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Innate movement rules in foraging bees: flight distances are affected by recent rewards and are correlated with choice of flower type

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Abstract The non-random movement patterns of foraging bees are believed to increase their search efficiency. These patterns may be innate, or they may be learned through the bees' early foraging experience. To identify the innate components of foraging rules, we characterized the flight of naive bumblebees, foraging on a non-patchy "field" of randomly scattered artificial flowers with three color displays. The flowers were randomly mixed and all three flower types offered equal nectar volumes. Visited flowers were refilled with probability 0.5. Flight distances, flight durations and nectar probing durations were determined and related to the bees' recent experiences. The naive bees exhibited area-restricted search behavior, i.e., flew shorter distances following visits to rewarding flowers than after visits to empty flowers. Additionally, flight distances during flower-type transitions were longer than flight distances between flowers of the same type. The two movement rules operated together: flight distances were longest for flights between flower types following non-rewarding visits, shortest for within-type flights following rewarding visits. An increase in flight displacement during flower-type shifts was also observed in a second experiment, in which all three types were always rewarding. In this experiment, flower-type shifts were also accompanied by an increase in flight duration. Possible relationships between flight distances, flight durations and flower-type choice are discussed.

Key words Bumblebees · Foraging · Movement rules · Innate behavior

Introduction

Foraging animals move in a non-random manner. A well-known example of a simple movement rule is "area-restricted search" (Tinbergen et al. 1967; see review by Bell 1991): after foraging on a highly rewarding food source, foragers tends to move a small distance. After receiving a small reward, or no reward at all, foragers move a larger distance. This movement pattern was also observed in bees foraging for nectar (Heinrich 1979; Waddington 1980, 1983; Dukas and Real 1993), and was termed "near-far search" (Selten and Shmida 1991; Motro and Shmida 1995). Area-restricted search may help bees to stay in rich areas, and avoid depleted areas, if nectar is distributed in patches. Moreover, the area-restricted search pattern creates nectar patchiness, which may later be exploited by the forager. Thus it may be selectively advantageous, and can be evolutionarily stable in foraging situations with many bees, even if the initial nectar distribution is uniform (Motro and Shmida 1995).

A second flight pattern in bees, which has been documented recently, is the association of flight duration with flower choice. Honeybees which foraged on four differentially rewarding artificial flowers required more time for shift flights (flights between individual flowers) than for stay flights, i.e., recurring flights to the same flower (Greggers and Menzel 1993; Menzel et al. 1993). Bumblebees foraging in a natural meadow were more likely to switch flower species following long flight intervals than after short flights (Chittka et al., in press).

Simple movement rules, such as the two rules described above, may be acquired through a gradual associative learning process, such as the learning mechanisms which lead to the formation of flower-species

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preferences (Gould 1993; Menzel et al. 1993). An alternative hypothesis is that these are innate, instinctive processes, and thus should be observable in bees with no previous foraging experience.

We attempted to test these hypotheses by monitoring the flight of *Bombus terrestris* (L.) workers with no previous foraging experience in an array of artificial flowers. We used flowers of three color displays, which were randomly intermingled, and were refilled according to a probabilistic random schedule immediately following foraging visits. We expected that the naive bees would fly longer distances after feeding on rewarding flowers than after encounters with empty flowers, if area-restricted search is an innate behavior. We also expected that flights that involved changes in flower type would be of longer duration than flights among flowers of the same type, if the association between flower-type choice and flight time is innate. We also investigated the bees' flight patterns in a second experiment, in which flowers of the three types offered a nectar reward each time they were visited (refilling probability = 1). This constant-reward experiment allowed us to eliminate possible interactions between the reward schedule and choice of flower type. We distinguished flights between flowers of the same color display and flights between flowers of different colors in this experiment as well.

Methods

Experiments were carried out in a 3 × 4 m flight room. Temperature ranged from 26 to 30 °C and relative humidity was 40–70%. The room was illuminated from 0630 to 1830 hours. Observations were conducted during November 1994 and June 1995, between 0800 and 1630 hours.

Colonies of naive *B. terrestris* were obtained from Kibbutz Yad-Mordechai, Israel. All individuals in the colony were marked within 3 days of emergence. Pollen was supplied without restriction, directly to the hive. The bees were allowed to fly freely in the room between observation sessions. The artificial flowers were covered, invisible and inaccessible to the bees between observation sessions. The bees were allowed to feed *ad lib* from an uncolored nectar feeder for 2–3 h after each observation session. Then the feeder was removed and the bees were starved until the next observation session, on the following morning. To minimize uncontrolled color learning between observation sessions we used (whenever possible) only black, white or grey equipment in the flight room. More details on the artificial flowers and the laboratory setup are given in Keasar et al. (in press).

Experiment 1 – variable rewards

Thirty morphologically identical artificial flowers were used for the experiment. Three flower types were created by placing a removable plastic landing surface, which was either white (10 flowers), blue (10 flowers) or green (10 flowers) on top of each flower. Therefore the only difference between the flower types was in color. We used three flower types because this is the minimal number which allows free foraging choices: whenever a bee leaves one of the flower types, it can choose between the two remaining types.

The flowers were placed on a 1.40 × 2.40 m table, in randomly chosen coordinates on a 6 × 20 position grid. The mean nearest-neighbor distance between flowers of the same color was 30.75 ± 19.41 (SD) cm, and the mean nearest-neighbor distance between flowers of different colors was 19.45 ± 8.60 (SD) cm. All of the flowers offered 1 µl scented 30% sucrose solution (“nectar”) at the beginning of each observation. After a flower had been visited by a bee, it was refilled automatically with probability 0.5 according to a predetermined random schedule. That is, flowers which had received a foraging visit were refilled with another 1 µl of nectar in approximately one half of the cases, and were left empty in the other half of the cases. The expected proportion of rewarding flowers therefore decreased gradually during the course of a bee's foraging activity, reaching 0.60 on a bee's visit no. 50, 0.52 at visit no. 100 and 0.50 at visit no. 150. Refilling occurred c. 2 s after the bee had flown away. Thus, bees which returned to previously visited flowers were also rewarded with probability 0.5. Refilling did not induce the bees to remain on the flowers, and did not interfere with their activity, since it took place after the bees' departure. In this manner we created a foraging area which included color-polymorphic rewarding and non-rewarding flowers at desired proportions, but no patchiness in nectar distribution.

A naive untrained worker, foraging singly, was allowed to visit the artificial flowers. Other individuals which approached the floral array were caught and caged until the end of the observation session. Data from the bees' first 150 flower visits were used for analysis. Flower number, time of the bee's head insertion and time of head withdrawal were recorded automatically for each foraging visit, so that a complete foraging record was obtained. We changed the colored plastic disks which served as landing surfaces, to prevent effects of odor marking, before another individual was allowed to approach the artificial flowers. Twenty bees from one colony were used in this experiment.

Experiment 2 – constant rewards

We used the same design as in the variable-reward experiment, except that now the flowers were programmed to refill after each foraging visit, so that reward probability was 1. A different random arrangement of flowers was used, so that the mean nearest-neighbor distance between flowers of the same color was 29.31 ± 24.16 (SD) cm, and the mean distance between two nearest neighbors of different colors was 20.87 ± 8.17 (SD) cm. We observed 22 bees from a different colony in this experiment.

Data analysis

The time between head insertion and head withdrawal from a flower was defined as probing duration. The time between head withdrawal from one flower and head insertion into the next flower was defined as inter-visit interval, and the straight-line distance connecting these flowers was regarded as flight distance. This represents an underestimate of the true flight distance because flight paths are usually not linear. A few inter-visit intervals and probing durations which were longer than 1000 s were treated as outliers, and were excluded from analysis. Inter-visit intervals which involved a return into the bee colony, and the flower visits which followed them, were excluded as well.

We calculated three series of data for each bee: probing times for all visits, inter-visit intervals and distances for all flights. The values within each data series (e.g., values of consecutive probing durations for a given bee) are not independent variables. For this reason we based the computation of standard errors on cluster sampling methods (Steel and Torrie 1981), where all measured values of a variable for a single bee were treated as one cluster. We used SAS 6.04 software (SAS Institute 1985) for some of the statistical analyses.

Table 1 Foraging parameters for the constant-reward (22 bees) and variable-reward (20 bees) experiments. Inter-visit intervals were computed for visits 41–150 in the constant-reward experiment, and visits 61–150 in the variable-reward experiment. Probing

duration was computed for visits 91–150 and 81–150 for the constant- and variable-reward experiments, respectively. Means \pm SE are reported

Parameter measured	Constant-reward experiment		Variable-reward experiment	
	Rewarded visits		Rewarded visits	Unrewarded visits
Flight distance (cm)	33.656 \pm 0.931		32.652 \pm 0.967	39.006 \pm 0.914
Inter-visits interval (s)	3.202 \pm 0.255		3.327 \pm 0.198	3.615 \pm 0.182
Probing duration (s)	4.029 \pm 0.353		6.467 \pm 0.587	4.271 \pm 0.367
Frequency of flower-type shifts	0.589 \pm 0.015		0.580 \pm 0.016	0.667 \pm 0.013

Table 2 Mean \pm SE flight distances (cm) as a function of the rewards obtained in the **a** two and **b** three last flower visits; data from the variable-reward experiment, $n = 20$ bees. The total

number of flights used for computations is given in parentheses. None of the differences between columns are statistically significant

		Flower $x-1$ was rewarding	Flower $x-1$ was non-rewarding
Flower x was rewarding		31.538 \pm 1.182 (665)	33.461 \pm 1.170 (774)
Flower x was non-rewarding		38.104 \pm 0.976 (774)	39.921 \pm 1.510 (724)

		Flower $x-2$ was rewarding	Flower $x-2$ was non-rewarding
Flower x was rewarding	Flower $x-1$ was rewarding	30.497 \pm 1.239 (289)	32.368 \pm 1.606 (378)
Flower x was rewarding	Flower $x-1$ was non-rewarding	34.722 \pm 1.650 (386)	32.179 \pm 1.317 (388)
Flower x was non-rewarding	Flower $x-1$ was rewarding	37.169 \pm 1.268 (374)	38.790 \pm 1.317 (399)
Flower x was non-rewarding	Flower $x-1$ was non-rewarding	38.749 \pm 1.554 (385)	40.844 \pm 2.309 (339)

Results

The effects of recent rewards

In the variable-reward experiment the bees visited both rewarding and non-rewarding flowers, while in the constant-reward experiment all visits were rewarded. Mean flight distances after rewarded visits did not differ significantly between the two experiments (Table 1, two-tailed t -test, cluster sampling, $t = 0.748$, $0.3 < P < 0.4$, $n_1 = 20$, $n_2 = 22$). However flight distances were longer when the previous flower was unrewarding than when it was rewarding (Table 1). This suggests that the bees used an area-restricted movement rule. We calculated, separately for each bee in the variable-reward experiment, the mean flight distance after leaving a rewarding flower and a non-rewarding flower, and the difference between those distances. The null hypothesis that these differences were zero was rejected (one-tailed, paired t -test, $n = 20$, $t = 7.462$, $P < 0.001$). We used the same statistical procedure in all cases where the behavior of the same individuals in two different situations was compared.

In order to evaluate the effects of the reward before last upon flight distance we first considered separately flights which followed a rewarded flower visit, and tested the effect of the reward before last on flight distance. For the sake of clarity we shall use the terms “flower x ”, “flower $x-1$ ” and “flower $x-2$ ” for the last visited flower, the flower before last and the flower second before last, respectively. Flight displacements which followed two consecutive rewards were not significantly shorter than displacements which followed an empty flower-full flower visitation sequence (Table 2a; one-tailed, paired t -test, $n = 20$, $t = 1.372$, $0.1 < P < 0.2$). Then we analysed separately the flights which followed a non-rewarding visit. Again, we found that flight distance in these cases was not significantly affected by the reward volume in flower $x-1$ (Table 2a; one-tailed, paired t -test, $n = 20$, $t = 1.095$, $0.2 < P < 0.3$). Similar pairwise comparisons revealed no significant effect of reward in flower $x-2$ on flight distances (Table 2b).

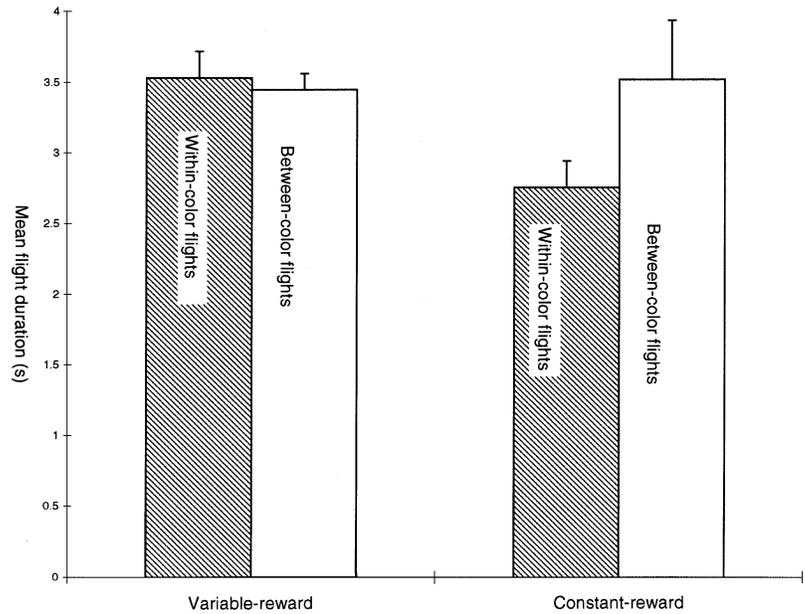
Inexperienced bees walked for a long time on the artificial flowers before head insertion, probably in search of the nectar. Long inter-visit intervals were

Table 3 Mean \pm SE frequencies of flower-type shifts as a function of reward obtained in the last two flower visits, data of the variable-reward experiment. The total number of flights used for com-

putations is given in parentheses. Only consecutive visits to the same flower type were included in the analysis. Differences between columns are not statistically significant

	Flower $x-1$ was rewarding	Flower $x-1$ was non-rewarding
Flower x was rewarding	0.568 \pm 0.031 (273)	0.583 \pm 0.030 (264)
Flower x was non-rewarding	0.638 \pm 0.029 (337)	0.647 \pm 0.032 (238)

Fig. 1 Mean flight durations (s) for within-type flights (hatched bars) and between-type flights (white bars). Computations are based on flights 61-150 for the variable-reward experiment 1, 41-150 for the constant-reward experiment. Error bars are 1 SE



recorded for the bees' first visits for this reason. Inter-visit intervals became shorter gradually, as the bees learned to handle the flowers, and stabilized after *c.* 60 visits for the variable-reward experiment and *c.* 40 visits for the constant-reward experiment. We therefore regarded only inter-visit intervals after stabilization as an approximate measure of flight durations. We have described a similar time-course for inter-visit intervals in a previous study (Keasar et al., in press).

Mean inter-visit intervals following rewarded and unrewarded visits are given in Table 1. The variable-reward and constant-reward experiments did not differ significantly in mean flight time following a rewarded visit (two-tailed *t*-test, $n_1 = 20$, $n_2 = 22$, $t = 0.926$, $0.3 < P < 0.4$). Within the variable-reward experiment, however, we found a significant increase in flight duration after visits to empty flowers as compared to flights after visits to rewarding flowers (one-tailed, paired *t*-test, $t = 2.148$, $P < 0.05$). This increase may be related to the elongation in flight distance following non-rewarded visits. To test for this possibility we computed the ratio flight distance/flight time (i.e., flight velocity) separately for each flight. We found no significant differences in the mean ratio between flights which followed rewarding visits and flights which followed non-rewarding visits. This finding supports the possi-

bility that the increases in flight distance and in flight duration following non-rewarding visits are interrelated.

Probing durations were also relatively long for inexperienced bees and gradually shortened as the bees acquired the probing technique. Probing times stabilized after approximately 80 visits for the variable-reward experiment and *c.* 90 visits for the constant-reward experiment. This time-course is also concordant with the measurements of Laverty (1994) on the acquisition of handling skills by bumblebees foraging on real flowers, and with our previous data (Keasar et al. 1996). We therefore used only probing durations after stabilization.

Probing times were significantly longer for rewarding flowers than for empty flowers in the variable-reward experiment (Table 1, paired *t*-test, $n = 20$, $t = 6.196$, $P < 0.001$). Probing times of full flowers in the variable-reward experiment were also significantly longer than in the constant-reward experiment (Table 1, *t*-test, $n_1 = 20$, $n_2 = 22$, $t = 3.635$, $P < 0.001$).

A characterization of flights within- and between flower types

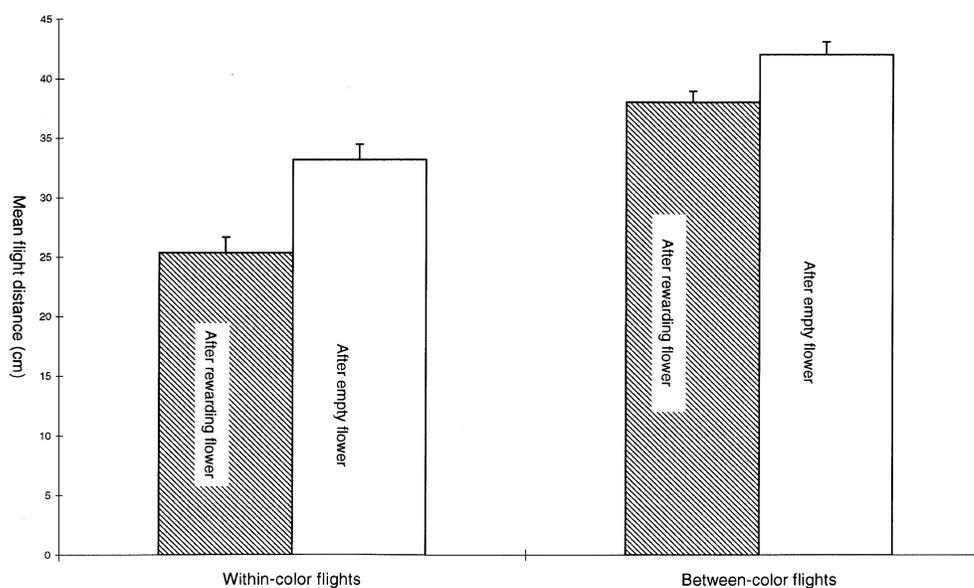
Flower-color shifts were significantly more frequent ($t = 3.721$, $P = 0.001$) after unrewarded visits than after

Table 4 Mean \pm SE flight distances (cm) for within-color flights and between-color flights. The total number of flights used for computations is given in parentheses. **a** variable-reward experiment, **b** constant-reward experiment

Visits considered	No. of flights considered	Within-color flight distance	Between-color flight distance	Significance of difference
1–150	2977	28.897 \pm 1.113	40.109 \pm 0.898	$P < 0.001$
1–60	1194	29.196 \pm 1.959	37.289 \pm 1.644	$P < 0.001$
61–150	1783	28.682 \pm 1.147	41.921 \pm 0.887	$P < 0.001$
1–60, excluding consecutive revisits	1092	37.355 \pm 1.876	37.289 \pm 1.644	$P = 0.929$
61–150, excluding consecutive revisits	1632	37.327 \pm 1.249	41.921 \pm 0.887	$P = 0.003$

Visits considered	No. of flights considered	Within-color flight distance	Between-color flight distance	Significance of difference
1–150	2977	24.874 \pm 0.976	39.786 \pm 1.111	$P < 0.001$
1–40	872	27.362 \pm 2.310	41.333 \pm 1.710	$P < 0.001$
41–150	2182	24.043 \pm 0.936	39.227 \pm 1.297	$P < 0.001$
1–40, excluding consecutive revisits	813	32.621 \pm 2.255	41.333 \pm 1.710	$P = 0.109$
41–150, excluding consecutive revisits	2220	28.579 \pm 1.123	39.227 \pm 1.297	$P < 0.001$

Fig. 2 Mean flight distances (cm) for within-type flights and between-type flights, following rewarded (*hatched bars*) and unrewarded (*white bars*) flower visits. Error bars are 1 SE



rewarded visits in the variable-reward experiment, but similarly frequent (two-tailed t -test, $t = 0.051$, $P < 0.9$) after rewarded visits in the two experiments (Table 1). The reward obtained in flower $x-1$ in the variable-reward experiment affected the frequency of flower-color shifts in the expected direction, but the effect was not statistically significant (Table 3). Data on cases of three successive visits to the same flower color were too few to allow examination of the relationship between the reward in flower $x-2$ and flower-color shifts.

Flight durations for between-color flights were significantly longer than for within-color flights

($P < 0.05$) in the constant-reward experiment. In the variable-reward experiment, however, the durations of between-color flights and within-color flights did not differ significantly (Fig. 1).

The distribution of flight distances was typically leptokurtic, indicating many flights between neighboring flowers (Waddington 1983). Flights between flowers of different colors were characterized by a longer mean displacement than flights between flowers of the same color, when all flights were taken into account (Table 4). We then considered initial flights (1–60 for the variable-reward experiment, 1–40 for the

constant-reward experiment) separately from the remaining flights. We computed flight distances for both groups of flights, in order to test for possible effects of the long initial inter-visit intervals on flight distances. Mean flight distances for between-color flights were significantly longer than for within-color flights in this case as well (Table 4). We also calculated flight distances for between-color flights and within-color flights, excluding successive flights to the same flower (flight distance = 0), because such flights are rare in natural situations (e.g., Best and Bierzychudek 1982). This comparison also shows an association between color shifts and long flight distances, except for the initial flights of the variable-reward experiment (Table 4). This flight pattern cannot be explained by the spatial arrangement of the flowers, since the three flower types were randomly intermingled in our experiments. Moreover, flowers in our array were likely to be next to a flower of a different color, as reflected by the nearest-neighbor distances (see methods). Random flights among neighboring flowers would result in many flower-type shifts. The prevalence of the opposite pattern, namely an association between flower-type shifts and long-distance flights, suggests non-random movement.

The combined association of reward and flower-type choice with flight distances

So far we have examined the association of two separate variables, reward and flower-type choice, with flight distance. In order to identify possible interactions between these variables we used the data of the variable-reward experiment to compute mean flight distances for the following cases:

1. Within-type flights which followed a rewarded flower visit
2. Within-type flights which followed a non-rewarded visit
3. Between-type flights which followed a rewarded visit
4. Between-type flights following a non-rewarded visit

Mean flight distances were largest for case 4, smallest for case 1 and intermediate for cases 2 and 3 (Fig. 2). We used analysis of variance to test for possible interactions between recent rewards and flower-type choice, which may have affected flight distance. We also wished to test for possible differences between individuals in the association between recent rewards, flower-type choice and flight distance. Therefore we employed three-way ANOVA, with flight distance defined as the dependent variable. The variation in flight distance was significantly affected (three-way ANOVA, $r^2 = 0.117$) by individual differences between bees ($F_{19, 2937} = 2.58$, $P < 0.001$), the reward obtained on the three last visits ($F_{7, 2937} = 5.06$, $P < 0.001$) and the bees' color shift decisions ($F_{1, 2937} = 91.00$,

$P < 0.001$). None of the interactions between the independent variables were significant.

Discussion

The bees in our study flew longer distances after visits to empty flowers than after visits to rewarding flowers (area-restricted search). Using area-restricted search may enable bees to forage within reward-rich areas when the nectar and pollen have a clumped spatial distribution. But in our experiment area-restricted search persisted even though nectar was distributed randomly, and the bees had not previously encountered any patchily distributed food source. This finding supports the hypothesis that area-restricted search in bees is an innate movement pattern, which can be applied optimally to diverse situations (Houston et al. 1982), rather than a learned response to local foraging conditions. We suggest that this innate area-restricted search pattern is not a detailed rule. It may not specify "how far" and may not include mechanisms to avoid revisitations. We expect, instead, that the detailed parameters of movement would be determined by the foraging situation, and implemented within the general area-restricted strategy.

Our second hypothesis was that the association between flower-type shifts and increased flight durations (Greggers and Menzel 1993; Menzel et al. 1993; Chittka et al., in press) is innate as well. The naive bees in the constant-reward experiment required more time for between-color flights than for within-color flights, as predicted by this hypothesis. However this pattern was not found in the variable-reward experiment. Thus the experiments do not show conclusively whether the association between flight durations and flower-type choice is an inborn flight rule.

An additional movement pattern which emerged in our experiments is that between-color flight were associated with longer flight distances than within-color flights. This association is also likely to be an innate movement rule, since it was observed in naive bees in the constant-reward experiment and in flights 61–150 of the variable-reward experiment. However, it was not demonstrated for the initial flights of the variable-reward experiment, when consecutive revisits were excluded. Possibly, for these flights, the effects of previous rewards on flight distances dominated the association between flower-type choice and flight distances. However, we cannot rule out the possibility that the bees somehow learned to associate flower-type shifts with long flights during the initial flights of the variable-reward experiment. Several possible mechanisms may underlie the correlation between flight distance and choice of flower type: long-distance flights may induce bees to shift to a different flower type, or shift decisions may spur them to increase flight distance.

Alternatively, both flight distance and flower-type choice may be affected by additional factors, which we did not measure. We are not able, with the present data, to distinguish between these alternatives. But we would like to speculate on the possible origin of the association between flower-type choice and flight distance: the “shift and fly-far” correlation seems inefficient in our experimental array of mixed flowers, where bees could easily have shifted between colors with a short-distance flight. However, in natural situations flowers are commonly arranged in monospecific clumps (such as inflorescences). In these situations, “flying far” often means shifting plant or plant species, while “flying near” means remaining on the same inflorescence or plant. Thus the two foraging components, “shift flower species” and “increase flight distance” may have become associated within the bees’ behavioral repertoire.

Following non-rewarded visits the bees flew longer distances, and switched flower type more often, than after visits to rewarding flowers. In natural situations, where “flying far” often means “shifting flower species”, the effects of reward on flight distance and on flower-type choice may be indistinguishable. Possibly, then, recent rewards can influence the bees’ choice of flower species in the field in two ways: by affecting flight distance, and thus the probability of encounter with other flower species (Selten and Shmida 1991); and by modifying the bee’s foraging preferences.

The bees’ choice of flower type was significantly affected by the reward obtained in the previous flower visit, but not by reward in the before-last visit. Flight distances were also significantly affected by the reward obtained in the previous flower visit, but not by rewards in immediately preceding visits. These results point to the last reward as an important single influence on the bees’ choices (Cresswell 1990; Real 1991; Kadmon and Shmida 1992, but see Waddington 1980; Dukas and Real 1993). More distant foraging history is probably integrated in a complex manner, and influences foraging decisions as well (Menzel 1968, Keasar et al. 1996). The three last rewards, the bees’ color choice decisions and individual differences between bees affected flight distances significantly, but all of these factors explained only 11.7% of the variation in flight distances. This supports our belief that flight distances are strongly influenced by long-term experience and additional factors, which we were not able to detect with our experimental setup.

Demas and Brown (1995) showed, in a laboratory study, that honeybees with previous foraging experience are predisposed to avoid returns to locations recently depleted of sugar solution. They suggest that this tendency may have been acquired during the bees’ prior foraging experience in the field, where depleted flowers do not replenish quickly. According to this suggestion, no avoidance of recently depleted flowers is

expected in the present study, where naive bees foraged on instantaneously refilling artificial flowers. Indeed, the frequency of recurring visits to the same artificial flower in our study was 8.50% for the variable-reward experiment, and 6.61% for the constant-reward experiment. Since the expected frequency of recurring visits for a randomly moving bee is only 3.33% (1/30), we conclude that the bees in the present study actually preferred to return to just-visited flowers. Thus, our experiments provide indirect support for the suggestion of Demas and Brown (1995) that the win-shift strategy in bees is an outcome of their foraging history.

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