The spatial distribution of nonrewarding artificial flowers affects pollinator attraction

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Many species of orchids that do not offer food rewards to pollinators bloom in clusters, early in the season, and are polymorphic for corolla colour. Previous studies suggest that the foraging behaviour of insect pollinators may select for early blooming and colour polymorphism. I tested whether pollinator behaviour can also favour aggregated flowering in these species, in a two-stage laboratory experiment on naïve bumblebees, *Bombus terrestris* (L.). In the first stage, the bees were allowed to forage on three colours of artificial flowers that contained sucrose rewards. In the second stage, I added nonrewarding flowers of a fourth colour and recorded the bees' visits to them. The four types of artificial flowers were either arranged in spatially distinct clusters, or were randomly intermingled. I used two reward schedules for each spatial arrangement: constant refilling of reward-containing flowers and probabilistic refilling. Bees that foraged on clustered flowers flew more often to the nonrewarding patch, and made more visits to nonrewarding flowers, than bees that foraged on intermingled flowers. This tendency was obtained both in the constant reward and in the probabilistic reward schedules. The results support the hypothesis that pollinator attraction may select for clustered, synchronized blooming in flowers that do not contain nectar and pollen rewards.

Several thousand orchid species (as well as other taxa) depend upon insect pollination, but offer no food reward to their pollinators. Many of these species attract pollinators by mimicking rewarding flowers that bloom at the same time, while other orchids function without models (Dafni 1986). The latter often bloom in clusters, early in the season, and are polymorphic, for example in corolla colour (Nilsson 1992).

The early blooming time and the display polymorphism of deceptive flowers may increase their ability to attract pollinators. Their early blooming coincides with the emergence of young bees. Thus, they may rely on pollination by naïve bees making their first exploratory visits to flowers (Nilsson 1980; Little 1983). The variability in display may also make it harder for inexperienced pollinators to learn to avoid the nonrewarding species, and thus enhance the reproductive success of these species (Heinrich 1975; Little 1983). Pollinators visit nonrewarding morphs more often when they are rare than when they are common and may thereby stabilize the polymorphism through frequency-dependent selection (Smithson & MacNair 1997).

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I investigated the third flowering characteristic of many nonmodel orchids, namely their synchronized, aggregated blooming, and its possible effects on pollinator behaviour. Although many other flower species bloom in patches the clustered flowering of deceptive orchids seems remarkable because of the low density and scattered dispersion pattern typical of many populations (Ackerman 1986).

Clustered blooming may have two advantages for nonrewarding plants. First, flowering patches may be detected more easily by pollinators than single flowering individuals (Heinrich 1979). Second, successful pollination is more likely if pollinators stay in the patch for several nonrewarded visits (see Feinsinger & Tiebout 1991; Kunin 1993 for data on reward-producing flowers). Alternatively, clustered flowering may be disadvantageous for nonrewarding flowers. Pollinators that have visited a patch of rewardless flowers may learn to recognize them, and may avoid them later in the season. Aggregation can also increase intraspecific competition for pollinators.

The reproductive success of nonrewarding orchids is generally pollen limited (e.g. Calvo 1993; O'Connell & Johnston 1998). Field studies suggest that nonrewarding flowers set more fruit as their population density increases (Laverty 1992; Fritz & Nilsson 1995;

Alexandersson & Agren 1996; Murren & Ellison 1996; Sabat & Ackerman 1996). Nonrewarding orchids that grow near rewarding flower species set less fruit than isolated orchids (Lammi & Kuitunen 1995). These findings suggest that it may be advantageous for nonrewarding plants to be clustered. However, these studies did not investigate the role of pollinator behaviour in the proposed density advantage.

I tested the hypothesis that blooming in groups increases the number of approaches by, and/or tenure of, pollinators on rewardless plants. Using artificial flowers, I simulated a situation where nonrewarding flowers start blooming after their bumblebee, *Bombus terrestris*, pollinators have already been exposed to rewarding flowers. I measured the bees' tendency to approach the nonrewarding flowers when rewarding and nonrewarding flowers were aggregated in patches and when the same numbers of flowers were randomly intermingled. I also measured the bees' tendency to visit several nonrewarding flowers in succession under both spatial arrangements.

METHODS

General Methods

I carried out experiments in a flight room measuring 3×4 m and 3 m high. Temperature ranged from 26 to 30°C and relative humidity was 40–70%. The room was illuminated from 0630 to 1830 hours with six D-65 neon light tubes. I conducted observations between October 1994 and October 1995, between 0800 and 1630 hours. Each bee was typically observed for 2–3 h.

I obtained colonies of naïve bumblebees from Kibbutz Yad Mordechai, Israel. The queens of the colonies that were used during the winter were treated by the suppliers to forego hibernation. Colony development and the behaviour of workers in these colonies resembled colonies reared in summer. All individuals in the colony were marked with numbered tags within 3 days of emergence. Pollen was supplied ad libitum, directly to the nest. Sucrose solution was dispensed by artificial flowers and by a petri dish feeder, as detailed below. I used 79 workers from four colonies, aged 2–33 days.

Artificial Flowers

I used 40 morphologically identical computer-controlled artificial flowers. These were tube-shaped and 10 cm tall. Each flower was placed above a box ($10 \times 10 \times 8$ cm) containing its electronic parts. A removable round plastic landing surface 3.7 cm in diameter was placed on top of each flower. I used landing surfaces of four colours (to the human eye: white, green, blue and yellow) to create the different colour displays. These colours were distinguishable by bumblebees, as they occupy separate loci in a colour-triangle representation of the bees' colour vision (Chittka et al. 1993; Keasar et al. 1997).

Figure 1 illustrates the design of the artificial flowers. Each flower consisted of a cylindrical container (g) that
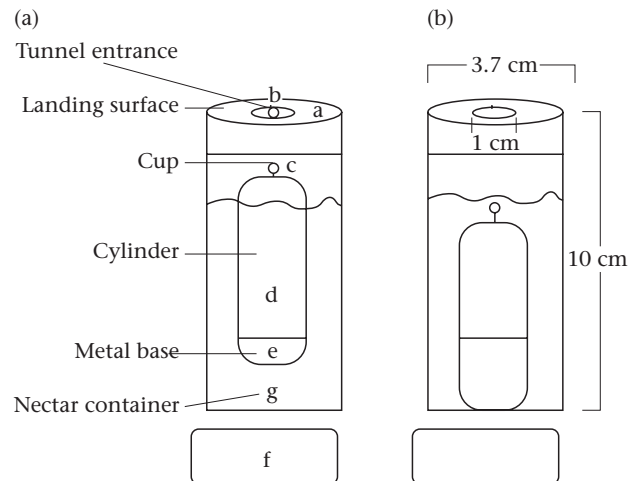

Figure 1. A side-view scheme of the artificial flowers. (a) Before refilling; (b) during refilling of a new serving of sucrose solution. See text for details and explanation of letters.

held sucrose solution. A plastic cylinder (d) with a metal base (e) floated inside this container. A miniature 'cup', calibrated to hold 1 µl of nectar, was attached to the top of the cylinder (c). A bee that landed on the flower had to insert its head through a narrow tunnel (b) to reach the droplet of nectar within the cup (c). The bee's head insertion and withdrawal were detected by a red-light photosensor within the tunnel and were recorded directly on to a computer. After the bee's departure, the electromagnet at the base of the flower (f) was activated for 1 s if the flower was scheduled to refill. This pulled the metal base of the cylinder (e) to the bottom of the container. The cup dipped into the sucrose solution and refilled with a new 1-µl serving (measuring error ± 20%). The cylinder floated back to its original position (Fig. 1) after the magnet was deactivated. This design elaborates on earlier electromagnetic artificial flowers used by Hartling & Plowright (1979). Refilling took place about 2 s after the forager's departure and did not interfere with the bee's foraging activity. Normally, no revisits took place before refilling, as the interval between visits was at least 3 s (Keasar et al. 1996). The magnet was not activated if the flower was not scheduled to refill after a foraging visit. In such cases the flower did not contain any sucrose reward when next visited by the forager. Preliminary experiments revealed that a full cup was completely emptied on each foraging visit, so that measurement of residual nectar was not necessary.

All blue, white and green flowers were full with 1 µl of 30% sucrose solution at the beginning of each observation session. After a foraging visit, the flowers were either refilled with the 1-µl nectar serving, or left empty. Refilling probability depended on experimental design (Table 1). The cups of yellow flowers, on the other hand, were always empty. Their cylindrical containers (Fig. 1) contained sucrose solution, however, so that they had the same odour as rewarding flowers. This was done to prevent the bees from detecting nonrewarding artificial flowers by fly-past inspection. Bees trained to colour-marked feeders prefer the most similar colours in later

Table 1. The parameters of visits by bumblebees to nonrewarding flowers

Flower arrangement and flower refilling probability	No. of bees	NR shifts*	All shifts†	NR shifts/All shifts	Mean run length‡	Total no. of visits	Visits to first arrival§
Patchy 1	20	2.40±0.25	19.75±1.55	0.122±0.015	3.15±0.52	7.55±1.57	3.7
Patchy 0.5	19	3.95±0.42	20.42±1.47	0.193±0.021	2.95±0.26	11.63±1.03	1.34
Intermingled 1	20	3.05±0.65	92.30±2.15	0.035±0.007	1.12±0.01	3.40±0.72	6.35
Intermingled 0.5	20	4.15±0.59	94.15±1.34	0.046±0.006	1.17±0.01	4.90±0.70	3.42

Means±SE are given, except for the last column, where median values are reported.
*Number of flights from a rewarding flower to a nonrewarding flower of a different colour in the four-colour array.
†Number of flights between flowers of different colours, whether rewarding or not.
‡Mean number of consecutive visits to nonrewarding flowers.
§Number of flower visits from when the nonrewarding flowers were exposed until they were first visited, normalized by the bee's tendency to change flower colours.

choice tests (Giurfa 1991; Giurfa et al. 1995). This suggests that the bees' tendency to choose the empty flowers may depend on their colour display and its similarity to the colours of rewarding flowers that they had visited earlier. I tried to reduce this effect by assigning the same colour display (yellow) to all empty flowers in all treatments.

Experimental Design

I tried to mimic a field situation where pollinators encounter some rewarding flowers before their first visits to rewardless flowers, by using a two-stage laboratory experiment. In the first stage, I allowed a naïve worker, foraging singly, to forage in a 'field' that contained three types of artificial flowers (10 blue, 10 white and 10 green) for 150 flower visits. The majority of bees made two to three trips to the nest and back to the floral array in the course of their 150 foraging visits. The flowers of the fourth type (10 yellow flowers) were covered with white plastic cups. At this stage the bees were able to fly above the covered flowers, but not to see or reach them.

In the second stage of the experiment, which began immediately after the bee had completed 150 flower visits, I exposed the yellow flowers ('nonrewarding flowers') with no interruption to the bee's activity. These flowers did not offer any nectar reward, while the reward schedule in the remaining flower colours was unchanged. I allowed the bee 150 additional visits to the four flower colours. I then removed the bee and kept it captive until the end of the observation session. Flower number was recorded automatically for each foraging visit. Thus the forager's visits to the nonrewarding flowers could be related to its foraging experience. Flower inspections that did not involve landing and head insertion were not recorded. I changed the coloured plastic disks that served as landing surfaces, to prevent effects of odour marking (Giurfa 1993; Goulson et al. 1998a) before another individual was allowed to approach the artificial flowers. However, there was no control over the possible use of scent marks by the same bee that had produced them. Each bee was used in one observation session only. All artificial flowers were covered at the end of each experimental session. The bees were then allowed to feed without restriction from a petri dish feeder that was placed on the table for 2–3 h. The feeder was then removed and the bees were deprived of food until the next observation session, on the following morning. Thus, experimental bees had previously fed from the petri dish feeder, but not from any artificial flower.

I measured the bees' tendency to visit nonrewarding flowers for two distribution patterns of the artificial flowers, and two reward schedules, using a 2×2 design. The artificial flowers (including the nonrewarding flowers) were either arranged in four clusters, one of each colour, on a table measuring 1.4×2.4 m, or randomly intermingled in a 6×20 position grid on the whole area of the same table (Fig. 2). The patchy arrangement was set up to mimic the natural distribution of flowers in a heterogeneous habitat, which allows blooming only in isolated patches. The intermingled arrangement tried to represent a more homogeneous habitat, such as a meadow. Colours were assigned randomly to the four possible locations, separately for each bee in the patchy arrangement. This was done to control for possible effects of location preferences, such as preferences to patches that were closer to the colony than others. Only one random arrangement pattern was used for each intermingled treatment. Visited flowers were refilled with probability 1 in two experimental treatments (constant reward schedule) and with probability 0.5 in the other two treatments (probabilistic reward schedule). I used 19 bees in the patchy probabilistic reward treatment and 20 for each of the other three treatments. The mean nearest-neighbour distance between flowers of the same colour in the intermingled constant reward treatment ± SD was 30.75 ± 19.41 cm and for flowers of different colours 19.45 ± 8.60 cm. In the intermingled probabilistic-reward schedule the mean nearest-neighbour distances were very similar, with means of 29.31 ± 24.16 and 20.87 ± 8.17 cm, for flowers of the same colour and of different colours, respectively. Figure 2 shows the nearest-neighbour distances for the patchy arrangement.

Data Analysis

The extent of visits to nonrewarding flowers depends on the bees' tendency to leave the rewarding flowers they
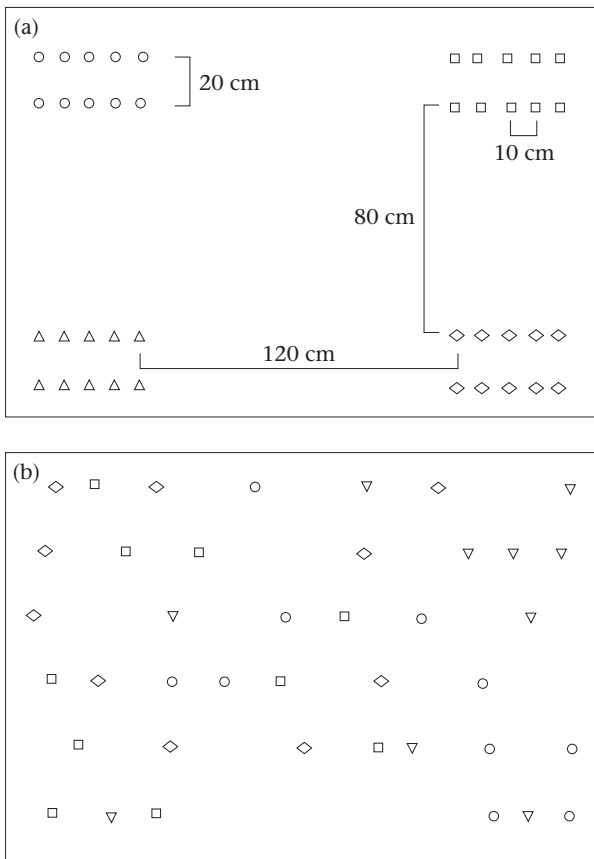
Figure 2. A scheme of the floral arrangement (a) in the patchy treatments and (b) the intermingled treatments. Each point represents one flower. Different symbols indicate different colours. The locations assigned to the four display colours were determined randomly for each bee in the patchy treatments. All the bees in each intermingled treatment were exposed to the same combination of locations and colours.

were visiting before, to switch to the nonrewarding flowers, and to visit more than one empty flower in succession. I estimated the frequency of these behavioural components by calculating the following parameters for each bee.

(1) NR shifts. The total number of colour shifts (i.e. flights) from a rewarding flower to a nonrewarding flower of a different colour.

(2) NR shifts/all shifts. Parameter 1 divided by the total number of flights between rewarding flowers of different colours in the four-colour array (colour shift flights). This parameter was used to estimate the bees' tendency to avoid nonrewarding flowers. Bees that do not discriminate against nonrewarding flowers are expected to make one-third of their colour shift flights to these flowers, while lower proportions indicate avoidance. The total number of colour shifts is reported as well (all shifts). Ratio estimate techniques were used for the computation of standard errors of the proportions. These techniques reflect the fact that the proportions are likely to be less variable than parameter 1 (Sampford 1962, pp. 105–112)

(3) Mean run length. The mean number of consecutive visits to nonrewarding flowers. I based computation of standard errors on cluster sampling, where all the runs of visits of each bee were treated as a cluster. Bees that made many runs of visits to empty flowers (large clusters) influenced the standard error more than small clusters (Sampford 1962, pp. 146–153).

(4) Total visits. The total number of visits to nonrewarding flowers (the sum of all consecutive visits following all flights from rewarding to nonrewarding flowers).

(5) Visits to first arrival. The number of flower visits from when the nonrewarding flowers were exposed until they were first visited (including the first visit to a nonrewarding flower), normalized by the bee's tendency to change flower colours. The normalization consisted of dividing the number of visits until first arrival to a nonrewarding flower by the bee's mean run length during the first phase of the experiment. Some of the bees did not visit the nonrewarding flowers at all during the 150 observed visits. For these bees, the number of visits until first arrival to a nonrewarding flower is greater than 150 and unknown. Therefore the mean value of this parameter for each treatment is not available and median values are reported instead.

Parameters 1–4 were measured in fairly large samples and were normally distributed, allowing analysis by parametric statistics. They were calculated as proportions of the total number of visits (150) in the second stage of the experiment. Visits and colour shift flights to nonrewarding flowers comprised only a low proportion (<10%) of the total number of visits in all experimental treatments. Since the arcsine transformation is not appropriate for the analysis of such small proportions (Zar 1996, page 282), I transformed the proportions using a slight modification of the Freeman–Tuckey transformation (1950, cited by Zar 1996, page 283). I used two-way ANOVA to evaluate the effects of reward schedule and spatial arrangement on the transformed proportions of number and proportions of flights from rewarding to nonrewarding flowers, mean run length and total number of visits to nonrewarding flowers. Two-tailed Wilcoxon two-sample tests were used to test the effects of spatial arrangement and reward schedule on the normalized number of visits until first approach to a nonrewarding flower.

RESULTS

The Effects of Spatial Arrangement

Bees that experienced a patchy flower arrangement arrived at the nonrewarding flowers sooner and visited them more (Table 1) than bees that were exposed to an intermingled arrangement. The total number of flights from rewarding to nonrewarding flowers was not significantly affected by the spatial arrangement of the flowers (Table 2). However, the total number of colour shifts was significantly higher when flowers were intermingled than when they were clustered. Consequently the proportion of colour shifts that were directed to the nonrewarding

Table 2. ANOVA results (*F* values) for the effects of spatial arrangement (clustered or intermingled) and flower-refilling schedule (probability 1 or 0.5) on the parameters of visits to nonrewarding flowers

	NR shifts $df=1,78$	All shifts $df=1,78$	NR shifts/All shifts $df=1,78$	Mean run length $df=1,72$	Total no. of visits $df=1,78$
Spatial arrangement	0.001	1473.43***	103.27***	98.07***	32.34***
Reward schedule	8.38**	0.44	9.91**	2.457	9.947**
Interaction	0.004	0.04	1.30	1.10	0.39
Complete model	2.80*	491.624***	37.77***	33.86***	14.027***
	$R^2=0.101$	$R^2=0.950$	$R^2=0.602$	$R^2=0.575$	$R^2=0.359$

For explanation of parameters see Table 1.
*$P<0.05$; **$P<0.01$; ***$P<0.001$.

flowers was significantly higher in the patchy arrangement than in the intermingled arrangement (Table 2). Mean run length was also significantly higher in the patchy treatments (Table 2). The total number of visits to nonrewarding flowers was significantly lower in the intermingled treatments than in the patchy treatments (Table 2). The normalized number of visits until first arrival to nonrewarding flowers was significantly higher in the intermingled treatments than in the patchy treatments (Wilcoxon two-sample tests: constant reward treatments: $U=280$, $N_1=N_2=20$, $P<0.05$; probabilistic reward treatments: $U=308$, $N_1=20$, $N_2=19$, $P<0.001$).

The Effects of Reward Schedule

Bees that experienced a probabilistic reward schedule (refilling probability 0.5) made significantly more colour shift flights to nonrewarding flowers than bees that foraged on rewarding flowers that always refilled (Table 2). The proportion of flights to nonrewarding flowers, and the total number of visits to these flowers, were also significantly higher in the probabilistic schedule than in the constant reward schedule (Table 2). Bees from the probabilistic reward treatments also made their first visit to nonrewarding flowers earlier than bees from the constant reward treatments (Wilcoxon two-sample tests: intermingled treatments: $U=283.5$, $N_1=N_2=20$, $P<0.05$, clustered treatments: $U=301$, $N_1=20$, $N_2=19$, $P<0.001$).

The proportion of colour shift flights that were directed to nonrewarding flowers was significantly lower than one-third for the intermingled treatments (two-tailed test for the difference between a sample mean and a parametric mean: reward probability 1: $Z=-9.613$, $P<0.001$, reward probability 0.5: $Z=10.630$, $P<0.001$) and for the patchy treatment with reward probability 1 ($Z=3.149$, $P<0.01$). On the other hand, the avoidance of the nonrewarding flowers was not statistically significant in the probabilistic patchy treatment.

DISCUSSION

The Effects of Spatial Arrangement

Foraging bumblebees visited nonrewarding artificial flowers more often when they were arranged in distinct clusters than when randomly intermingled. Field studies

report a positive correlation between the local population density of nonrewarding orchids and their reproductive success, measured by removal of pollinia and fruit set (Laverty 1992; Fritz & Nilsson 1995; Alexandersson & Agren 1996; Murren & Ellison 1996; Sabat & Ackerman 1996). My results corroborate these findings by direct observations of pollinator visits to nonrewarding flowers. In addition, they suggest that the spatial distribution of nonrewarding flowers affects their attraction to pollinators even when their total number is kept constant. These factors have not been treated separately in field studies on orchid pollination.

The total number of switches from rewarding to nonrewarding flowers was not significantly affected by the spatial arrangement of the flowers. However, the proportion of colour shift flights directed to nonrewarding flowers was significantly higher in the patchy treatments than in the intermingled treatments. This suggests that colour-switching bees avoided nonrewarding flowers more when they were intermingled than when they were clustered. Bees in the patchy treatments also made longer runs of consecutive visits to nonrewarding flowers than in the intermingled treatments. Keasar et al. (1997) found a similar effect of spatial distribution on the bees' tendency to perform runs of visits in rewarding artificial flowers. These findings may reflect the larger travel costs between flowers of different displays in the patchy treatments than in the intermingled treatments (Charnov 1976; Bernstein et al. 1991). Field studies also show that the spatial distribution of flowers affects the tendency of pollinators to switch between species. Bumblebees and butterflies tend to switch when their encounter rates with the species on which they had previously foraged are low (Chittka et al. 1997; Goulson et al. 1997). Field and laboratory experiments also indicate that long-duration flights between flower visits are correlated with switches between flower species (Greggers & Menzel 1993; Chittka et al. 1997). My results show a similar trend: more switches from nonrewarding flowers to rewarding flowers occurred when empty flowers were intermingled and thus less likely to be encountered. The behavioural observations are supported by the finding that bees' eyes are limited to resolving the colours of objects with a visual angle of less than 2–5°. The bees in my experiment flew a few centimetres above landing surfaces 3.7 cm in diameter, so that their colours could be resolved only up to a distance of about 35 cm (Giurfa et al. 1996; Greggers

& Maulhagen 1997). Therefore, after leaving a flower, bees could only see a few neighbouring flowers simultaneously. This visual limitation is also expected to cause more colour switching in intermingled treatments than in patchy treatments.

My results are consistent with the working hypothesis that clustered blooming of rewardless flowers, such as orchids, may confer a pollination advantage. A possible mechanism for the increased proportion of colour shift flights to nonrewarding flowers in patches is that their colour display was more conspicuous and visible than the display of the intermingled flowers. Following similar reasoning, plants or inflorescences with many reward-containing flowers would receive more pollinator visits than plants with few flowers. Seed sets generally increase with the number of flowers per patch, plant or inflorescence (Willson & Price 1977; Schemske 1980; Bell 1985; Sih & Baltus 1987; Cruzan et al. 1988; Campbell 1989; Andersson 1991; Eckhart 1991; Krannitz & Maun 1991; Kunin 1992). The total number of pollinator visits increased with increasing display size, and probably contributed to pollination success, in some field studies (e.g. Klinkhamer et al. 1989; Ohara & Higashi 1994; Dreisig 1995; Goulson et al. 1998b), as in the present experiment. In other field studies, pollinator attraction to the whole plant increased less than proportionately (Andersson 1988) or was not influenced (Robertson & MacNair 1995) by display size. These conflicting results raise the question whether increased pollinator attraction can explain the increased seed set in large patches. Indeed, pollinator visits per flower are generally unaffected or decline with increasing patch size (Augspurger 1980; Bullock et al. 1989; Klinkhamer et al. 1989; Dreisig 1995). This suggests that attracting more pollinators to a large patch does not necessarily result in higher fitness per plant.

Total 'field size' (2.4 × 1.4 m) and frequencies of the colour displays were identical for both spatial arrangements. Thus, overall spacing and frequency-dependent selection probably did not confound the effects of spatial arrangement. The position of nonrewarding flowers was randomized for each bee in the patchy treatments, but not in the intermingled treatments. Therefore, choices biased by flower position cannot be ruled out in the intermingled treatments. For example, all bees within a treatment may have preferred empty flowers that were placed, by chance, close to each other; or they may have avoided some flowers because of their location. Such biases, if they exist, are expected to reduce the behavioural variability within each intermingled treatment. Another possible confounding effect may have resulted from placing the four flower types in the corners of a rectangular table in the patchy treatments (Fig. 2). During the first stage of the experiment, the bees could have learned that the rewarding flower patches are located in the corners of the experimental table. In addition, the shape of the new patch and its location in the fourth corner matched the situation in the other three corners in the second stage, when the nonrewarding flowers were uncovered. This may have led to more visits to the nonrewarding flowers than in the intermingled environment, as an effect of generalization.

My study shows that pollinators are willing to visit nonrewarding flowers repeatedly in their first 2–3 h of foraging. However, this choice pattern may change as the pollinators become more experienced. In particular, bees may learn to discriminate nonrewarding flowers faster when they are clustered than when singly dispersed (Sabat & Ackerman 1996). This should be investigated in further experiments with longer observation periods.

My results also raise questions regarding how much clustering is needed to attract bees to nonrewarding flowers. One aspect of the question is how the density of clustered nonrewarding flowers affects their attraction to pollinators. This can be tested experimentally by changing the distances between flowers in the nonrewarding patch, or by slightly intermingling them with rewarding flowers that surround them. Another aspect is whether pollinator attraction to nonrewarding flowers is affected by the spatial distribution of the rewarding flowers in their vicinity. This can be examined by intermingling the rewarding flowers while the nonrewarding flowers are arranged in a patch, or by placing the empty flowers randomly in patches of rewarding flowers.

The Effects of Reward Schedule

Bumblebees that were rewarded with probability 0.5 in green, blue and white flowers visited the nonrewarding flowers more often than bees that were rewarded on each visit to these flowers. This may reflect the bees' tendency to avoid food sources that have a low reward mean, high reward variability, or both. My study did not contain treatments that differed in reward variability but had identical mean rewards. Therefore, it cannot be used to study the effects of risk sensitivity on the pollination prospects of nonrewarding flowers (Real 1992). Bees from probabilistic treatments also switched more frequently between blue, green and white flowers than bees in constant reward treatments. Visits to empty flowers were followed by a switch more often than visits to rewarding flowers (Keasar et al. 1996). Similar findings from field experiments suggest that the amount of reward in the last-visited flower affects the switching decisions of insect pollinators (Chittka et al. 1997).

Bees visited the nonrewarding artificial flowers repeatedly even when always rewarded in the other three flower types. Such visits cannot be explained as shifts in flower colour after unrewarded experiences. An alternative interpretation is periodic sampling of alternative food sources that does not depend on immediate past experience (Tamm 1987; Shettleworth et al. 1988). Rewardless flowers may benefit from periodic sampling by their pollinators regardless of their spatial distribution.

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