Temporal reward variability promotes sampling of a new flower type by bumblebees

Tamar Keasar [a,*], Uzi Motro [b], Avi Shmida [b]

[a] Department of Biology and Environment, University of Haifa–Oranim, Tivon, Israel
[b] Department of Evolution, Ecology and Behavior, and Center for Rationality, The Hebrew University, Jerusalem, Israel

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Foraging bumblebees focus mainly on one flower species (their 'major'), and occasionally visit other flowers ('minors') that are less rewarding. Minoring allows tracking of potential alternative resources that might become more profitable with time. This is expected to provide an adaptive benefit under unstable foraging conditions, but to reduce foraging efficiency when resources are steady. We tested how predictability of food sources affects minoring and foraging success, using *Bombus terrestris* workers that fed on sucrose solution in artificial flowers. Bees exposed to three colour-distinct flower types with fluctuating food rewards performed more minoring (visits to a fourth, nonrewarding flower type) than bees that encountered a stable reward schedule. This difference was mostly due to a higher frequency of flower type shifts in the fluctuating-reward treatment. Flowers of the highest-rewarding type were visited less frequently in the fluctuating-reward than in the stable-reward treatment. This suggests that the fluctuating-reward schedule limited the bees' ability to track the most profitable flower type. Intervals between successive visits were longer in the fluctuating-reward than in the stable-reward treatment, possibly because the fluctuating schedule required time-consuming neural processing. As expected, the number of minoring visits correlated negatively with the number of colour shifts and with foraging success in the stable-reward treatment. In the fluctuating-reward treatment, on the other hand, sucrose intake rates were independent of minoring and colour shift frequencies. We suggest that novelty seeking by foragers can evolve when food sources offer fluctuating rewards, which reduce foraging success but also the cost of exploring new resources.

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Foragers sample and learn the availability and quality of their food sources when making dietary choices. Under stable foraging conditions, individuals identify high-quality patches and food types through sampling, and later exploit these resources preferentially. The timing and extent of sampling under constant laboratory conditions have been characterized in several studies of birds and fish (e.g. Krebs et al. 1978; Godin & Keenleyside 1984; Milinski 1984; Abrahams 1989; Gotceitas & Colgan 1991). Patch sampling has been implicated in important individual and group foraging patterns, such as risk sensitivity and the ideal free distribution (Kacelnik & Krebs 1985; Stephens & Krebs 1986, Stephens 1993; Thuijsman et al. 1995).

Sampling also allows foragers to track temporal changes in resource quality (Tamm 1987; Shettleworth et al. 1988; Hall et al. 2007; Dunlap & Stephens 2012). Sampling effort varies among individuals (Milinski 1984), and is affected by the total time available for

foraging (Krebs et al. 1978). Several authors (including Houston et al. 1982; McNamara & Houston 1985; Stephens 1987; Krebs & Inman 1992; Cohen 1993; Thuijsman et al. 1995; Eliassen et al. 2007; Stephens 2007) have constructed theoretical models of foraging as an activity that involves sampling, and have discussed the costs and benefits of food source sampling in patchy environments. Essentially, sampling increases the prospects of discovering profitable new food sources, at the expense of time spent foraging at familiar sources, and thus results in an exploration–exploitation trade-off. Sampling levels are therefore expected to be influenced by the foragers' perceived benefit of exploiting known food sources versus the anticipated profitability of harvesting food sources that are yet unknown.

Sampling has been proposed as an interpretation for the diet choice specializations of nectar- and pollen-collecting bumblebees in the field (Heinrich 1976, 1979b). Inexperienced individuals visit several flower species, and gradually restrict most of their foraging to flowers of a single common and highly rewarding species (the 'major'). Meanwhile they keep visiting flowers of one or a few additional species (the 'minors') at low frequency. The 'major' often differs between individual foragers, accounting for the wide variety

* Correspondence: T. Keasar, Department of Biology and Environment, University of Haifa–Oranim, Tivon 36006, Israel.
E-mail address: tkeasar@research.haifa.ac.il (T. Keasar).

of flower species exploited by the whole bee colony. A forager may persist on the same 'major' for several days, as long as it offers high profitability. This distinguishes 'majoring' from flower constancy, a tendency to visit flowers of a single species in succession within a short foraging trip while ignoring better alternatives (Raine & Chittka 2007). As the composition of the flowering community changes over time, foragers change their majors, often by gradually increasing their exploitation of one of the minors (Heinrich 1976). Minoring has been suggested to constitute an adaptive sampling strategy that allows foragers to track changes in the profitability of flower species, and adjust their diets accordingly (Heinrich 1979a, 1983; Waser 1983). A theoretical analysis predicts that minoring would contribute to foraging success, and thereby to fitness, when foraging conditions change over time. When the profitability of food sources is constant, on the other hand, the optimal strategy is to concentrate on the major species exclusively once it is identified, since there is no exploration payoff from minoring (Oster & Heinrich 1976). The predictions arising from this hypothesis are that: (1) bees that forage in fluctuating environments will minor more than bees that experience stable foraging conditions; and (2) the relationship between individual minoring level and feeding success will depend on the stability of foraging conditions. Specifically, (2a) under stable conditions, foraging success will increase as minoring decreases and (2b) the correlation between minoring level and foraging success will not be negative under changing foraging conditions. This is because too little minoring will limit resource tracking and will reduce harvesting rates. Higher minoring rates are expected to increase the forager's tracking and foraging success, while still higher minoring will involve over-exploitation of low-reward resources and lower foraging intake. The relationship between minoring and foraging success is thus predicted to resemble a bell-shaped function, but the width and skew of the function can vary with foraging conditions.

In spite of much research on bee foraging, the above predictions still require experimental testing. To address this aim, we manipulated the stability of food rewards for bumblebees and measured the bees' resulting allocation of foraging effort to high-reward (majoring) versus nonrewarding (minoring) feeding patches. Using *Bombus terrestris* workers foraging on artificial flowers, we first confirmed that exposure to fluctuating food rewards increased visit frequency to a nonrewarding flower type. We then tested for correlations between individual foraging success (measured as the percentage of rewarded visits and the percentage of visits to the most profitable flower type) and the frequency of minoring visits for bees, within each reward schedule.

METHODS

Experiments were carried out in a 3×4 m flight room. The temperature range was $26–30\,°C$ and relative humidity was 40–70%. The room was illuminated during 0630–1830 hours. Colonies of naïve *B. terrestris* were obtained from kibbutz Yad Mordechai, Israel. All individuals in the colonies were marked within 3 days of emergence. Pollen was supplied ad libitum, directly to the hive. The bees also fed ad libitum on a 50% sucrose solution from a feeder inside the colony. The feeder was removed from the colony ca. 12 h before each observation session and was returned after the session ended.

Artificial Flowers

Forty morphologically identical artificial flowers (described in detail in Keasar 2000) were used for experiments. Briefly, each flower consisted of a cylindrical container that held a 30% sucrose solution, and a 1 µl miniature cup that was refilled when programmed to dip into the sucrose solution container. Only foragers

that landed on the top part of the flowers and probed them correctly were able to gain access to this cup and feed. The flowers either dispensed 1 µl ($\pm$20%) of sugar solution or no sugar solution at all. Each artificial flower was equipped with a photodetector that was activated when the foraging bee inserted its head into the flower. The photodetector signals were automatically recorded as computer files, allowing us to track flower visit sequences for each forager. A removable coloured plastic landing surface of 3.7 cm diameter was placed on top of each flower. Display colours were human-white (10 flowers), human-green (10 flowers), human-blue (10 flowers) and human-yellow (10 flowers). These colours are distinguishable by bumblebees, as they occupy separate loci in a colour triangle representation of the bees' colour vision (Keasar et al. 1997).

All flowers were full at the beginning of each bee's foraging session. After the bee took off from a visited flower, it was either refilled or left empty according to a probabilistic schedule that varied with experimental treatment (see below for design of the experiment). Repeated head insertions into a single flower, with no flight between probes, were treated as a single visit, and the flower could refill only after the bee's departure.

The artificial flowers were arranged in four colour-distinct patches on a 1.40×2.40 m table (Fig. 1). The four flower colours were randomly assigned to the four patches, separately for each bee. This was done to minimize possible biases caused by location preferences of the bees and the unequal distances between patches.

Experimental Design

A two-stage experimental design was used. In the first stage we allowed a naïve worker, foraging singly, 150 flower visits in an array that contained 30 artificial flowers of three colour-distinct types (blue, white and green). Ten additional flowers, marked yellow,
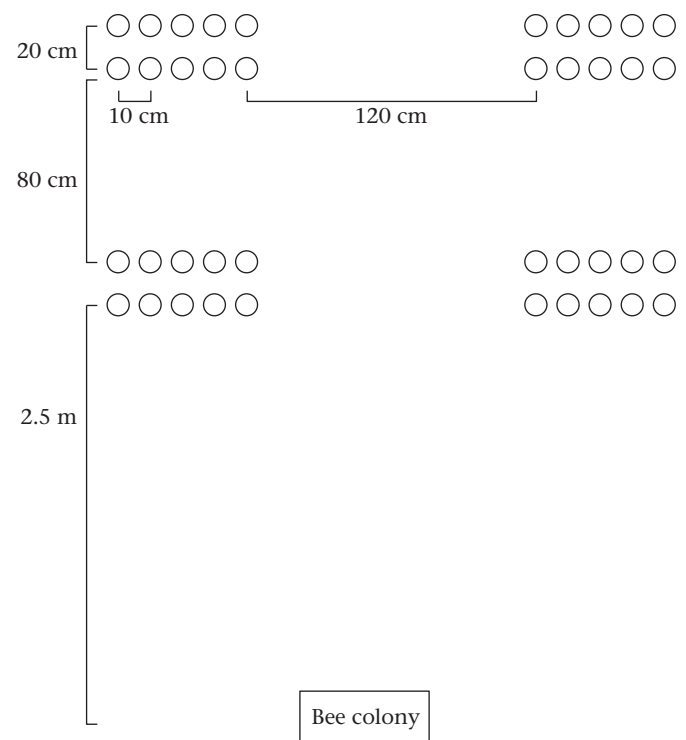

Figure 1. The arrangement of the artificial flowers. The flowers were arranged on a table in a flight room. Their refilling probabilities and colours varied between patches. Refilling probabilities in the stable-reward treatment were 0.9, 0.3, 0.3 and 0. In the fluctuating-reward treatment, refilling probabilities were changed during the experiment as detailed in Table 1. Flower colours were white, green, blue and yellow.

were covered, invisible and inaccessible to the bees at this stage. In the second stage of the experiment, which began immediately after the bee had completed 150 flower visits, we exposed the yellow flowers (test flowers, see Table 1) with no interruption to the bee's activity. This mimicked a field situation in which a new flower species comes into bloom in a familiar foraging area. The test flowers did not offer any nectar reward, while the reward schedule in the remaining artificial flowers was kept unchanged. Thus visits to the test flowers would contribute to exploration (but not to exploitation) of the bees' food resources, at the expense of exploiting familiar food types. We allowed the bee 150 additional visits to flowers of the four colours. We then removed the bee and kept it captive until the end of the observation session. Flower number, time of the bee's head insertion into each flower and time of head withdrawal were recorded automatically for each foraging visit. Thus the forager's visits to the test flowers were recorded, and could be related to its foraging experience. We changed the coloured plastic disks that served as landing surfaces, to prevent effects of odour marking, before another individual was allowed to approach the artificial flowers. A 300-visit observation session typically required about 2 h.

Refilling schedules of the artificial flowers depended on experimental treatment: in the stable-reward treatment ($N = 19$ bees), flowers of one of the three rewarding types were refilled with probability 0.9, and the two others were refilled with probability 0.3 throughout the experiment. The position of the high-rewarding flower type was varied randomly among bees. In the fluctuating-reward treatment ($N = 20$ bees), each of the three flower types was refilled with probability 0.9 for 100 visits, and with probability 0.3 in the remaining 200 visits, as detailed in Table 1. Thus, the location and colour of the high-reward flower type changed twice during the experiment in this treatment, but the spatial arrangement of the floral array remained unchanged. The total mean reward of the array was identical in both treatments. Both refilling schedules were characterized by reward variability within patches (not all flowers within a patch offered sucrose at any point in time) and between patches. The fluctuating-reward treatment included also temporal variability in rewards, which did not occur in the stable-reward treatment.

Data Analysis

Visits to the nonrewarding test flowers, which were exposed in the second stage of observations, was used as a measure of the bees' minoring effort. The extent of minoring depends on the bees' tendency to leave the patches with other flower types, arrive at the test flowers and visit a series of test flowers after arrival. We estimated the total minoring effort, and each of its components, by computing the following parameters for each bee: (1) number of visits to test flowers; (2) number of colour shifts; (3) number of arrivals at the test flowers, divided by number of colour shifts (this parameter was used to estimate the bees' tendency to avoid the test flowers, after departing from one of the other flower colours; bees that do not

discriminate against the nonrewarding test flowers are expected to make one-third of their colour shift flights to these flowers, while lower proportions indicate avoidance); (4) mean number of consecutive visits to test flowers (mean run length); (5) latency to the first arrival to the test flower patch, expressed as the mean number of visits since the first exposure of the test flowers until they were first visited; (6) the mean number of visits between the bee's first and second arrivals at the test flower patch; and (7) the mean number of visits between the bee's second and third arrivals at the test flower patch.

Some of the bees did not visit the test flowers at all during the 150 observed visits. For these bees, run lengths in the test flowers and the number of visits until first arrival are unknown. Excluding these cases reduced sample sizes to 14 in the stable-reward and 19 in the fluctuating-reward treatment for parameters 4 and 5. Samples for parameters 6 and 7 include only individuals that arrived at the test flower patch twice (parameter 6: stable reward: $N = 6$; fluctuating reward: $N = 14$) or three times (parameter 7: stable reward: $N = 2$; fluctuating reward: $N = 10$).

We calculated the proportion of rewarded visits and the proportion of visits in the most profitable flower type (with reward probability 0.9), out of all visits to the three rewarding flower types for each bee. These parameters, used as measures of foraging success, were correlated with the number of visits to test flowers, for each treatment separately, using Pearson correlations.

Flower handling times and intervisit intervals (flight durations, measured as time between head withdrawal from a flower and head insertion into the next) decrease as foragers gain experience (Keasar et al. 1996a). In the set of artificial flowers used here, they typically stabilize after ca. 80 visits. We computed the mean handling time of rewarding flowers and the within-patch intervisit interval for visits 201–300 for each bee as measures of their steady state durations, and compared them between treatments. Two-tailed t tests were employed for the comparisons.

RESULTS

Minoring under Stable- versus Fluctuating-reward Conditions

Bees in the fluctuating-reward treatment made significantly more visits to the nonrewarding test flowers than in the stable-reward treatment (Table 2). This was due to a higher number of switches between flower patches in the fluctuating-reward treatment. Bees in both treatments avoided the test flowers, that is, directed significantly fewer than a third of their colour shift flights to them ($t_{18} = 54.08$, $P < 0.0001$ for the stable-reward treatment; $t_{19} = 42.64$, $P < 0.0001$ for the fluctuating-reward treatment). The proportion of colour transitions that involved visits of test flowers was marginally significantly higher in the fluctuating-reward treatment than in the stable-reward treatment (Table 2). The number of consecutive visits in the test flower patch was not affected by treatment. The latencies to the first, second and third arrivals at the test flower patch did not differ between the treatments either. Latencies to arrivals at the test flower patch increased with experience in the fluctuating-reward treatment, but not in the stable-reward treatment (Table 2).

Minoring and Foraging Success

Bees from both treatments experienced the same reward schedule during their first 100 visits of the experiment. Accordingly, they visited the highest-rewarding flower type (reward probability 0.9) at similar frequencies during the first 100 visits of the experiment (Fig. 2; t test: $t_{37} = 0.07$, $P = 0.94$). During later visits, the proportion of visits to the high-reward flower type

Table 1
Refilling probabilities of the artificial flowers in the fluctuating-reward treatment

Visit no.	Type of artificial flower patch			
	Test	Rewarding 1	Rewarding 2	Rewarding 3
1–100	Inaccessible	0.9	0.3	0.3
101–200	Inaccessible in visits 101–150, nonrewarding in visits 151–200	0.3	0.9	0.3
201–300	Nonrewarding	0.3	0.3	0.9

Table 2
Parameters of minoring (visits to a nonrewarding test flower patch)

Foraging parameter	Mean±SD (Sample size)		Significance of difference
	Stable-reward	Fluctuating-reward	
1. Number of visits to test flowers	3.68±1.05 (19)	6.40±0.71 (20)	$t_{37}=2.17, P=0.037$
2. Number of patch shifts	30.74±2.81 (19)	44.45±3.24 (20)	$t_{37}=3.18, P=0.002$
3. Proportion of patch shifts directed to test flower patch	0.039±0.007 (19)	0.058±0.006 (20)	$t_{37}=1.99, P=0.054$
4. Number of consecutive visits in test flower patch	2.86±0.48 (14)	2.82±0.23 (19)	$t_{31}=0.07, P=0.948$
5. Latency to first arrival at test flower patch	38.79±27.64 (14)	26.89±22.73 (19)	$t_{31}=1.36, P=0.093$
6. Latency to second arrival at test flower patch	48.50±21.34 (6)	30.93±18.37 (14)	$U=58.5$ $P=0.179$
7. Latency to third arrival at test flower patch	22.50±0.71 (2)	36.20±20.47 (10)	$U=10.0$ $P=1$

Parameters 1–3 were calculated for all bees. The computation of parameters 4–7 excludes individuals that did not arrive at the test flower patch once (parameters 4–5), twice (parameter 6) or thrice (parameter 7). Sample sizes are reported in parentheses. Treatments were compared using two-tailed *t* tests (parameters 1–5) or Mann–Whitney *U* tests (parameters 6–7).

increased in the stable-reward treatment, but not in the fluctuating-reward treatment. Over the whole 300 visits of the experiment, the stable-reward bees visited the most profitable flower type significantly more frequently ($t_{37}=4.602$, $P<0.001$) than foragers in the fluctuating-reward treatment. Accordingly, individuals in the stable-reward treatment also obtained a sucrose reward in a greater proportion of their visits (mean ± SD: 0.71 ± 0.02) than in the fluctuating-reward treatment (0.56 ± 0.01; $t_{37}=6.28$, $P<0.001$). The mean sucrose volumes collected by a forager during the experiment were 211.89 ± 28.23 µl in the stable-reward treatment and 166.95 ± 14.74 µl in the fluctuating-reward treatment. In both treatments, the high-reward flower type received significantly more than a third of the visits (stable reward: $t_{18}=13.88$, $P<0.001$; fluctuating reward: $t_{19}=23.87$, $P<0.001$), and thus was preferred to the two rewarding flower types with lower refilling probabilities.

In the stable-reward treatment, the number of visits to test flowers was inversely correlated with the percentage of visits to the high-reward flower type (Pearson correlation: $r_{18}=-0.557$, $P=0.013$; Fig. 3) and with the percentage of rewarded visits ($r_{18}=-0.780, P<0.001$; Fig. 4). These percentages were calculated from the total number of visits to rewarding flower types, and are therefore independent of the number of visits to the test flowers. No significant correlation between minoring levels and measures of foraging success was found in the fluctuating-reward treatment (percentage of visits to high-reward patch: $r_{19}=-0.118$, $P=0.62$; percentage of rewarded visits: $r_{19}=-0.175$, $P=0.46$).

Handling Times and Intervisit Intervals

Mean steady-state flower handling times were significantly shorter in the stable-reward treatment (3.73 ± 0.42 s) than in the fluctuating-reward treatment (5.43 ± 0.38 s; $t_{37}=2.99$, $P=0.005$). These durations were not confounded by differences in rewards between treatments, because only visits to rewarding flowers were analysed. Within-patch intervisit intervals did not differ between treatments (stable-reward: 2.92 ± 0.22 s; fluctuating-reward: 3.22 ± 0.24 s; $t_{37}=2.09$, $P=0.36$). As only intervisit intervals between same-coloured flowers were considered, this measure is not affected by differences in colour shift frequencies between the treatments. The time between two successive head insertions into a flower (the sum of handling time and intervisit interval) was shorter for stable-reward individuals (6.65 ± 0.54 s) than for fluctuating-reward bees (8.65 ± 0.59 s; $t_{37}=2.50$, $P=0.02$), probably because of the longer handling times in the fluctuating-reward treatment.

DISCUSSION

This experiment simulated situations in which foraging bumblebees with some prior experience encounter a new food source, which differs in colour and location from the familiar foraging options. We measured the foragers' allocation to exploitation of the familiar food sources (majoring) versus exploration of the new
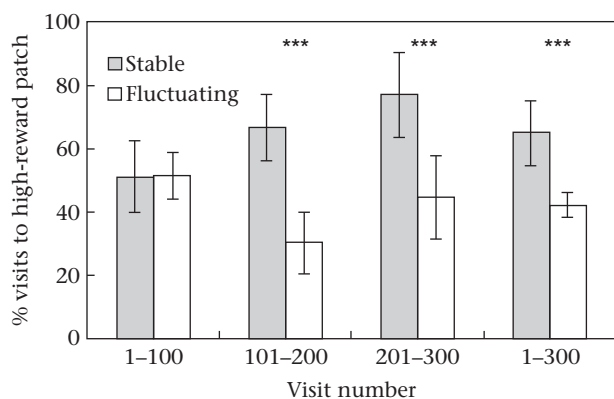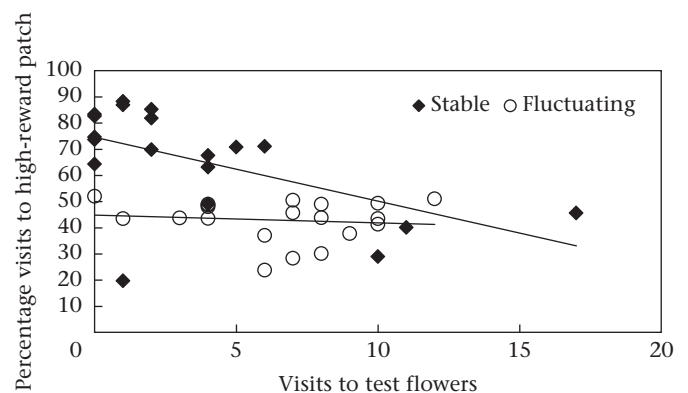
Figure 2. Mean and SD percentage of visits directed to the high-reward patch (refilling probability 0.9), calculated over each third of the experiment and over its whole duration. Asterisks denote significant differences (*t* tests: $P<0.001$) between the stable-reward treatment and the fluctuating-reward treatment. Data were collected for 19 bees in the stable-reward and 20 bees in the fluctuating-reward treatment.

Figure 3. Percentage of all visits directed to the high-reward patch (refilling probability 0.9) out of visits to the three rewarding patches versus number of minoring visits to the test flowers. Each data point depicts a bumblebee worker (stable-reward treatment: $N=19$; fluctuating-reward treatment: $N=20$). Linear regression equations are $y=-1.50x+76.92$ for the stable-reward treatment, and $y=-0.27x+58.58$ for the fluctuating-reward treatment.
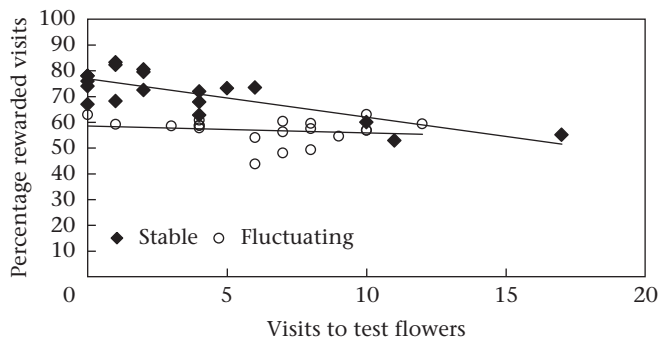
Figure 4. Percentage of all visits that yielded a sucrose solution reward out of visits to the three rewarding patches versus number of minoring visits to the test flowers. Each data point depicts a bumblebee worker (stable-reward treatment: $N = 19$, fluctuating-reward treatment: $N = 20$). Linear regression equations are $y = -2.44x + 74.63$ for the stable-reward treatment, and $y = -0.30x + 44.88$ for the fluctuating-reward treatment.

flower type (minoring). We tested whether this allocation is affected by reward stability of the familiar food sources, and whether it correlates with foraging success. In a previous project, we investigated how the spatial distribution of the artificial flowers and reward variability within food sources affects minoring (Keasar 2000). In the present study, we captured two novel aspects of the bees' foraging environment: variability in rewards among food sources, and temporal fluctuations in their profitability.

Minoring has been interpreted as an adaptive behaviour that allows bumblebees to track changing food resources. In nature, the abundance and quality of food for bees vary over space and time (Pleasants & Zimmerman 1979; Real & Rathcke 1988; Thomson et al. 1989; Waser & Mitchell 1990). New plant species come into bloom while others stop flowering. The 'majoring–minoring' strategy allows bumblebees to monitor the quality of previously encountered food sources and to evaluate new resources. Tracking of food sources through minoring is expected to be beneficial when foraging conditions fluctuate, but to reduce foraging efficiency when food sources provide constant rewards (Oster & Heinrich 1976). In agreement with these predictions, the mean number of minoring visits was higher under fluctuating rewards than under stable ones, and increased minoring was associated with lower foraging efficiency in the stable-reward treatment.

No negative correlation between minoring level and foraging success was predicted for the fluctuating-reward treatment, and the experiment's results conform with this prediction as well. There was no clear relationship between the number of minoring visits and the proportion of rewarded visits when food patches varied in time. A possible interpretation is that the trade-off between exploitation and exploration in the fluctuating-reward treatment generated a range of minoring levels that are similarly and moderately successful, rather than resulting in a single optimal minoring strategy. In other words, the utility function associated with different levels of minoring was a rather low and flat one in the present experiment. Consistent with this interpretation, foraging success in the fluctuating-reward treatment was lower than in the stable-reward treatment. The lack of correlation between minoring frequency and foraging success in the fluctuating-reward treatment may also reflect the fact that bees were never rewarded in the experiment's test flowers. In the field, on the other hand, minor flower species are likely to provide some reward when visited. We predict that minoring under field conditions will become more profitable with increasing rewards in the minor species. This prediction was not tested in the present experiment, which aimed to measure exploration of the test flowers independent of exploitation of any food rewards.

At the proximate level, minoring visits may reflect errors in identifying or approaching the high-rewarding food source. From a learning perspective, the frequency of errors is expected to increase when the high-rewarding flower type is more difficult to identify, as in the fluctuating-reward treatment. Indeed, the high-rewarding food source was chosen less often in the fluctuating-reward treatment, suggesting that the bees missed it more often than in the constant-reward treatment. A second, complementary, interpretation views the bees' choices in the experiment as patch-leaving decisions, rather than choices of flower types. The patch time choices of bumblebees are compatible with a countdown mechanism: the bees' motivation for patch switching increases with time in a foraging patch, but decreases upon receiving a food reward (Lefebvre et al. 2007). In our experiment, the bees received fewer rewards in the fluctuating-reward treatment than in the stable-reward treatment. This may have motivated them to leave patches more frequently, leading to a greater number of arrivals at the test flowers. Finally, recent studies of traplining by foraging bumblebees suggest an additional interpretation of the difference between our experimental treatments. Bumblebees learn to develop regular foraging routes that link familiar flowers (e.g. Ohashi et al. 2007; Lihoreau et al. 2012). This behaviour improves the bees' overall foraging efficiency and increases exploitation at the expense of exploration. Traplining is disrupted, however, if the spatial distribution (Lihoreau et al. 2012), and possibly also the rewards of flowers, are changed. This could cause bees to perform more minoring when rewards are fluctuating than when they are stable.

Bees from the fluctuating-reward treatment foraged more slowly than those in the constant-reward treatment. This is reflected in the longer flower handling times, which were independent of differences in reward volumes. Bees have been shown to forage more slowly when performing tasks that involve long-term memory retrieval, such as switching between food sources that differ in colour (Keasar et al. 1996b; Chittka et al. 1997; Raine & Chittka 2007) or morphology (Chittka & Thomson 1997). Possibly, memory retrieval and data processing involved in tracking the fluctuating-reward schedule reduced the speed of foraging in the present study, compared to the easier tracking task in the stable-reward treatment. Shortening of flight paths by traplining (Lihoreau et al. 2012) in the stable-reward treatment is unlikely, as intervisit intervals did not differ significantly between the treatments.

Viewing minoring visits as incorrect choices in learning tasks is supported by comparison of the present results with an earlier study (Keasar 2000). Bumblebees were presented with three equally rewarding types of artificial flowers. Their rates of visits to a nonrewarding flower type were measured, using the same design as in the present experiment. In one treatment, flowers of the rewarding types were always refilled (constant rewards), while in a second treatment refilling probabilities were 0.5 (variable rewards). As in the stable-reward treatment of the present experiment, the reward schedules did not change over the whole experiment. Unlike in the present experiment, none of the rewarding flower types was more profitable than the others. The bees directed a higher proportion of their colour shift flights (means of 0.12 with constant rewards, 0.19 with variable rewards) to the test flower patch, compared to the stable-reward treatment of the present study (0.04). They also performed more visits to the test flowers (7.55 with constant rewards, 11.63 with variable rewards) compared to the current experiment (3.68). The comparison between the experiments suggests that experiencing equal profitability among familiar flower types increased the bees' minoring effort. From a learning perspective, bees that experienced stable between-colour reward differences associated a single colour with high reward.

Bees exposed to three equally rewarding flower types, on the other hand, had to learn three colour associations, or alternatively learned to ignore the colour cue as a predictor of reward. These latter learning tasks may be more difficult for foragers, accounting for more minoring visits that indicate erroneous patch choices. The difficulty of associating several colours with food rewards has been demonstrated in two earlier experiments: in one study honeybees, *Apis mellifera*, were consecutively trained to artificial feeders of three colours, and were then presented with targets of the trained colours paired with targets of untrained colours. The bees chose the trained and the untrained targets at similar frequencies (Menzel 1969). In the second study bumblebees learned to discriminate between one nonrewarding floral type and either one, two or three rewarding floral types that differed only in colour. The bees' learning rates were higher in experimental sessions with fewer numbers of rewarding floral types (Dukas & Real 1993). The results of both studies suggest that when bees forage on an increasing number of floral types, their ability to discriminate between these and nonrewarding types is reduced.

The association between reward stability and minoring in the present experiment can thus be explained on two levels. On a mechanistic level, fluctuating rewards may complicate the bees' learning task, leading them to more erroneous flower choices (i.e. choices of test flowers). On an evolutionary level, minoring reduces foraging efficiency and is disadvantageous when food sources are constant, but not when their quality fluctuates. Bumblebees forage under variable and fluctuating conditions in nature; hence natural selection is expected to maintain a wide range of minoring levels within and between colonies. This reasoning may apply to foragers of additional taxa as well. We thus predict that foraging on unstable food sources will increase risky, novelty-seeking or sampling behaviours that promote exploration of new resources in additional species.

Flower constancy, the tendency of bees to visit flowers of a single species within a foraging bout, can be viewed as the flip-side of minoring: foragers that are highly flower-constant will necessarily perform little minoring, and this might cause them to miss high-quality food sources. A recent review points out that bees are more flower-constant when foraging on high-reward food sources than on poor ones (Grüter & Ratnieks 2011). A possible interpretation is that foraging on rich food sources reduces the potential gain from exploring alternative ones; thus constancy is an adaptive foraging strategy in profitable environments (Grüter & Ratnieks 2011). This interpretation is consistent with our finding of a negative correlation between foraging success and minoring levels in the constant-reward treatment. To our knowledge, the effects of stable versus fluctuating reward schedules on flower constancy are still unknown.

Our laboratory set-up was simpler than the bees' natural foraging environment in several respects. We used fewer flowers and flower types and constrained the bees to a small foraging arena. We also varied the profitability of the flowers over a bee's single foraging session, rather than over days or weeks, as in nature. It would be useful to repeat our experiment at a larger spatial and temporal scale, to test for the generality of our findings.

While the present study focused on individual foraging performance, it is important to keep in mind that the whole colony acts as the unit of selection in nature; hence colony performance rather than individual foraging efficiency is expected to be optimized. In the context of the exploitation–exploration trade-off, it may be adaptive to produce some foragers that mainly major on familiar food sources (exploiters), while others allocate more efforts to minoring and discovery of new flower patches and species (explorers). This implies that the consistent variation in learning capacities among foragers within a colony (recently demonstrated by Raine & Chittka 2012) could be adaptive. Discovery of new profitable

food sources by the explorers could be communicated to their nestmates through excitatory runs, pheromones and increased honey storage (Dornhaus & Chittka 2001, 2005). How majoring and minoring are balanced on a colony scale has yet to be elucidated.

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