another bee. In contrast, the frequency of visits to inflorescences that had definitely been visited (either by the same bee, a conspecific or another species) was consistently lower (Fig. 1). Comparisons of the frequency of rejection of randomly selected inflorescences with those previously visited by bees reveal that this difference is consistently significant (Table I), with overall 78% of inflorescences being rejected when they had just been visited by another bee. There was no difference in the frequency with which individuals of *B. terrestris* rejected inflorescences visited by themselves compared with those visited by conspecifics ($\chi^2_1=1.41$, NS); however, the strength

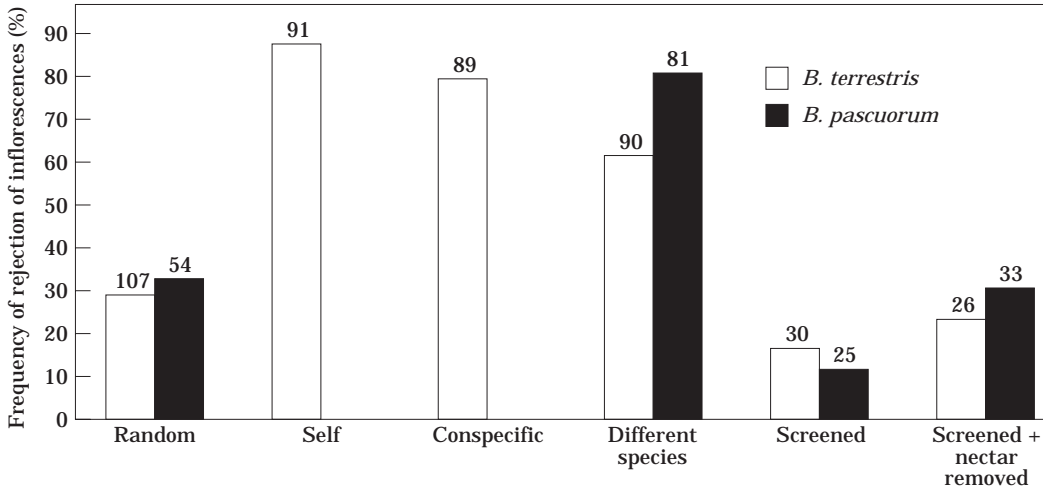


Figure 1. Frequency of rejection of inflorescences when presented to foraging bumblebees, according to the history of the inflorescence; random: chosen at random from the area in which the bees were foraging; self: previously visited by the same bee; conspecific: previously visited by a conspecific; different species: previously visited by a different species of *Bombus*; screened: inflorescence screened from insect visitors for 1 h; screened+nectar removed: as previous treatment but nectar removed from flower before presentation. Sample sizes above the bars refer to the number of trials. The frequency of rejection of inflorescences by *B. pascuorum* was not examined for the categories 'self' or 'conspecific'.

Table I. Chi-square comparisons (with Yates' correction) of the proportion of inflorescences rejected by foraging bees to assess whether bees are able to distinguish between inflorescences that have been recently visited versus inflorescences chosen at random ($df=1$)

Inflorescence	Test bee	
	<i>B. terrestris</i>	<i>B. pascuorum</i>
Visited by same bee versus random	37.6**	—
Visited by conspecific versus random	25.1**	—
Visited by other species versus random	9.1*	18.6**

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

of the response appeared to differ between inflorescences visited by conspecifics (including themselves) versus *B. pascuorum*, with more rejections of inflorescences visited by conspecifics ($\chi^2_1 = 11.14$, $P < 0.001$). Also, *B. pascuorum* were more likely to reject inflorescences visited by *B. terrestris* than *B. terrestris* were to reject inflorescences visited by *B. pascuorum* ($\chi^2_1 = 4.86$, $P < 0.05$).

Manipulation of Nectar Volume

Rejection of inflorescences that had been screened from insects for 1 h was consistently low for both bee species (overall 19.6%; Fig. 1). There was no evidence that bees were able to distinguish inflorescences that contained nectar from those that had been emptied of nectar ($\chi^2_1 = 0.01$, NS and $\chi^2_1 = 0.40$, NS for *B. terrestris* and *B. pascuorum*, respectively).

DISCUSSION

Nectar rewards between flowers are highly heterogeneous and unpredictable over time since flowers are emptied at unpredictable intervals by visiting insects (Real & Rathcke 1988; Cresswell 1990; Waser & Mitchell 1990). On sunny days when foraging insects are most active the majority of flowers may be empty at any one time (e.g. Wetherwax 1986) which clearly poses a challenge to foragers attempting to obtain a high rate of reward. Bumblebees adjust their foraging behaviour in response to patchiness of rewards, adjusting turning rates and movement distances so that they quickly leave unrewarding patches and

remain for longer in patches that provide a high reward (Heinrich 1979; Kato 1988). Non-random foraging by bees (for example systematic or directional searching or trap-lining) can improve efficiency by minimizing visits to flowers that they have just emptied (Levin et al. 1971; Pyke 1978; Corbet et al. 1984; Kadmon 1992; Giurfa & Núñez 1993). The reduced incidence of multiple encounters with the same inflorescence (compared with expected values for a strategy of random visits) found in our study further confirms that bumblebees use a strategy of systematic searching among inflorescences on the same plant. Such strategies are of little benefit, however, when intra- and/or interspecific competitors are abundant so that many flowers have been emptied by other individuals.

An ability to detect flowers that have recently been visited by conspecifics has clear benefits in saving time that would otherwise be spent in entering and probing these unrewarding flowers (Kato 1988; Schmitt & Bertsch 1990). Where a guild of bee species share a nectar resource it is presumably also advantageous to be able to detect flowers visited by other species. There is convincing evidence for the existence of both attractant and repellent scent marking of flowers in various bumblebee species and honey bees (Cameron 1981; Free & Williams 1983; Marden 1984; Kato 1988; Schmitt & Bertsch 1990; Giurfa 1993). We found that bumblebees could not detect nectar levels in inflorescences that had not been visited, and so readily accepted inflorescences that had been depleted of nectar artificially. Thus they are unlikely to be using either direct vision of nectar, detection of humidity gradients or nectar scent to discriminate between inflorescences (Thorp et al. 1975, 1976; Kevan 1976; Corbet et al. 1979). The flower structure of *S. officinale* would in any case render these explanations unlikely since the nectaries are entirely enclosed within the corolla, and bees can gain access only by forcing apart the anther bases that form a barrier across the inside of the tubular corolla (although robbing holes provides a limited direct view of nectaries). Nevertheless, bees were able to detect and reject with a high degree of accuracy flowers that had been previously visited by themselves, conspecifics or other species. Since bumblebees are known to scent-mark flowers to communicate with conspecifics (Schmitt & Bertsch 1990), we suggest that scent marking is

the most parsimonious explanation for this selective rejection.

To our knowledge this is the first evidence for the reciprocal use of (putative) scent marking by two species. Since bumblebees did not forage randomly (cf. Zimmermann 1982) they rarely encountered inflorescences that they themselves had just visited, so that the evolutionary benefit of leaving scent marks is not immediately apparent. Presumably the primary benefit of marking is through benefits to siblings. However, given the abundance of bumblebee species at the study site, and the small size of bumblebee colonies (compared with honey bees), the majority of beneficiaries are probably not siblings. Competition between bumblebee species is known to occur elsewhere (Inouye 1978; Pyke 1982), and we suggest that it probably occurs at the study site since visit rates are high and at any one time a large proportion of flowers contain no nectar (D. Goulson, unpublished data). *Symphytum officinale* was also the only abundant nectar source available to bumblebees at the study site in June and July. Thus scent marking benefits both siblings and probable competitors. Of course, it is possible that scent marking did not evolve as a benefit to the marker or her siblings, but rather that foraging bees can simply detect the scent of preceding bees.

Previous research on scent marking in *B. terrestris* suggests that long-term (>20 h) marks are placed on rewarding flowers and increase the probability of subsequent visits (Schmitt & Bertsch 1990). The experimental conditions were very different from ours, since Schmitt & Bertsch used captive bees and artificial flowers. Possibly bees use both long-term attractants and/or short-term repellents depending on the conditions encountered. If competitors are able to recognize both sorts of mark then attractants may not be favoured when competitors are abundant as they will magnify the strength of competition. Clearly further research is necessary to identify which compounds are involved. We cannot rule out with certainty the possibility that other detection mechanisms are involved in distinguishing between flowers. Our data suggest that bees are able to recognize flowers recently visited by both conspecifics and heterospecifics with approximately equal accuracy, but different compounds may be produced by each species. Much-cited studies of competitive interactions in bumblebees

have not considered the possibility that scent marking may be involved in interspecific interactions (Inouye 1978; Pyke 1982). Studies of other bumblebee species and in other bumblebee communities are required to elucidate the generality of repellent marking, its importance in determining foraging patterns, and its role in competitive interactions between species.

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