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The Foraging Movements of Bumblebees on Vertical "Inflorescences": An Experimental Analysis

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Summary. The bumblebees, *Bombus edwardsii*, move upward while visiting consecutive flowers on artificial "inflorescences". This response is unrelated to the vertical patterning of rewards in the flowers of inflorescences. However, when rewards are greatest in the bottommost flowers the bees learn to start lower and leave before reaching the topmost (empty) flowers. Conversely, when rewards are greatest in the topmost flowers they tend to start in the middle of the inflorescence and depart from the top. When rewards are equal in all flowers bees start near the bottom and depart near the top of inflorescences. These behavioral patterns tend to maximize the number of visits to rewarding flowers while minimizing visits to non-rewarding flowers, thereby enhancing foraging returns.

Introduction

Wherever bumblebees have been observed foraging from flowers arrayed on vertical inflorescences, they first visit the lower flowers and then move upward (Epling and Lewis, 1952; Benham, 1969; Kevan, 1971; Heinrich, 1975, 1979; Pyke, 1978). In the plants examined (e.g., *Delphinium, Epilobium*) flowers open sequentially from the bottom of the inflorescence and the rate of production of nectar is highest in the older, lower, female flowers. Bees starting at the bottom would visit the most rewarding flowers first, and they could depart before visiting the least rewarding, male flowers at the top.

Both Pyke (1978) and Heinrich (1979) infer that the bumblebees' foraging behavior at inflorescences has significance in maximizing the rate of energy gain. Percival and Morgan (1965) and Pyke suggest that the bees' tendency to move upward is a direct response to the nectar rewards available. However, the same behavior is observed at inflorescences having no more nectar in the bottom flowers than in the top (Pyke, 1978; Heinrich, 1979). The upward movement may thus also function in systematizing foraging to prevent re-visits to just-emptied flowers. The two hypotheses (which may not be mutually exclusive) cannot be resolved from field observations. It is necessary to know the precise reward-spectrum each bee has encountered on each flower of its foraging career in order to disentangle the foraging mechanisms. We here report on the responses of bumblebees foraging on inflorescences under controlled laboratory conditions.

Methods and Materials

Most of the bees (newly emerged queens of *Bombus edwardsii*) were taken from a hive in the laboratory, while some were captured during December in Berkeley, CA, from bushes of *Manzanita* sp. The bees were individually caged in wooden boxes with glass covers.

Observations were carried out on individual bees foraging from six artificial inflorescences hung side by side (separated by 12 cm) from a wire inside a 76 × 76 × 76 cm screen cage. The distribution of sugar solution rewards in the flowers of the inflorescences was varied as indicated in the Results.

The artificial inflorescences consisted of strips of dark green plexiglass (23 mm × 190 mm). Each strip had a row of five 1 mm diameter holes (39 mm apart). The holes were each surrounded by four thin strips of blue tape ("petals") to form a star-pattern (Fig. 1). The reflectance of these "flowers" and of the green plexiglass substrate upon which they were mounted are given elsewhere (Heinrich et al., 1977). Food rewards (30% sucrose solution) were dispensed into the center-hole of flowers from a 50 µl syringe with a PB 600 Hamilton push button repeating dispenser. Flowers without food reward (where indicated) were filled with water rather than sucrose solution to prevent possible visual discrimination between rewarding and non-rewarding flowers.

The bees were familiarized with the artificial flowers before

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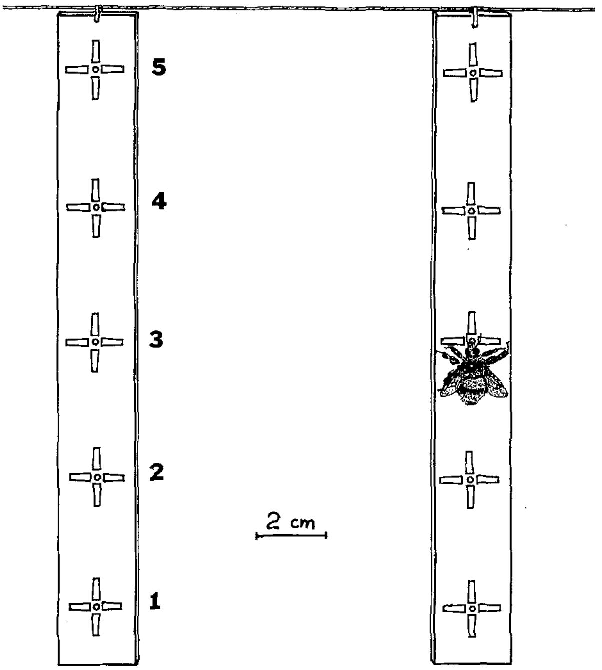

Fig. 1. Artificial "inflorescences" used in the experiments, showing spacing and numbering of flowers on each inflorescence, and spacing of inflorescences suspended horizontally across the foraging cage

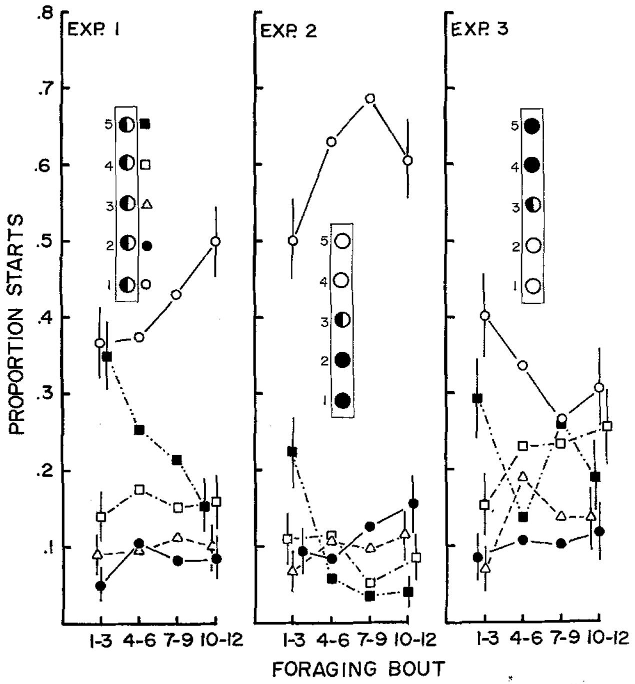

Fig. 2. Proportion of starts at the different flowers of the inflorescences (indicated in key at left) as a function of foraging experience. The distribution of nectar rewards in three experiments is indicated in keys (○ no nectar, ◐ 1 µl sucrose solution, ● 2 µl sucrose solution). Bars in the first and last foraging bouts are the 95% confidence intervals about the means. Statistics on the other foraging bouts were approximately similar, but they have not been drawn on the graph for purposes of clarity in presentation

their foraging responses were tested on the vertical inflorescences. Six inflorescences were laid side by side, abutting each other, on the floor of the cage and each flower contained 1 µl sucrose solution. A bee was caged in an inverted 50 ml beaker over one of the middle flowers. After the bee discovered (accidentally) the sucrose reward, the beaker with the bee was moved from one to another neighboring flower as flowers were probed and emptied. After several flowers had been visited the bee foraged spontaneously after the beaker was removed. The bee's foraging responses were then tested on the vertical inflorescences. Only one bee was allowed to forage at a time. All of the inflorescences were washed and refilled (as indicated in the individual experiments) after each foraging bout of a bee. Foraging bouts of any one bee were separated by at least a half-hour. Different bees were used for each set of experiments.

Results

The bumblebees exhibited apparently normal foraging behavior at the artificial inflorescences in the foraging cage. They flew between inflorescences and between flowers, and they probed into both sucrose- and water-filled flowers. However, their behavior varied greatly as a function of experience in relation to different reward distributions.

We investigated four aspects of the bees' behavior. 1) The proportion of approaches to inflorescences that start on flower 1 (the bottom flower), 2,···, 5 (the topmost flower). 2) The proportion of departures from flower 1, 2,···5 to another inflorescence. Linear regression analyses were used here to determine if these proportions changed with experience (number of foraging bouts). 3) The directions (up or down) of successive floral visits on the inflorescence. 4) The propensity to pass by flowers without probing.

When confronted with equal rewards (1 µl, 30% sucrose solution) in all five flowers of each inflorescence naive bees tended to start at the bottom flowers and move up, and this tendency increased with experience. The proportion of starts at the bottom flower (# 1) increased from a mean of about 0.4 in the early bouts (data pooled for bouts 1–3) to over 0.5 in bouts 10–12 (Fig. 2). The positive slope of the resulting regression line is significant (Table 1). However, the proportion of starts at the topmost flower (# 5) decreased from 0.28 to 0.14. Approximately 0.65 of departures were from flower # 5 (Fig. 3). Only departures from flower # 2 increased significantly with experience (Table 2).

When we provided 2 µl sucrose solution in the two bottommost flowers (# 1 and # 2), 1 µl in # 3, and placed water in the two uppermost flowers, the

Table 1. Regression analyses. y=proportion of *starts* at one of the five flowers (an analysis for each flower); x=foraging bout (1–12). Data pooled for all bees used in an experiment

Flower position	Regression equation	Level of significance[a]	r	N
Experiment 1. All flowers have equal rewards				
1	$y=0.01x+0.393$	*	0.164	105
2	$y=0.002x+0.075$	ns	0.065	105
3	$y=0.0007x+0.099$	ns	0.028	105
4	$y=0.002x+0.141$	ns	0.066	105
5	$y=-0.015x+0.292$	***	−0.285	105
Experiment 2. Rewards highest in bottom flowers				
1	$y=0.014x+0.494$	**	0.261	96
2	$y=0.008x+0.067$	**	0.248	96
3	$y=0.004x+0.073$	ns	0.158	96
4	$y=-0.006x+0.136$	*	−0.196	96
5	$y=-0.020x+0.230$	***	−0.487	96
Experiment 3. Rewards highest in top flowers				
1	$y=-0.012x+0.412$	*	−0.227	96
2	$y=0.003x+0.086$	ns	0.105	96
3	$y=0.007x+0.096$	*	0.179	96
4	$y=0.008x+0.163$	*	0.191	96
5	$y=-0.006x+0.242$	ns	−0.117	96

r = Pearson correlation coefficient
N = Number of variable pairs

[a] Significance level of slope (H_0: slope=zero); ns=not significantly different from zero ($P>0.05$), * $P<0.05$, ** $P<0.01$, *** $P<0.001$

Table 2. Regression analyses. y=proportion of *departures* from one of the five flowers (an analysis for each flower); x=foraging bout. Data pooled for all bees used in an experiment

Flower position	Regression equation	Level of significance[a]	r	N
Experiment 1. All flowers have equal rewards				
1	$y=-0.002x+0.154$	ns	−0.043	105
2	$y=0.004x+0.036$	*	0.188	105
3	$y=0.003x+0.047$	ns	0.149	105
4	$y=-0.0001x+0.077$	ns	−0.005	105
5	$y=-0.005x+0.686$	ns	−0.105	105
Experiment 2. Rewards highest in bottom flowers				
1	$y=0.001x+0.214$	ns	0.028	96
2	$y=0.007x+0.058$	**	0.249	96
3	$y=0.010x+0.046$	***	0.312	96
4	$y=0.010x+0.083$	***	0.334	96
5	$y=-0.028x+0.598$	***	−0.497	96
Experiment 3. Rewards highest in top flowers				
1	$y=-0.009x+0.155$	**	−0.283	96
2	$y=-0.003x+0.064$	*	−0.174	96
3	$y=-0.0004x+0.063$	ns	−0.014	96
4	$y=-0.0008x+0.058$	ns	−0.038	96
5	$y=0.014x+0.661$	**	0.254	96

r = Pearson correlation coefficient
N = Number of variable pairs

[a] Significance level of slope (H_0: slope=zero); ns=not significantly different from zero ($P>0.05$), * $P<0.05$, ** $P<0.01$, *** $P<0.001$

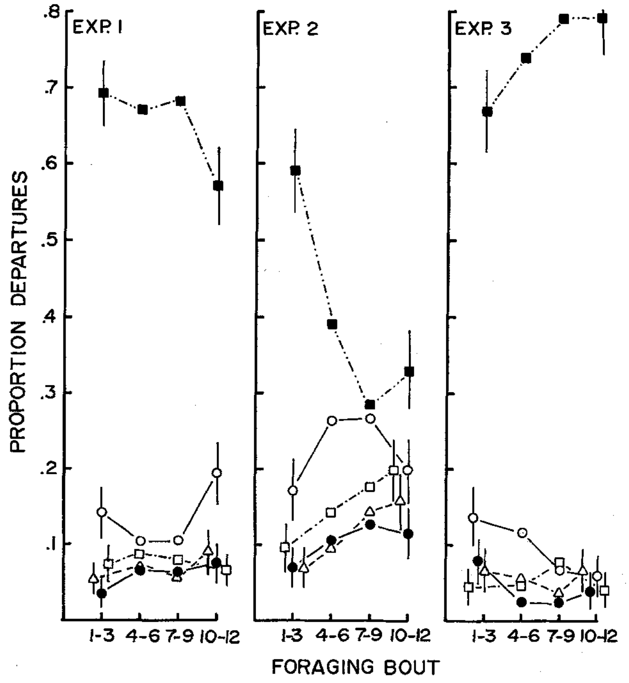

Fig. 3. Proportion of departures at the different flowers of the inflorescences as a function of foraging experience. Designations as in Fig. 2

bees started at the bottom flowers as before, but the tendency to start at flower # 1 increased from 0.5 to about 0.65 from foraging bouts 1–3 to 10–12 (Fig. 2, Table 1). The proportion of starts at flowers # 2 and # 3 remained low (0.05–0.15) but the trend to increase with experience is statistically significant (at # 2). In their first three foraging bouts the bees sometimes (0.2) started at the topmost (non-rewarding) flower, but by their 4–6 foraging bout they only started at the topmost flower on the average 0.05 of the time. The proportion of starts at flower # 4, the other non-rewarding flower, also decreased with experience. Departures were initially (in the first 3 foraging bouts) as high from the topmost flower (# 5) as before when all flowers were rewarded, but by the 10th foraging bout departures at flower # 5 had decreased to about 0.30. Departures from the middle flowers, # 2, # 3, and # 4, increased with experience (Table 2), with the proportion of departures from # 4 (0.2) twice that from # 2 (0.11) during foraging bouts 10–12. In contrast to the results obtained when the rewards are equal in all flowers, the bees started and departed lower on the inflorescence.

In the third experiment 2 µl of sucrose solution

Table 3. Direction of movement on successively visited flowers on inflorescences as a function of foraging experience at different distributions of nectar rewards. Experiment 1 = 1 μl sucrose solution in each of the five flowers. Experiment 2 = rewards in bottom flowers. Experiment 3 = rewards in top flowers

	Experiment	Proportion of moves (observed number)	
		Up	Down
Bouts 1–6	1	0.87 (1180)	0.13 (184)
	2	0.86 (1072)	0.14 (180)
	3	0.85 (901)	0.15 (158)
Bouts 7–12	1	0.94 (1142)	0.06 (69)
	2	0.95 (1029)	0.05 (57)
	3	0.91 (921)	0.09 (97)

Table 4. Tendency to skip flowers while moving up or down on inflorescences

Number of flowers skipped	Proportion (observed number)			
	0[a]	1	2	3
Movement up	0.975 (6089)	0.021 (129)	0.004 (22)	0.001 (5)
Movement down	0.930 (693)	0.052 (39)	0.014 (10)	0.004 (3)

[a] Movement to closest flower on the inflorescence

was provided in each of the top two flowers and 1 μl in flower # 3, while the unrewarded, bottom two flowers were filled with water, as before. The bees clearly responded to this distribution of rewards. As in the other experiments they started at the bottom flower (# 1) 0.4 of the time during the first three bouts, however, that proportion decreased with experience (Fig. 2, Table 1). The proportion of starts at flowers # 3 and # 4 increased with experience. Nearly 0.25 of the starts were at flowers # 4 by bouts 10–12, the highest level reached in the three experiments. Departures from the top flower (# 5) increased with experience (Table 2); by bouts 10–12 the bees departed 0.8 of the time from # 5 (Fig. 3). Departures from the two bottom flowers decreased to a very low level with increased experience. Thus, when the rewards are highest towards the tops of inflorescences the bees start higher (relative to the other two reward distributions) on the inflorescences and usually depart from the top flower.

In the three experiments, each with different reward distributions, the bees had the same propensity to move upward. Furthermore, the proportion of upward moves was significantly ($P < 0.001$) greater during foraging bouts 7–12 than in the first six bouts (Table 3). The bees were more likely to move downward when rewards were concentrated near the top of the inflorescence and they started nearer to the top. On both upward and downward moves the bees exhibited a strong tendency to visit the closest flowers. On 99.6% of moves up, and 98.2% moves down, the bees passed by no more than one flower (Table 4).

Discussion

We have demonstrated that the bumblebees, *Bombus edwardsii,* move upward on artificial "inflorescences", as they do on natural flowers. This propensity is practically unchanged relative to the vertical patterning of the nectar rewards. However, the bees are highly responsive to varying reward patterns by changing the positions of starting and leaving an inflorescence.

We do not know why bees predominantly move upward. It may be because, while maintaining an upright orientation in order to fly between flowers, they have a better view of the flowers above them than those below, and they then fly to those they can most readily see. In addition, in many natural inflorescences the flowers are angled slightly downward, and when backing out of such a flower the bee is oriented up toward the other flowers of the inflorescence. Still another consideration is that bumblebees are negatively geotactic (Jander and Jander, 1970), thus, they spontaneously walk upward against gravity when other directional cues are absent.

Bees foraging on the inflorescences in the present study rarely passed by flowers. This "rule" of visiting the closest flower, which was also described by Pyke (1978), resulted in the bees making several visits per inflorescence rather than skipping about between flowers on different inflorescences.

With the constraint that the bees move *upward* to the *closest* flowers, the start and departure positions (relative to the vertical patterning of the nectar rewards) seem to maximize the number of visits to rewarding flowers and minimize visits to non-rewarding flowers. When rewards are greatest at the bottom of the inflorescence bees start near the bottom but depart before reaching the top, empty flowers. When rewards are greatest at the top they start higher up on the inflorescence above the lower, empty flowers. And finally, when the rewards are evenly distributed in the five flowers, bees start low and depart from the top, thus tending to visit all of the flowers on the inflorescence. These adjustments in the start and departure positions would appear to enhance the rate of nectar intake.

Proctor and Yeo (1972), Pyke (1978), and others have speculated that outcrossing is enhanced by the patterns of nectar volume normally observed in plants in nature with bumblebee-pollinated vertical inflorescences (highest volumes in bottom flowers) relative to the usual spatial patterning of the sexes of the flowers (female flowers toward bottom, male flowers toward top). Outcrossing is affected as pollen is first deposited on the stigmas of the bottom flowers, and the bees' behavior (to start at the bottom) is thought to be mediated by nectar patterns. Clearly, in light of the results presented here, this would appear to be the case. When rewards are highest toward the bottom, bees start low on inflorescences; thus the chances of an initial pollen-laden visit to a female flower (and pollination) would be expected to be highest. It appears, therefore, that many plants have capitalized on the bees' "rules of movement" since their architecture enhances cross-pollination given the bees' response patterns.

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