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A test of spatial memory and movement patterns of bumblebees at multiple spatial and temporal scales

James G. Burns and James D. Thomson
Evolutionary Ecology Group, Department of Zoology, University of Toronto,
Toronto, Ontorio M5S 3G5, Canada

Naive bumblebee foragers appear to use movement rules at small spatial and temporal scales, but it is not clear whether these rules determine movement patterns as the scales increase. One strategy for efficient foraging used by bumblebees is near-far search, involving short flights when in good patches of flowers and longer flights when in poor patches. Bumblebees also demonstrate the use of a spatial memory strategy by returning repeatedly to patches of flowers, and even following the same route between flowers, over periods of days. We attempted to determine at what spatial scales bumblebees use spatial memory while foraging within a patch and after how many flower visits spatial memory outweighs near-far search. Bumblebees in the laboratory foraged on a 4 × 4 array of artificial flowers with distances ranging from 10 to 80 cm between flowers in two simple spatial patterns. The proportion of visits to flowers containing a sucrose reward was monitored for either 100 or 400 flower visits in two separate experiments, after which the locations of the rewarding and nonrewarding flowers were interchanged, producing a mirror image. A drop in accuracy after the mirror image switch would indicate that the bees had memorized the location of rewarding flowers. Mirror image tests, and comparisons to a simulation model of near-far search based on actual flight distances, indicate that naive bumblebees used near-far search on flowers 10 cm apart but increasingly used spatial memory as experience and spatial separation increased. Bumblebees thus have multiple tactics available to forage efficiently in different environments.
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There are two fundamentally different ways in which an animal can concentrate its foraging effort in particularly rewarding areas. First, it can keep track of rewards it has received and use spatial memory to return preferentially to the more rewarding locations. Alternatively, it can employ simple heuristic movement rules that do not depend on spatial memory at all. The latter approach seems to require less cognitive ability (Gigerenzer and Todd, 1999) and has been particularly well studied in insects such as bees. At small spatial scales and over short foraging periods, both bumblebees and honeybees use heuristic foraging tactics that produce short flights when in an aggregation of nectar-rewarding flowers but longer flights when encountering an aggregation of poor flowers (Dukas and Real, 1993; Heinrich, 1979; Keasar et al., 1996; Pyke, 1978; Waddington, 1980). This tactic, called near-far search (Motro and Shmida, 1995), tends to enhance foraging efficiency in aggregated habitats by keeping the forager in nectar-rich areas.

The use of heuristic tactics over the short term, however, does not imply the lack of ability to use spatial memory over the longer term. Presently, the evidence suggests that apid bees have only a weak short-term spatial memory for flowers they have recently visited (honeybees: Brown et al., 1997; Isnec et al., 1997; bumblebees: Redmond and Plowright, 1996). This may account for the use of heuristics when a bumblebee is familiarizing itself with a new foraging environment. However, there is good evidence that bumblebees have a strong long-term spatial memory, in that they repeatedly return to the same foraging areas (Osborne et al., 1999; Osborne and Williams, 2001), remember and return to highly rewarding plants (Cartar, 2004), and sometimes repeat the same sequence of plant visits on each foraging trip over several days (Manning, 1956; Thomson et al., 1982; Williams and Thomson, 1998). There is also ample evidence that other pollinators can remember rewarding locations, especially when a large amount of nectar is provided (honeybees: Huber et al., 1994; hummingbirds: Brown and Gass, 1993; Healy and Hurly, 1995; Hurly, 1996; Sutherland and Gass, 1995). We used simple experiments to examine the circumstances in which bumblebees begin to rely on spatial memory within a foraging patch and depend less on simple heuristic tactics. We hypothesize that bumblebees will rely more on spatial memory as experience increases, as well as when flower spacing is greater (because individual flowers are easier to discern and remember).

Bumblebees may be able to switch between near-far search and spatial memory use as their experience increases, in a fashion analogous to animals that switch navigational tactics with experience. For instance, naive giant tropical ants (*Paraponera clavata*) initially use chemical trails to find food sources and to return to the colony but switch to visual cues as they gain experience (Harrison et al., 1989). Ants using visual cues run twice as quickly between sites as those following chemical trails. Although a heuristic foraging tactic such as near-far search can produce success above chance levels, it may not deliver the same performance as a tactic based on spatial memory which can consistently bring a bumblebee to rewarding flowers.

Depending on its circumstances, a bumblebee forager in the wild may encounter resources that are sufficiently stable over time and space for it to benefit from spatial memory or so unstable that memory provides no advantage over a heuristic tactic. To determine which tactics are used in particular situations, an iterative process is appropriate. First, observations of natural bee behavior help generate hypotheses to explain the behavior, and then details of both bee cognitive capabilities and the

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Address correspondence to J.G. Burns. E-mail: jgburns@zoo.utoronto.ca.

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behavioral hypotheses are tested with manipulative laboratory experiments. These experiments then inform subsequent studies of bee behavior in nature. In this study, we target the second stage to investigate bumblebee foraging tactics. Our experiments involved bumblebees foraging within a patch of artificial flowers, with aggregations of renewing nectar rewards and aggregations of flowers without reward, over a period during which the locations of flowers remained constant to provide an opportunity for the use of spatial memory. When bees are using near-far search, we expect to observe (1) longer flights after visiting unrewarding flowers and shorter flights after visiting rewarding flowers and (2) above-chance accuracy in choosing rewarding flowers, which would be unaffected by changes in the location of rewarding flowers between foraging periods. If bumblebees use spatial memory, we would expect to see a decrease in the accuracy of rewarding flower choice when the location of rewarding flowers is changed after a period of learning. This study assesses the relative use of spatial memory and near-far search in foraging bumblebees at multiple spatial and temporal scales in the laboratory.

MATERIALS AND METHODS

Experiments were conducted in a 3 × 8 × 2–m indoor flight cage with multiple two-dimensional and three-dimensional landmarks (colored cardboard boxes and posters) on the walls and floors of the cage to help the bumblebees navigate (Cartar and Real, 1997; Pyke and Cartar, 1992). Fifty individually marked workers from two colonies of *Bombus impatiens* (supplied by Biobest, Canada), a common, generalist pollinator in eastern North America, were used. Workers from each colony were represented in each treatment group, and no obvious differences in behavior were observed between colonies. No bee took longer than 4 h to complete its experimental run. Pollen was supplied ad lib within each colony.

Pretraining

Bees fed from 5-ml polyethylene test tubes (hereafter, "flowers") held upright in green cylindrical foam holders (10 cm diam, 12 cm tall) mounted on 80-cm-high metal rod stands. Bumblebee workers were pretrained as a group onto flowers containing 24% reagent-grade sucrose solution provided ad lib during the day so that they learned to recognize the flowers as nectar sources for the experiment. Flower positions for pretraining differed from those used in training and experiments.

Training

Each experimental subject was individually trained for one foraging trip (generally 20–30 flower visits before returning to the colony) on a horizontal 4 × 4 array of flowers, at the same spatial separation as its assigned treatment (see below), with 4 μl of 50% sucrose solution in each flower. We believe our arrays represent "within-patch" foraging because, although it is difficult to define a "patch," the spatial scales are much smaller than those seen separating distinct flower patches in nature. Each flower visit, defined by the bumblebee going to the bottom of the tube, averaged 7 s for entry and exit, plus 5 s ingestion time. After each flower visit, an observer inside the cage replaced the visited tube with a fresh, nectar-loaded one, to eliminate scent marks left by the bumblebee (Goulson et al., 2000). The observer remained in one location (acting as a stationary landmark), outside the array but inside the flight cage, while the bumblebee flew between flowers. The observer replaced each visited flower while the bee was inside the subsequent flower and then returned to his position before the bee reemerged. Thus, there was no resource depletion in the rewarding aggregations of flowers. We saw no evidence that the bumblebees were disturbed by the observer.

One hundred-visit experiments

Bumblebees foraged individually for 100 flower visits on one of the four spatial arrays. The first three treatments involved splitting a 4 × 4 array of flowers spaced at 10, 40, or 80 cm into "Halves" of 2 × 4 flowers (Figure 1a). One half had rewarding flowers (4 μl 50% sucrose solution) and the other half unrewarding flowers (4 μl water). In the fourth treatment, rewarding and unrewarding flowers were divided into "Quarters," spaced 80 cm apart (Figure 1b). There is thus a strong spatial autocorrelation of nectar reward, with rewarding flowers being close to other rewarding flowers (and unrewarding to unrewarding). The Quarters treatment was intended to increase the difficulty of remembering locations of rewarding flowers by increasing the evenness of the distribution of the rewarding flowers.

Two performance variables were measured for all treatments: "accuracy," defined as the proportion of visits made to rewarding flowers in a run of 50 visits, and "flight distance," defined as the straight-line distance between flowers. Flight distance was standardized for each treatment by designating a flight to one of the closest possible flowers as one unit, a flight that skips over one flower in a row as two units, and so on. Turning angle, a variable often used to provide insight into bee foraging tactics (e.g., Waddington, 1980), was not considered in our study because the structure of the flower array forced frequent turns due to the large ratio of edge to inner flowers (i.e., 12 edge versus 4 inner flowers).

After 100 flower visits, the flower array was switched to its "mirror image" for 50 visits (after Sutherland and Gass, 1995). A bumblebee that has learned the spatial location of rewarding flowers should (1) show a steady increase in accuracy before the switch, (2) perform above accuracy levels predicted by a Monte Carlo simulation of the near-far search (described below), and (3) continue to visit the previously rewarding locations after the mirror image switch until it learns that they have become unrewarding. If bumblebees are using a nonspatial memory–based tactic (e.g., near-far search), we expect (1) their flight distance to increase after visiting unrewarding flowers (to fly away from the spatial aggregation of unrewarding flowers), (2) their accuracy to be above chance (at levels predicted by a Monte Carlo simulation) because they remain in aggregations of rewarding flowers that do not experience resource depletion, and (3) their accuracy to be unaffected by the mirror image switch. Avoidance of unrewarding flowers cannot be interpreted as remote detection of reward because these bumblebees could not remotely detect the difference

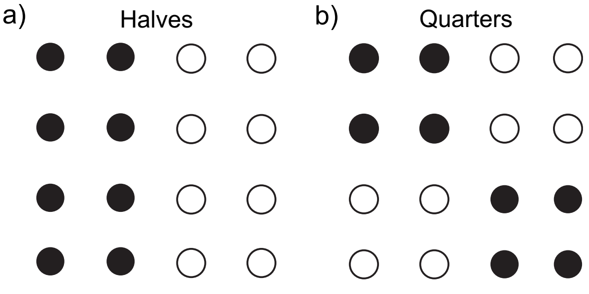

Figure 1
The two types of spatial distributions of rewarding (filled circles) versus unrewarding (unfilled circles) flowers. Flowers were separated by 10, 40, or 80 cm in the Halves treatments and by 80 cm in the Quarters treatment.

between sucrose solution and water (Marden, 1984; Burns JG, unpublished data).

Testing for near-far search requires comparing flight distance after rewarding versus unrewarding flower visits. Dukas and Real (1993) found that multiple consecutive unrewarding visits had a greater effect on bumblebee flight distance than just one unrewarding visit. Thus, we recognized three categories of visit, depending on whether the flower previously visited was (1) rewarding, (2) unrewarding, or (3) part of a string of two or more consecutive unrewarding flowers. Preliminary analyses had indicated that there was no difference in flight distance between single and multiple rewarding visits in a row ($p > .3$), so these were all pooled and classified simply as rewarding visits.

To reduce any effects of unintended cues from the flowers themselves (e.g., undetected unique visual markings or scents), 50% of the flower stands were switched every two foraging trips using a random selection procedure at each switch. Possible olfactory cues in the air, such as the chemicals known to be released by the Nasanov gland of honeybees at rich nectar sources (Gould JL and Gould CG, 1995), were dispersed by running an electric fan in the cage while the bumblebee was in the colony between foraging bouts.

Four hundred-visit experiments

To determine whether bees' use of tactics depended on their levels of experience, we ran a second set of experiments in which subjects foraged for 400 visits prior to the mirror image switch. We choose 400 visits because pilot experiments indicated that accuracy typically reached an asymptote by this point. Bees were then left to forage for 100 visits after the mirror image switch, an adequate number of visits to determine whether performance dropped after the switch. In addition to the two performance variables measured in the 100-visit experiments, we recorded whether the first flower visited in a foraging trip was a rewarding flower or not. This proportion should be higher if bees are using spatial memory to select flowers.

Statistical analysis

To analyze accuracy, with replication over bees, we broke each bee's foraging sequence into consecutive blocks of 50 visits (using block lengths of 25 visits did not qualitatively affect the analysis). Paired t tests were used to compare the proportion of rewarding visits in the final block of the initial foraging period versus the first block of the mirror image test within treatments in both experiments, and (in the 400-visit experiments) to compare the proportion of first visits to rewarding flowers before and after the mirror image test. In an effort to detect whether first visits were the result of learned motor patterns (a sequence of movements that develop with repetition, e.g., Collett et al., 1993), we visually searched foraging trip data for repeated visit sequences. To determine whether there was any effect of experience on flight distance (dependent variable) in 400-visit experiments, we performed a multivariate repeated-measures ANOVA with two repeated independent factors: visit period (visits 1–100, 101–200, 201–300, 301–400, and 1–100 of the mirror image test) and visit type (rewarding visit, one unrewarding, two unrewarding, and three or greater unrewarding visits in a row). To test whether the proportion of visits to rewarding flowers increased (dependent variable) with spatial separation of flowers (independent variable), we compared the accuracy of visits 351–400 of each treatment with ANOVA and post hoc Tukey-Kramer tests to determine whether performance increased with increased spatial separation of flowers. To improve conformity with the normality assumptions of these tests, proportion data were arcsine transformed and flight distances were log transformed.

Monte Carlo simulation

As an alternative analysis to tease apart spatial memory from near-far search, we created a Monte Carlo simulation model determining the accuracy of flower choice, in the absence of memory use, with parameters based on the actual flight distance data. The model allows us to test if the accuracy observed in the experiment could have been produced by a combination of simple "near-far" movement rules that specified only how far a bee would fly as a function of its recent reward experience. The results of the simulation thus produce a memory-null model that provides the expected level of accuracy given the observed movement rules. Any deviations above this level of accuracy, prior to the mirror image switch, would further support the use of spatial memory. The model selected the distance to be flown after a visit based on the type of visit (rewarding, unrewarding, etc.) just experienced. The simulated bee then flew to a randomly selected flower within the constraint of the selected distance. We ran 5000 simulated foraging bouts for each bumblebee based on the frequency distribution of its own flight distances for each type of visit during the experiment. For example, suppose an experimental bee made 90% of its subsequent visits to the closest flower after visiting a rewarding flower, 5% to the next closest, and so on. The simulation for that bee would then prescribe a 90% chance for the simulated bee to visit the closest flower after it visits a rewarding flower. If the foraging area has an aggregated distribution of rewarding flowers and the bees displayed behavior consistent with the near-far search, the model should produce levels of accuracy greater than chance. The observed accuracy from the experiments was compared with these 5000 null equivalents. We then calculated the probability, using Stouffer's method for combining one-sided probabilities (Rosenthal, 1991), for the randomization test for each bee that the observed accuracy could have been produced by near-far movement rules. We tested whether each bee performed more accurately than the null model and then combined the probabilities across bees for the final probability.

RESULTS

One hundred–visit experiments

The proportion of visits to rewarding flowers dropped significantly from the last 50 visits of the initial foraging period to the first 50 visits of the mirror image test in the 40- and 80-cm Halves treatments (40-cm Halves: $n = 6$, $t = 4.69$, $p = .002$; 80-cm Halves: $n = 6$, $t = 3.13$, $p = .012$; Figure 2). This is consistent with bumblebees using their spatial memory of locations of the rewarding and unrewarding flowers after an average of 1.5 h of foraging in these two treatments. Bumblebees in the 10-cm Halves and 80-cm Quarters treatments did not forage less accurately after the mirror image switch (10-cm Halves: $n = 6$, $t = 0.24$, $p = .410$; 80-cm Quarters: $n = 6$, $t = 1.76$, $p = .069$; Figure 2), indicating less memory for the rewarding sectors of the flower arrays in those designs.

Four hundred–visit experiments

When bees had a longer period in which to memorize the rewarding locations, accuracy dropped significantly in all treatments after the mirror image switch, indicating spatial memory for rewarding locations in all treatments during 3–4 h of foraging (10-cm Halves: $n = 8$, $t = 3.46$, $p = .005$; 40-cm

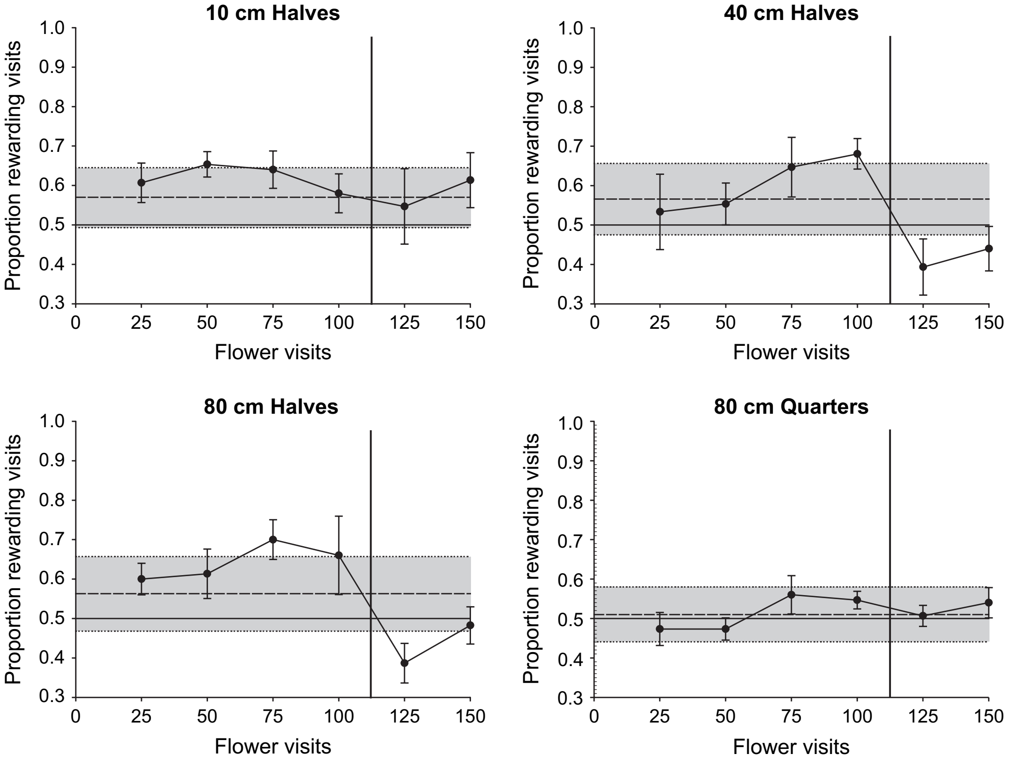

Figure 2
The decline in the proportion of visits to rewarding flowers after the mirror image switch (represented by the vertical lines) indicates the use of spatial memory in the 40- and 80-cm Halves treatments. Bumblebees in these two treatments also visited significantly more rewarding flowers in the 50 visits before the mirror image switch than predicted by the near-far search simulation model (the mean accuracy of the model is denoted by the dashed line and 95% confidence limits denoted by the gray box). In the 10-cm Halves and 80-cm Quarters treatments, the consistency in the proportion of visits to rewarding flowers before and after the mirror image switch indicates that bumblebees did not remember the location of rewarding and unrewarding flowers after 100 visits. Data points are mean accuracy for bees over blocks of 25 flower visits. Error bars represent one standard error.

Halves: $n = 6$, $t = 4.05$, $p = .005$; 80-cm Halves: $n = 6$, $t = 17.63$, $p < .001$; 80-cm Quarters: $n = 6$, $t = 4.75$, $p = .003$; Figure 3). The time to complete the experimental runs did not differ among treatments ($F_{3,20} = 1.35$, $p = .28$). Bumblebees in the 80-cm Halves treatment performed significantly more accurately than those in the 10-cm Halves and 80-cm Quarters treatments in the final 50 visits before the mirror image test (post hoc Tukey-Kramer test, $\alpha = 0.05$). The proportion of first flower visits of a foraging trip that went to rewarding flowers was also significantly greater prior to the mirror image switch in the 40-cm Halves, 80-cm Halves, and 80-cm Quarters treatments but not in the 10-cm Halves treatment (10-cm Halves: $n = 8$, $t = 1.36$, $p = .108$; 40-cm Halves: $n = 6$, $t = 3.87$, $p = .006$; 80-cm Halves: $n = 6$, $t = 7.79$, $p < .001$; 80-cm Quarters: $n = 6$, $t = 7.00$, $p < .001$; Figure 4). An alternative explanation for the pattern of observed first flower visits might be that the bees were following a learned motor pattern. If so, the drops in accuracy observed in the mirror image tests could arise from a bee employing a learned motor pattern to begin in a specific area. This would provide an advantage before, but not after, the mirror image switch to a bee using a near-far search strategy. However, subsequent visits were not part of a trapline or other learned motor pattern as visit sequences were clearly not repeated. Another reason to reject the alternative explanation is that removing the first three visits (to decrease the effect of first visits) from each foraging trip did not qualitatively change any of the mirror image test results. We reason as follows: if a bee were using a learned motor pattern to arrive in the originally rewarding patch, and it then switched to near-far search, it would be likely to fly out of the (now) unrewarding patch after several unrewarding visits in a row. That the bees remained in the unrewarding patches after the first three flower visits indicates that they remembered those flower locations as previously rewarding.

Flight distance did not vary by visit period in the 400-visit experiments ($F_{3,20} = 0.21$, $p = .88$), indicating that the bumblebees flew the same distance after a particular visit type regardless of the number of total flower visits or even the mirror image switch. Therefore, we removed visit period from the multivariate repeated-measures ANOVA and ran the analysis with visit type as the only repeated factor (dependent variable: flight distance, independent variables: visit type and treatment). Two main results emerged. First, bumblebees in the 10-cm Halves treatment flew longer relative distances than did those in the other treatments, regardless of the visit type (treatment: $F_{3,22} = 39.24$, $p < .0001$; Figure 5). Second, bumblebees in each treatment flew farther after unrewarding visits than after a rewarding visit (visit type: $F_{3,20} = 34.89$, $p < .0001$; Figure 5), consistent with a near-far search tactic. There was, however, a significant interaction between treatment and visit type (treatment × visit type: $F_{9,48.8} = 2.75$, $p = .011$), indicating that bumblebees in the 10-cm Halves treatment responded more strongly to unrewarding visits than did bumblebees in the other treatments, particularly the 80-cm Quarters treatment. This interpretation is supported by two observations: (1) A multivariate repeated-measures ANOVA without the 80-cm Quarters treatment and the interaction

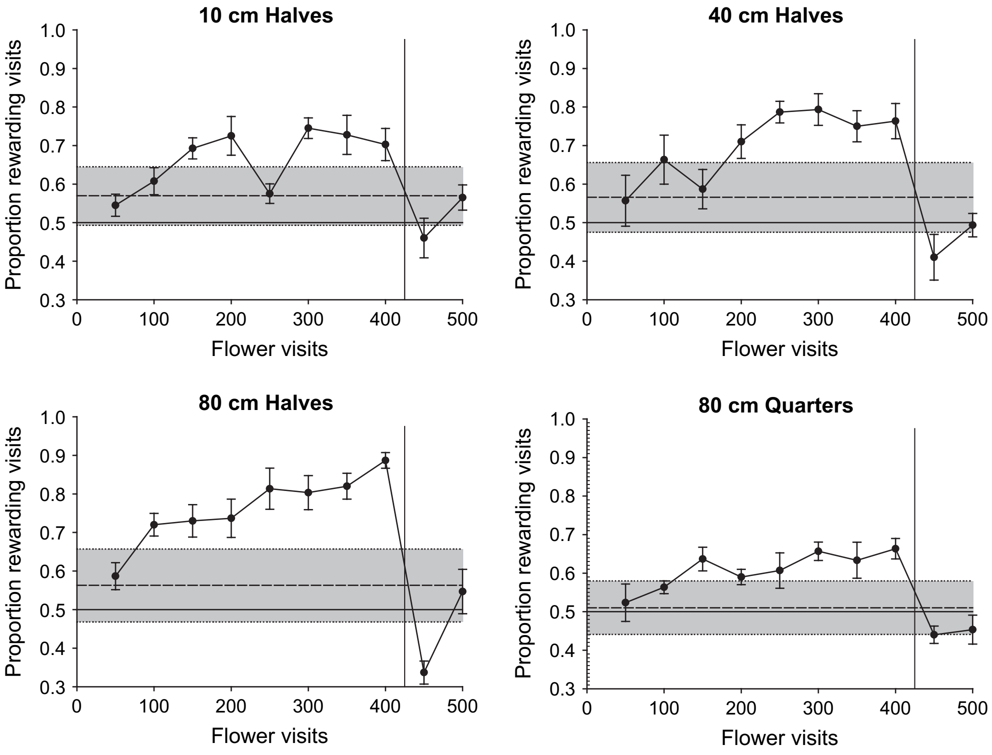

Figure 3
After 400 flower visits, bumblebees in all treatments use spatial memory to increase their accuracy of choosing rewarding flowers, as indicated by the significant drop in accuracy after the mirror image switch (indicated by vertical lines). Accuracy was also greater than that predicted by the near-far search simulation model (mean is denoted by the dashed line and 95% confidence limits denoted by the gray box). Data points are mean accuracy for bees over blocks of 50 flower visits. Error bars represent one standard error.

was no longer significant ($F_{6,30} = 1.29$, $p = .293$); (2) A series of post hoc multivariate repeated-measures ANOVAs with visit type (independent variable), performed on each treatment independently (Bonferroni corrected to $\alpha = 0.0125$), indicate that flight distance (dependent variable) increased significantly in all treatments except at 80-cm Quarters (10-cm Halves: $F_{3,5} = 17.26$, $p < .005$; 40-cm Halves: $F_{3,3} = 10.78$, $p < .005$; 80-cm Halves: $F_{3,3} = 16.48$, $p < .0001$; 80-cm Quarters: $F_{3,3} = 3.2$, $p = .054$).

In the 400-visit experiments, because our analyses were consistent with both near-far search and spatial memory use, we asked whether there were any other indicators to differentiate the two tactics. We reasoned that if bees are able to remember their locations as their experience grew they should be more likely to visit rewarding flowers after making multiple errors. In this case, they would fly to the location of rewarding flowers rather than just "searching" for them. Therefore, we ran a multivariate repeated-measures ANOVA looking at the proportion of rewarding visits after three unrewarding visits (dependent variable) in a row over the four visit periods (1–100, 101–200, 201–300, and 301–400 flower visits) (independent variables: period and treatment). We also analyzed the linear trend of this relationship. There was no significant flower distance treatment effect, but as bees gained experience, they became more likely to follow three unrewarding flower visits in a row with a visit to a rewarding flower (Figure 6; treatment: $F_{3,22} = 0.67$, $p = .578$; period: $F_{3,20} = 2.63$, $p = .078$; period × treatment: $F_{9,48.8} = 0.79$, $p = .629$; linear trend: $F_{3,22} = 5.26$, $p = .032$). We interpret this as another line of evidence for the use of spatial memory: experienced bees that had strayed from the rewarding sectors seemed to know where to go to remedy the problem.

Monte Carlo simulation

The simulation model results paralleled the mirror image tests in each experiment and treatment (100-visit experiment—10-cm Halves: $n = 6$, $z = 1.29$, $p = .098$; 40-cm Halves: $n = 6$, $z = 2.31$, $p = .010$; 80-cm Halves: $n = 6$, $z = 2.59$, $p = .005$; 80-cm Quarters: $n = 6$, $z = 0.69$, $p = .243$; 400-visit

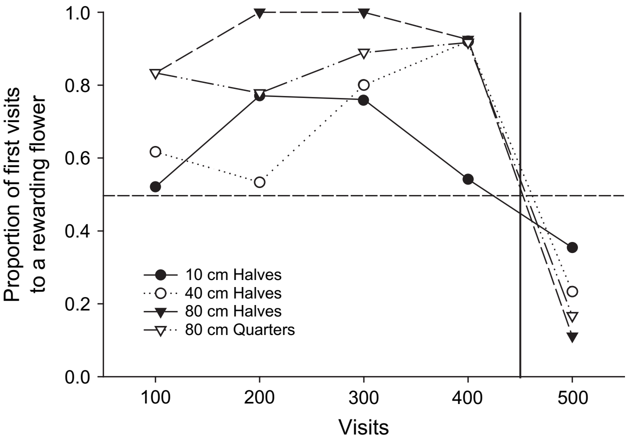

Figure 4
In further support of spatial memory use, the proportion of first flower visits of a foraging trip going to a rewarding flower drops significantly after the mirror image switch in the 40-cm Halves, 80-cm Halves, and 80-cm Quarters treatments. Vertical line represents mirror image switch.

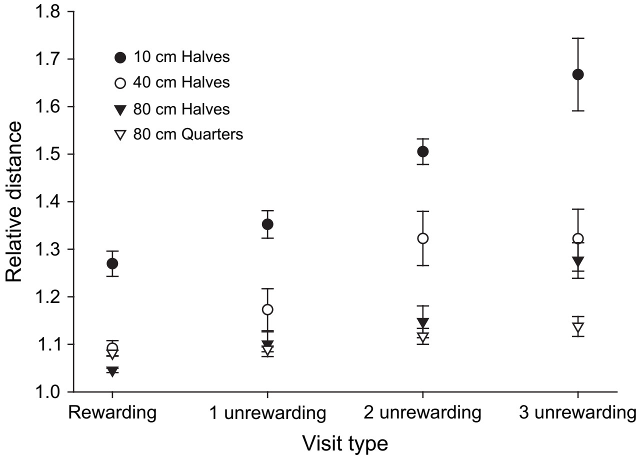

Figure 5
As the number of unrewarding flower visits in a row increases, bumblebees fly a greater distance to the next flower. Relative distance is in "flower units," where one unit is a flight to the closest flower and two units is a flight that skips one flower and ends on the next flower in that line. Bumblebees are also more likely to fly a relatively far distance when flowers are separated by 10 cm than when farther separated.

experiment—10-cm Halves: $n = 8$, $z = 3.08$, $p = .001$; 40-cm Halves: $n = 6$, $z = 3.10$, $p < .001$; 80-cm Halves: $n = 6$, $z = 5.67$, $p < .001$; 80-cm Quarters: $n = 6$, $z = 1.73$, $p = .042$). Figures 2 and 3 show the accuracy of bumblebees over time compared to the predictions of the simulation model.

DISCUSSION

In these experiments, bumblebees used both near-far search and spatial memory tactics. They used near-far search in the early stages of foraging on flowers separated by only 10 cm; as their experience increased, however, they increasingly depended on their spatial memory for locating rewarding flower locations. Our spatial pattern design was simple, but it demonstrates that bumblebees can adjust their foraging tactics after only a few hours. Nature is obviously more spatially complex. In particular, the distinction between rich and poor flowers in nature is not likely to be nearly as clear-cut and consistent as in our experiment. However, nectar resources in the environment can be aggregated, depending on factors such as the actions of nectivores (Pleasants and Zimmerman, 1979; Waser and Mitchell, 1990; Zimmerman, 1981), and wild bumblebees can live several days to weeks, long enough to learn patterns of reward in their environment if those patterns are stable enough. Even so, natural aggregations of flowers with distinctly higher nectar secretion rates would sometimes be empty due to recent draining by other visitors. In our experiments, such depletion never occurred. Our bumblebees did not, however, switch to the most efficient tactic available in our setup: flying back and forth between two rewarding flowers. Whether they would have used this tactic after greater lengths of time is unknown. In any case, the behavior we observed was consistent with natural exploratory flight patterns, and so the lack of local nectar depletion did not seem to affect our experiment.

Further, we suggest that accuracy increased as flower separation increased, within the Halves treatments, because the difference in location of individual flowers became easier to discern for the bumblebees. Our explanation is mechanistic. A nonexclusive alternative using functional reasoning, suggested by Pyke (1978; see also Schmid-Hempel P and Schmid-Hempel R, 1986), predicts that spatial memory use should increase as flower distance increases because knowledge of rewarding locations is more valuable with greater search times. Using Harder's (1988) equation for the rate of net energy uptake with measurements of differences in flight time (~1 versus ~2 s in 10- versus 80-cm separation, respectively) and handling time (7 s for unrewarding flowers and 12 s for rewarding flowers), we calculate an approximately 8% lower rate of energy gain when flight times increase from 1 to 2 s (this is robust to all accuracy levels over 0.10). An 8% difference is modest, but it might be an important consideration. We cannot weigh this energetic advantage against the advantage of easier cognitive decision making but suspect that the latter should not be ignored.

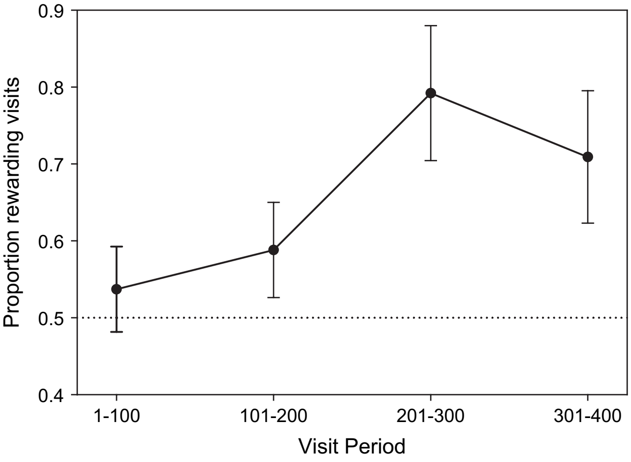

Figure 6
The proportion of visits to rewarding flowers after visits to three unrewarding flowers in a row increases as bumblebees gain experience with the array. The linear trend is significantly positive (linear trend of repeated-measures ANOVA: $F = 5.26$, $p = .032$).

Overall, the movement patterns observed in the 100-visit experiments are consistent with near-far search and are similar to previous studies that have focused on spatial scales of 30 cm or less and time scales fewer than 210 visits (Dukas and Real, 1993; Heinrich, 1979; Keasar et al., 1996). The correspondence of the results for our mirror image tests and simulation model provides confidence in our assessment that near-far search was being used in the first 100 visits of the 10-cm Halves treatment. But in all the Halves treatments, flight distances were consistent with near-far search from beginning to end of each trial, even though the mirror image switches, Monte Carlo simulations, and patterns of first visits all indicate the use of spatial memory. One piece of evidence supporting spatial memory use is that the proportion of visits to rewarding flowers after a run of three unrewarding visits increased over time. This indicates that the long flights taken in those circumstances after experience had been gained were not "searches" but rather directed flights to rewarding flower locations stored in memory. Flight distance can thus be a poor indicator of near-far search and could lead to incorrect conclusions about the movement tactics being used by pollinators.

Qualitatively different performance was observed in the first 100 visits of the 80-cm Quarters treatment compared to the Halves treatments. Although accuracy fell within the boundaries of a near-far search tactic as in the 10-cm Halves treatment, the flight distance patterns do not match. Distance flown after unrewarding visits was only slightly longer than after a rewarding visit. Near-far search is more efficient in aggregated habitats because short flights are more likely to stay within an aggregation of rewarding flowers. Thus, a possible explanation for our observation is that the bumblebees somehow quickly detected that rewarding flowers were less aggregated in the Quarters treatment and used near-far search to a lesser extent.

Our results differ from previous studies in how bumblebees acted on information from the last event experienced or from a longer series of events. In our study, flight distance increased as the number of unrewarding flowers previously visited in a row increased but was not affected by the number of rewarding flowers visited in a row. The reaction to strings of unrewarding flowers suggests that bumblebees place more value on information gathered from multiple flower visits than on information from a single flower visit (Chittka et al., 1997; Dukas and Real, 1993), but the reaction to strings of rewarding flowers suggests otherwise. This pattern could arise, for example, if a bumblebee's attention to its spatial location is differentially affected by rewarding versus unrewarding flowers, in that attention decreased as it visited rewarding flowers but then increased as it encountered unrewarding flowers. Our results, however, fall between those of two related studies. Dukas and Real (1993) reported, similar to our results, that flight distance increased as the string of unrewarding flowers in a row grew, but they also observed a decrease in flight distance with an increase in the number of rewarding flowers visited in a row. Keasar et al. (1996) observed that bumblebees responded in a manner consistent with near-far search, but it made no difference whether the bees had previously visited one versus up to three unrewarding (or rewarding) flowers. Unfortunately, there are numerous methodological differences among the studies, the most apparent being in the species of bumblebee: *Bombus bimaculatus* (Dukas and Real, 1993) and *B. impatiens* (this study) are both North American members of the subgenus *Pyrobombus* and have similar foraging ecologies (Gegear R, personal communication). The European bumblebee *Bombus terrestris* (Keasar et al., 1996) particularly differs from the other two in being a frequent nectar robber (Goulson, 2003). Also, in the experiments of both Dukas and Real (1993) and Keasar et al. (1996), rewarding and unrewarding flowers were randomly distributed, unlike our aggregated distribution.

Overall, our results support the notion that spatial memory can be an important component of bumblebee foraging behavior at scales from inflorescences to patch, as has been reported for similar studies with hummingbirds (Brown and Gass, 1993; Hurly, 1996; Sutherland and Gass, 1995). There is evidence from natural systems that bumblebees remember patches (Heinrich, 1976; Manning, 1956; Osborne and Williams, 2001) and perhaps even individual plants (Cartar, 2004; Thomson, 1988; Williams and Thomson, 1998; but see Klinkhamer et al., 2001). The specifics of the environment and spatial distribution of flowers likely determine the scale at which bumblebees use their spatial memory (Thomson et al., 1982). To explore this, future research should utilize both laboratory and field experiments. Laboratory manipulations including more naturalistic nectar-reward schedules or more complex spatial aggregations could help determine either how long bumblebees require to learn the locations of flowers or when the patterns are beyond their spatial learning abilities. Laboratory studies, however, are likely to be limited to within-patch foraging strategies. Field experiments at larger scales can take advantage of naturally occurring variation in reward level and/or manipulate nectar rewards in naturally occurring plants (e.g., Cartar, 2004) to create highly rewarding patches versus less rewarding patches. Utilization of newer technologies such as harmonic radar will aid in tracking bee movements and foraging strategies through these patches over extended periods.

The foraging tactic switch reported here is analogous to adjustments seen in navigational tactics as an animal gains experience. For instance, some ants use chemical trails or path integration when first foraging but can learn visual landmarks as they travel along their route. Their initial navigation tactic acts as a "scaffold" on which the learning of landmarks is built (Collett et al., 2003). We suggest that near-far search can act as a scaffold on which bumblebees accumulate long-term spatial information of floral reward in order to improve their foraging efficiency. This scaffold serves bees adequately in situations where they lack local experience, and it will continue to be an efficient tactic in cases where nectar depletion by competing foragers means that an intrinsically richer aggregation will sometimes present little reward. But if certain aggregations are statistically better and if bees linger within a particular area long enough to form associative memories of reward and location, then these memories will increasingly come into play. Bees therefore should not abdicate the use of near-far search but can add a new component of sophistication to their foraging repertoire by employing spatial memory.

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