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

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Foraging bumblebees focus mainly on one flower species (their ‘major’), and occasionally visit other flowers (‘minors’) that are less rewarding. Minorng 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 minorng 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 minorng (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 minorng 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 minorng 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; Abrahams & 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

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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). Minor foraging 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 minor foraging 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 minor foraging (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 minor foraging level and feeding success will depend on the stability of foraging conditions. Specifically, (2a) under stable conditions, foraging success will increase as minor foraging decreases and (2b) the correlation between minor foraging level and foraging success will not be negative under changing foraging conditions. This is because too little minor foraging will limit resource tracking and will reduce harvesting rates. Higher minor foraging rates are expected to increase the forager's tracking and foraging success, while still higher minor foraging will involve over-exploitation of low-reward resources and lower foraging intake. The relationship between minor foraging 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 minor foraging 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

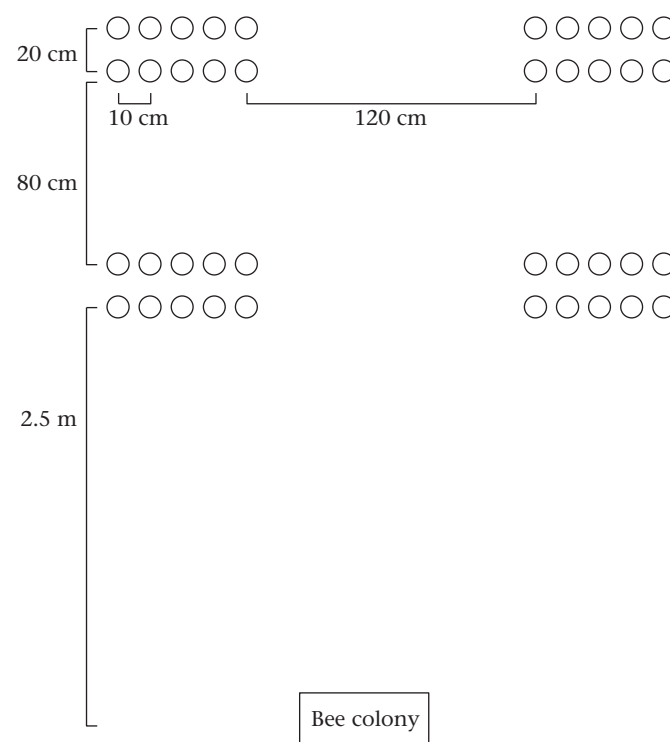
that landed on the top part of the flowers and probed them correctly were able to gain access to this cup and feed. The flowers either dispensed 1 µl (±20%) of sugar solution or no sugar solution at all. Each artificial flower was equipped with a photodetector that was activated when the foraging bee 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.

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