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Original Article

Trapline foraging by bumble bees: VII. Adjustments for foraging success following competitor removal

Kazuharu Ohashi,[a] Alison Leslie,[b] and James D. Thomson[b]
[a]Graduate School of Life and Environmental Sciences, University of Tsukuba, Tsukuba, Ibaraki 305-8572, Japan and [b]Department of Ecology and Evolutionary Biology, University of Toronto, 25 Harbord Street, Toronto, Ontario M5S 3G5, Canada

Animals collecting food from renewable resource patches scattered in space often establish small foraging areas to which they return faithfully. Such area fidelity offers foraging advantages through selection of profitable patches, route minimization, and regular circuit visits to these patches ("trapline foraging"). Resource distribution under field conditions may often vary in time, however, especially when competitors suddenly vanish and a number of patches become available for their neighbors. Previous studies suggested that site-faithful foragers of bumble bees quickly respond to such unexpected events by readjusting their foraging areas, although it is not clear how much their foraging performance was improved, beyond the simple relaxation of competitive pressure, or how they manifest such flexibility while persistently using certain foraging areas or paths. Here, we conducted indoor flight-cage experiments with bumble bees and found that a bee, when encountering a loss of its competitor, improved its foraging performance to a greater extent than expected from a simple relaxation of competitive pressure by increasing the size of its foraging area. Moreover, bees with better-established traplines achieved greater foraging areas after the loss of competitors, suggesting that bees do not necessarily need to "sample" neighboring patches to monitor temporal changes in environments. We discuss how periodical returns and route memory associated with accurate reward values could allow inherently conservative trapliners to make flexible adjustments, by effectively monitoring their circumstances and quickly readjusting to detected changes. *Key words: Bombus*, competition, conservatism, flexibility, readjustment, resource intake rate, trapline foraging. *[Behav Ecol]*

INTRODUCTION

Animals collecting food from renewable resource patches scattered in space often establish small individual foraging areas or territories to which they return faithfully over many days or weeks (Ribbands 1949; Manning 1956; Linhart 1973; Gill and Wolf 1975; Heinrich 1976; Davies and Houston 1981; Thomson et al. 1982; Waddington 1983; Paton and Carpenter 1984; Thomson 1996; Comba 1999; Makino and Sakai 2004). Such area fidelity allows animals to accumulate local knowledge and forage preferentially on more profitable patches (Makino and Sakai 2007), while traveling along the shortest possible route (Lihoreau et al. 2010). Moreover, certain site-faithful animals repeatedly make circuits through a particular set of patches in a predictably nonrandom order, referred to as "trapline foraging" (Janzen 1971; Davies and Houston 1981; Thomson et al. 1982; Lemke 1984; Racey and Swift 1985; Thomson et al. 1987; Garber 1988; Gill 1988; Thomson 1996; Janson 1998; Ohashi et al. 2007; Saleh and Chittka 2007; Ohashi et al. 2008). Trapline foraging reduces the variance of return intervals in each patch, which should confer benefits in 3 ways to an animal that is competing for resources that replenish in a decelerating way: 1) it increases the chances of encountering accumulated resource before its competitors (Ohashi and Thomson 2005; Ohashi et al. 2007), 2) it keeps resource standing crops low and discourages intruders (Possingham 1989; Ohashi and Thomson 2005), and 3) it gets to patches before the slowing refilling rate diminishes too much (Ohashi and Thomson 2005; Ohashi et al. 2008).

Resource distribution for these animals, however, may vary in time on a weekly or even daily basis. In field conditions, individual foragers frequently vanish from a food site due to death, resignation, or emigration (Rodd et al. 1980; Schmid-Hempel and Wolf 1988, Thomson 2004), which makes it possible for the remaining neighbors to use the recently abandoned patches. If site-faithful foragers could quickly detect such changes in circumstances and readjust their foraging areas by recruiting newly opened, more profitable patches while abandoning some of their former favorites, therefore, they might gain long-term competitive advantages through constant improvement of performance.

A few previous studies on bumble bees have provided empirical support for this idea. Thomson et al. (1987) performed competitor removal experiments in bumble bees foraging on a field population of *Aralia hispida* and found that bees shifted their foraging locations toward dense and more profitable flower patches in the removal area. Based on similar removal experiments in a large flight arena, Makino and Sakai (2005) also suggested that competition from other conspecifics forced bumble bees foraging on *Salvia farinacea* to concentrate on fewer plants than when

Address correspondence to K. Ohashi. E-mail: kohashi@biol.life.tsukuba.ac.jp.

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they foraged alone. Thomson et al. (1987) further discovered that remaining bees in the removal experiment came to collect more floral resources and make quicker trips than bees in competitive situations. Although these results are highly suggestive and intuitive, direct evidence has not yet been provided to demonstrate that a more successful readjustment of a bee's foraging area leads to a higher performance in food collection. Moreover, it is not clear how much improvement was achieved by these readjustments in addition to a simple relaxation of competitive pressure, because the gradual removal of nearly 50 competitors (as in Thomson et al. 1987) made it difficult to distinguish the effects of behavioral changes from those of competitive release.

Furthermore, these experiments have prompted another interesting question, concerning how animals make flexible responses to unpredictable resource fluctuations while persistently using certain foraging areas or paths. Although previous authors have repeatedly shown that flower foragers possess both flexibility and persistence in their spatial use (Manning 1956; Thomson et al. 1987; Gill 1988; Thomson 1996; Garrison and Gass 1999; Cartar 2004), it is not certain how they balance between such inherently opposed proclivities. To make an effective readjustment in spatial-use patterns, these animals will first need to detect changes in competitive circumstances, and then will need to take proper actions so that they can improve their performance. Bumble bees are known to make occasional visits to peripheral patches outside their foraging areas (Thomson et al. 1982, 1997). Such sampling visits to neighboring patches of familiar flowers have been suggested to function as a low-cost monitoring system to detect changes in surroundings (Thomson et al. 1987); also, they are necessary for evaluating unfamiliar patches during the process of reformation (Ohashi and Thomson 2005). If more sampling of peripherals necessitates less persistent use of patches, however, such monitoring may inevitably preclude animals from efficiently exploiting patches already included in their foraging areas (Thomson et al. 1987) or, conversely, faithful animals may suffer from sluggish reactions to changes in resource availability. If this is the case, how do animals negotiate a potential trade-off between flexibility for future prospects and persistence for current success?

We therefore conducted indoor flight-cage experiments on the patterns of spatial use by bumble bees (*Bombus impatiens*) foraging from arrays of automated feeders (Ohashi et al. 2008, 2010). By challenging a bee with a sudden removal of its competitor to exploit nectar sources with different renewing rates, we addressed the following specific questions: 1) Do bees change their spatial-use patterns when they encounter an abrupt loss of neighboring competitors, and if so, how? 2) Do the remaining bees readjust their foraging areas in ways that increase their performance, and if so, is the increase more than would be expected from simple relaxation of competitive pressure? and 3) Do animals face a trade-off between effectively tracking changing resources and efficiently exploiting sets of patches, and if so, how do they deal with it?

METHODS

We worked indoors in a flight cage measuring 788 (length) × 330 (width) × 200 (height) cm. Temperature ranged from 26 to 30 ˚C. The room was illuminated with normal fluorescent bulbs (0900–1900). Our subjects were workers from commercial colonies of *B. impatiens* Cresson (supplied by Biobest, Leamington, Canada). Colonies were maintained in nest boxes and connected to the cage with a transparent entrance tunnel fitted with gates, so that we could control the entry of bees into the cage. Pollen was supplied ad libitum every day, directly to the colony. Sucrose solution was dispensed by electric artificial flowers and by a training flower (see below). We used 22 and 30 workers from each of the 2 colonies, which did not significantly differ in their body size (length of radial cell in forewing: Welch's $t = -0.14$, $P = 0.89$).

Artificial flowers and monitoring system

We used an experimental system that has been developed for tracking and identifying multiple bees foraging on 16 feeders. Each feeder (hereafter, "flower") is a vertical box made of clear Plexiglas, with a small electric clock motor mounted at its top. The motor turns an axle (1.50 or 3.15 mm in diameter, depending on the secretion rate desired) at 1/30 rpm, winding up a thread that is clipped to one end of a 50 cm length of flexible tubing (3.0 mm in internal diameter) that contains unscented 30% (w/v) sucrose solution (hereafter, "nectar"). The other end of the tube terminates in a steel needle inserted into a "nectar bucket" (a hole 5.5 mm in diameter, 7.0 mm in depth) drilled in a horizontal platform halfway up the box. As the motor pulls upward, the nectar oozes out through the needle and accumulates in the bucket at a constant rate (1.1 or 2.3 µL/min). Each nectar bucket was topped with a U-shaped block of plastic painted blue, so that bees could easily find and learn to extract nectar from it.

For automatic tracking and identification of individual foragers, we used infrared light-emitting diodes (infrared LEDs) and phototransistors in combination with a Radio Frequency Identification (RFID) system. By wiring phototransistors and RFID readers on nectar buckets to an interface board in a personal computer, we built a data acquisition system that automatically wrote arrival and departure times to 0.1 s, flower ID, and bee ID data to 1 disk file. At the opening of each U-shaped block, an infrared LED produced a beam that was sensed by a phototransistor. When a bee crawled through the opening, it masked the beam and registered a signal on the phototransistor output to the computer (flower ID and arrival time). In response to the signal from the phototransistor, moreover, the computer activated the U-shaped block's overhead RFID reader and interrogated a passive 2.5-mm square and 0.58-mm thick RFID chip (the Coil-on-Chip RFID system®, Hitachi Maxell, Ltd, Tokyo, Japan) glued onto the bee's thorax (bee ID). When the beam was reconnected, the phototransistor sent the departure time to the computer. We could also record on/off timing of the electric motors for the artificial flowers by pressing a specific key, as well as directly enter additional information from the keyboard, such as the accumulated number of foraging trips made by each bee. More details of the artificial flowers and the data acquisition system have been described in Ohashi et al. (2010).

Between experiments, we used a training flower to let bees learn where to find nectar. The training flower had the same shape and color as the 16 automated flowers described above, but the "bucket" communicated to a 3-cm wick made from a cotton dental roll, the other end of which was dipped in 20% (w/v) nectar in a plastic vial attached underneath the stage. Bees could extract nectar from the surface of the wick until they were satiated.

Experimental procedures

We set out 16 artificial flowers in a diamond-shaped array (Figure 1). The interflower spacing of 0.95 m was chosen to be far enough that neighboring flowers would be distinguishable to the bees as different "patches" or "plants" (Thomson

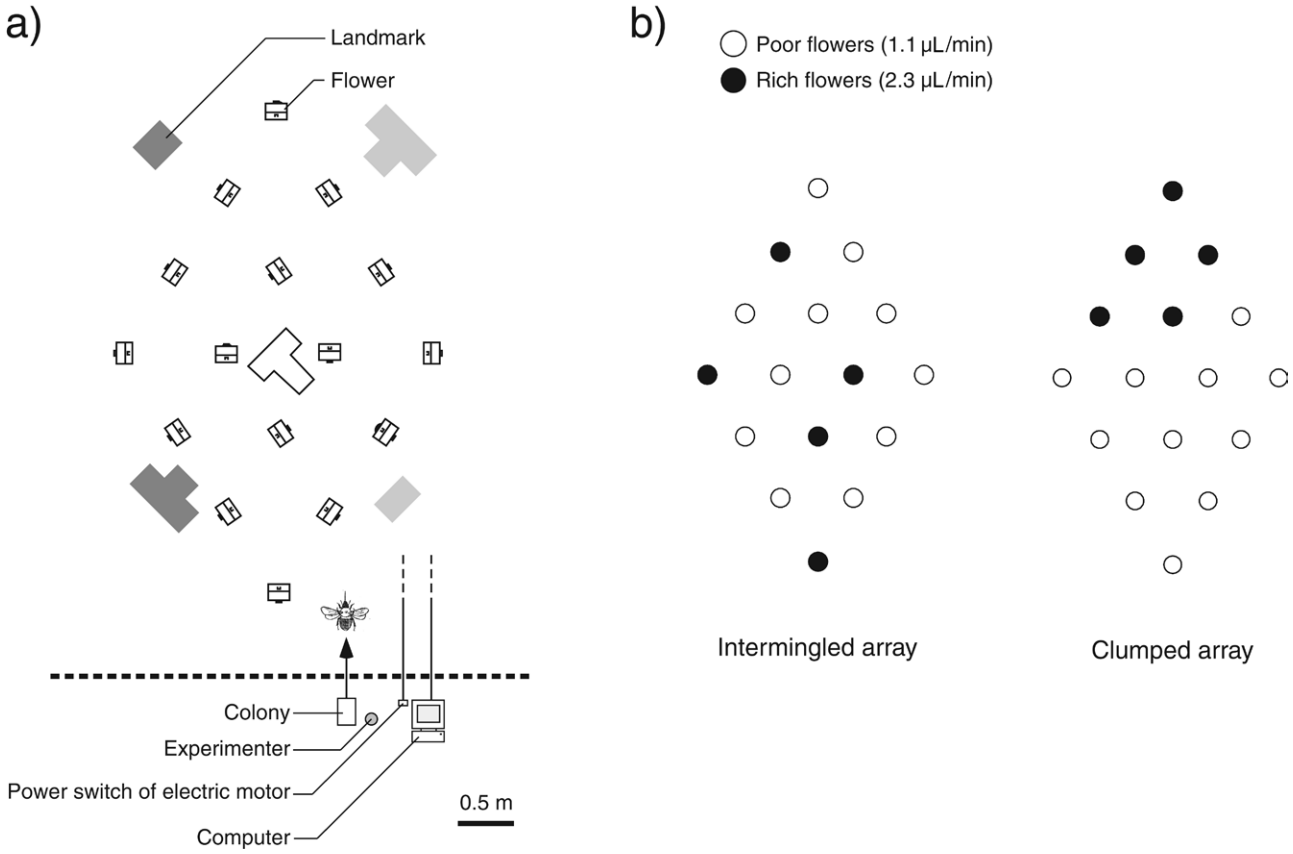

Figure 1
Experimental setup. (a) A schematic view from above of the diamond-shaped array of 16 electric artificial flowers with 5 artificial landmarks in the flight cage and (b) 2 types of spatial arrangements of rich (nectar secretion rate = 2.3 µL/min) and poor (1.1 µL/min) flowers adopted in the experiments: "intermingled" and "clumped" array, respectively.

et al. 1982; Burns and Thomson 2006). The design of our flower, with its tower behind the flower stage, might limit bees' departure directions even though its transparency would allow bees to see through it. To minimize such effects, we arranged the peripheral flowers so that their backs faced outside of the array. We also rotated the 4 middle flowers every 10 trips in randomly chosen directions (−90°, 90°, or 180°), so that bees' departures from these flowers were not biased toward particular directions throughout the experiments. We used four 0.5-m-high artificial landmarks with different combinations of color and shape, made of cardboard boxes and colored paper: 2 rectangular prisms, 1 yellow and 1 purple, and 2 T-shaped columns, also in yellow and purple. We set out each of them within 0.9 m from the array (Figure 1a). On the floor inside the array, we also placed a flat 0.5-m-long landmark cut from a light blue styrofoam board in a T shape.

We also added spatial heterogeneity of reward value into the array, by assigning high nectar secretion rate (2.3 µL/min) to 5 "rich" flowers and low nectar secretion rate (1.1 µL/min) to 11 "poor" flowers. These flowers were identical in their appearance, except for the 1.65 mm difference in their axle diameters that would be indistinguishable to bees in our conditions. The rich and poor flowers were arranged in either of 2 patterns: " intermingled" or "clumped" (Figure 1b).

Before running an experiment, we connected the colony to the cage and let bees forage freely on the training flower. During the training, the 16 artificial flowers were turned off and individually covered with dark brown cloth bags to prevent access. The training flower was located away from any locations of artificial flowers used in the experiments. On non-experiment days, we left the colony open from 1000 to 1700. This procedure allowed bees to associate the U-shaped blue plastic block with nectar rewards, but they remained naive to the spatial array of flowers. When several bees began "regular foraging" (i.e., visiting the flower directly after entering the cage, returning to the nest briefly to deposit their nectar loads, and repeating the same process), we glued 2.5-mm square RFID chips onto their thoraces. Regular foragers typically ran through the gated tunnel connecting the colony and the cage more quickly than others and could be easily identified. When traffic was too busy to keep track of individuals, we lightly marked motivated foragers with acrylic paint on the thorax.

On experiment days, we let bees forage on the training flower for 30–60 min in the morning ("warming-up phase") to refresh their experience of being rewarded on the flower with the U-shaped block. Among the tagged bees that started regular foraging, we chose several for the trial and uniquely marked them on the abdomen with acrylic paint. We managed to choose bees of similar size for each trial to minimize bias in their potential competitive abilities. The training flower and the cloth bags on the 16 artificial flowers were then removed. With a syringe, we drained accumulated nectar from all nectar buckets so that the first visit to each flower would not fill a bee's honey stomach. At the beginning of the trial, therefore, only a trace of nectar was left in each

flower. Thus the first bee visit would drain the nectar amount to 0, after which it accumulated with time while the motors were on.

We then performed the experiment in each of intermingled and clumped array (Figure 1b), imposing the following "removal" or "solo" treatments. These combinations of treatment and array type were randomly assigned to 31 trials. There was no statistical bias between the 2 colonies in assignment of treatment (2-sided Fisher's exact $P = 0.44$) or array type (2-sided Fisher's exact $P = 0.48$).

Removal

This design simulated a situation in which 2 equally experienced bees competed for nectar within a food site, and then one of them quit. After the warming-up phase, we let the 2 bees out to start foraging simultaneously. On release, bees would usually fly around in the cage, but begin to forage systematically within a few minutes. We would catch a slow-starting bee in a plastic vial and guide it into one of the flowers, which often initiated active foraging. If more than 15 min elapsed without visiting a flower, we chose another bee for the trial. Because bees often started out sampling flowers slowly, we avoided nectar overflow by turning on the electric motors after the bee visited the first 10 flowers. When the bee finished its first foraging trip and returned to the hive, we turned off the motors and waited until it reemerged. Throughout these trials, we switched the motors off except when bees were actively foraging. Until both bees made at least 30 trips ("competitive phase"), we diverted all the other bees to a small box (17 × 22 × 10 cm) connected to the nest with a gated tunnel and let them collect nectar from a cotton wick inserted in a plastic petri dish topped with the U-shaped blue plastic block and filled with nectar. This procedure kept the other bees motivated for foraging during the competitive phase. After the competitive phase, we arbitrarily chose 1 of the 2 bees and let it forage alone until it made 30 trips ("postremoval phase"). In this way, we observed 10 and 11 pairs of bees in the intermingled and the clumped arrays, respectively. Because *B. impatiens* and some other bumble bees exhibit no nestmate recognition at hives and food sites (Breed et al. 2007; Lefebvre and Pierre 2007; Ohashi K, Thomson JD, personal observation), we assume that the outcomes would be the same if the bees were not nestmates.

Solo

As the control, we let a bee make 60 solo trips in the array. Corresponding to the 2 phases in the removal treatment, we refer to the first half (1st–30th trips) as the "former phase" and the second half (31st–60th trips) as the "latter phase," respectively. We performed this treatment for 5 bees in the intermingled and the clumped arrays, respectively.

Note that the design of the flowers was intended to create a continuous and uniform supply rate while the motors were running, but that in practice we turned off the motors while the bees were not foraging. This manual intervention, which was necessary to prevent nectar overflow, created a nonlinear pattern of nectar accumulation in flowers; as the elapsed time since last visit increased at a flower, its rate of nectar accumulation gradually decreased (rich flower: Kendall's tau = −0.42, $n = 238$ visits, $P < 0.0001$; poor flower: Kendall's tau = −0.44, $n = 412$ visits, $P < 0.0001$; see also Ohashi et al. 2008).

After each trial, we immediately placed the bee in a clean plastic vial and froze it at −20 °C. We measured the length of the radial cell on the right forewing as an index of body size. We also inspected the hindgut contents under a microscope at ×400 for the intestinal trypanosome *Crithidia bombi* Lipa and Triggiani. *Crithidia* infections sometimes occur in commercial stocks and can affect behavior (Gegear et al. 2005; Otterstatter et al. 2005; Gegear et al. 2006).

Data analysis

The recorded data occasionally showed 2 or more successive visits to the same flower by the same bee; these arose when bees atypically ducked below the beam in the tunnel or when they briefly departed from the flower. We treated all such on-and-off records on a flower as single visits and summed their durations to estimate the probing time. For each flower visit made by a bee, we computed "travel speed between flowers" as the distance per second between departure from the previous flower and arrival at the current flower. We also determined "turning angle" as the difference between the arrival direction and the departure direction at the flower, which may range from −180° to +180° with 0° indicating a straight movement. A bee faces different sets of angle options, depending on its current position in the array. To account for these positional effects, we ranked each choice according to its directionality within the available options and divided the rank by the number of options. Straighter movements scored higher ranks, and clockwise and counterclockwise turns were not distinguished. For example, if a bee chose the 2nd straightest movement among 9 available options at 1 of the 2 acute-angled corners of the diamond array (Figure 1), the measurement would be 2/9 = 0.11. We referred to this measurement as "relative angle rank." Turning angle has been suggested as a good indicator of the length of a bee's foraging circuits, because longer circuits generally consist of straighter paths between patches (Ohashi et al. 2007, 2008).

We subsequently estimated the amount of nectar a bee gained at each visit, assuming that 1) nectar accumulated in flowers with time at a constant rate (1.1 or 2.3 µL/min) as long as the motors were running, 2) all the accumulated nectar was taken at single visit, and 3) nectar secreted during a visit was also taken by the bee. Nectar crops encountered at the initial 2 visits to each flower (after the motor was first turned on for the day) were omitted. We then obtained averages of all the variables for the last 80 visits (roughly the average number of visits in 2 foraging trips) of the competitive phase, the first 80 visits ("transitional period") and the last 80 visits ("stabilized period") of the postremoval phase made by a bee that continued to forage in the removal treatment. We computed the corresponding values for the solo treatment by using the last 80 visits from each of the former and the latter phases (averages for the first 80 visits of the latter phase in the solo treatment were not used for the analyses).

For each trial, we also assessed 5 characteristics of a bee's spatial use using the last 80 visits of the competitive (or former) phase and those of the postremoval (or latter) phases, respectively. First, we measured the size of a bee's foraging area (hereafter, "foraging range") using a rarefaction method, originally developed for assessing species richness (Hurlbert 1971):

$$\sum_{i=1}^{16}\left[1-\frac{{}_{80-V_i}\mathrm{C}_n}{{}_{80}\mathrm{C}_n}\right]$$

where V_i is the number of observed visits to ith flower, n is the number of randomly chosen visits, and ${}_{80}\mathrm{C}_n$ is the "choose" function of 80 and n (also known as the combination or binomial coefficient):

$${}_{80}\mathrm{C}_n=\binom{80}{n}=\frac{80!}{n!(80-n)!}$$

That is, the number of ways that n visits can be chosen from the observed 80 visits. This index represents the average number of flowers that is included in n visits randomly and independently drawn from the observed 80 visits. By substituting

n = 40 into the above formula, we calculated the expected number of flowers in a sequence when a bee makes 40 visits (roughly the average number of visits per trip). Although the rarefaction method is designed to compensate for variation in sampling effort, which did not apply here, we preferred it to other diversity measures (e.g., Simpson's index) because the expected number of flowers used per trip gives a more direct picture of a bee's foraging range. Second, we calculated the coefficient of variation (CV) of return cycle (the number of flowers visited before returning), using all return visits made within each trip. The CV of return cycle was suggested by Thomson et al. (1997) as the best simple index of foraging-route repeatability or traplining. In this paper, we used the CV of return cycle multiplied by −1 as the index of repeatability (hereafter, "route repeatability"). Third, we determined the location of a bee's foraging area as the "centroid" (or "center of gravity") of each set of 80 visits in the removal treatment, computed from x- and y-coordinates and visit frequencies of all the flowers in the array. We obtained these values for the competitive and the postremoval phases of the bees that continued to forage (the remained bees), as well as for the competitive phase of the removed bees. We then measured the distance between the centroids of the paired bees during the competitive phase, and also the distance between the centroid of the remained bee during the postremoval phase and the old centroid of the removed bee (hereafter, "centroid distance to competitor" or "CDC"). Fourth, we obtained the centroid of rich flowers in the array, and measured its distance to the centroid of the remaining bee during the competitive and the postremoval phases (hereafter, "centroid distance to rich flowers" or "CDR"). Fifth, we measured a bee's preference for rich flowers as the relative visitation frequency to rich flowers multiplied by 16/5. This index should approach one if a bee chose flowers randomly, with greater values indicating higher levels of preference for rich flowers. Finally, we calculated the gross rate of nectar intake (total amount of nectar gain divided by total time spent on interflower movements and probing flowers) for each trip as an overall measure of a bee's foraging success.

Statistical analysis

We tested whether and how bees' spatial-use patterns and foraging performance at the end of the competitive (or former) phase changed through the transitional period to the stabilized period of the postremoval (or latter) phase. We compared all the variables calculated for the competitive (or former) phase, the transitional period of the postremoval phase, and the stabilized period of the postremoval (or latter) phase with Wilcoxon signed-rank tests (Sokal and Rohlf 1995), treating the trials as pairs. Comparisons between the last 80 visits of the competitive phase and those of the stabilized period of the postremoval phase would allow us to exclude fluctuations in data during the very early stages of a bee's foraging career, as well as to detect net changes after the bee became adjusted to the postremoval situation. On the other hand, changes between the competitive phase and the transitional period of the postremoval phase, and changes between the transitional and the stabilized periods of the postremoval phase, would inform us about the direction and intensity of the bee's immediate and delayed responses to competitor removal, respectively. We applied Benjamini and Hochberg's (1995) false discovery rate control to correct for 3 comparisons in each variable, which gave almost identical results with more conservative corrections such as Holm's (1979) sequential Bonferroni method. We also asked how and whether bees subjected to the 4 combinations of treatment (removal/solo) and phase (competition/postremoval or former/latter) differed in the aspects of their spatial use and foraging performance, using an adjusted Tukey–Kramer comparison where repeated measurements for individual bees were considered in calculating the standard error of the difference. We pooled data from the intermingled and the clumped arrays in these analyses, because our preliminary surveys with generalized linear mixed model (GLMM) analysis for spatial-use patterns and foraging performance (Crawley 2002) had revealed that inclusions of array type (intermingled/clumped) as an explanatory variable always increased the Akaike information criterion (AIC) by more than 4, indicating that the array difference adds little to the explanatory power for bees' spatial behavior and performance in different treatments and phases (see also Table 1).

Next, we examined which spatial-use aspects of bees' readjusted foraging areas were most influential in determining their foraging performance after the competitor removal, by using generalized linear model (GLM) analysis with an identity link function and a gaussian (normal) distribution function (McCullagh and Nelder 1989). We considered the following 10 factors as the potential candidates for the explanatory variables: foraging range, route repeatability, average turning angle, preference for rich flowers, centroid distance to the removed competitor (CDC), CDR, average travel speed between flowers, and array type (intermingled or clumped) during the stabilized period of the removal treatment, together with body size and *Crithidia* infection (number of protozoan cells in 1 μL of feces sample) of individual bees. We used the average nectar crop per flower during the stabilized period of the removal treatment as the response variable representing bees' foraging performance, instead of gross rate of nectar intake sharing the same denominator variable with travel speed between flowers (i.e., travel time between flowers).

We avoided a direct application of model selection in GLM to the data set with 10 explanatory variables, because it implicitly assumes that explanatory variables are highly independent from one another. When the assumption is not met, model selection may not properly exclude "noise" variables that affect the response variable largely through spurious correlations with the other variables, or may fail to incorporate the truly influential variables whose effects are suppressed by the others (see Mac Nally 2000 for details). This problem cannot be detected by checking the variation inflation factors, unlike the well-known "multicollinearity problem" (Mansfield and Helms 1982), and becomes exacerbated with greater numbers of explanatory variables. As a complementary analysis to GLM, therefore, we preliminarily performed hierarchical partitioning (Chevan and Sutherland 1991; Mac Nally 2000; Walsh and Mac Nally 2003) to narrow the candidates. We employed log-likelihood as a goodness of fit measure and averaged the incremental improvement in fit by the addition of a given variable to all the 2^9 possible models with that variable compared with the equivalent model without that variable (Chevan and Sutherland 1991). This averaging effectively excludes spurious effects that would appear only in combination with certain variables. The average for each variable (X_i) is called the "independent effect" (I_i), corresponding to the sum of direct (partial) and indirect effects in path analysis. The sum over 10 variables (ΣI_i) equals the difference in fit between the full model (i.e., $Y = a + b_1X_1 + ... + b_{10}X_{10}$) and the null model (i.e., $Y = a$). Mac Nally (2002) recommended randomization tests on I values for identifying significantly important variables. Instead, we adopted a more conservative way to avoid type II errors due to small sample size; because we had 10 potential candidates, we excluded variables with 10% or smaller contribution of independent effects ($100 \times I_i/\Sigma I_i$) as probable noise or unimportant variables. We then

exhausted all possible models from the remaining variables and selected the most parsimonious one with the smallest AIC in GLM analysis, to leave out variables whose effects on the response variable were mostly indirect.

Finally, of the spatial-use patterns that developed during the competitive phase, we asked which were most influential in achieving a successful rearrangement of foraging areas after the competitor removal, by using GLM analysis with an identity link function and a gaussian distribution function. We used the response variable that we had identified in the above 2 analyses as being the most changed and influential; this turned out to be the foraging range during the stabilized period of postremoval phase (see Results). We considered the following 10 factors as the candidates for the explanatory variables: foraging range, route repeatability, average turning angle, preference for rich flowers, centroid distance to the removed competitor (CDC), CDR, average travel speed between flowers, and array type (intermingled or clumped) during the competitive phase, together with body size and *Crithidia* infection of individual bees. After narrowing these candidates with hierarchical partitioning (as above), we exhausted all possible models from the remaining variables and selected the most parsimonious one with the smallest AIC in GLM analysis.

RESULTS

Changes in spatial-use patterns

Bees significantly expanded their foraging areas during the postremoval phase in the removal treatment, but not during the latter phase in the solo treatment (Figure 2a and Table 1). This expansion started after the removal, and gradually progressed to the significant level as the bees accumulated more experience in the postremoval situation (Table 1). The foraging area reached similar sizes in both arrays by the stabilized period, although the overall change was not significant in the clumped array (Table 1). Bees with larger foraging areas tended to have smaller turning angles (average relative angle rank) during the stabilized period (Kendall's tau with data pooled for the intermingled and the clumped arrays = –0.32, n = 21 bees, P = 0.042), but the overall change in turning angles after the removal did not reached the significant level in either array (Table 1).

On the other hand, bees changed the other aspects of spatial use only slightly after the competitor removal (Table 1). A bee's foraging area tended to move toward the "removal area" that had been formerly occupied by its competitor in both arrays, as indicated by the slight decrease (~10 cm) in the centroid distance to the competitor's foraging area (CDC), but these trends were too weak to be significant in our modest-sized data set (Table 1). Throughout the experiments, moreover, bees responded minimally in terms of relative foraging efforts on rich flowers in either array, as indicated by the nonsignificant decrease in preference for rich flowers as well as in the CDR (Table 1). Similarly, only a little increase was observed for the route repeatability, indicating that bees maintained their initial levels of traplining regardless of the relaxation of competition (Table 1). Finally, the adjusted Tukey–Kramer comparison revealed that only foraging range during the competition phase in the removal treatment was significantly lower than the stabilized period of the postremoval phase and the solo treatment (Figure 2a). None of the other aspects of spatial use significantly differed between the competition and the stabilized period of the postremoval phases, or between the removal and the solo treatments (the adjusted Tukey–Kramer tests).

Changes in foraging performance

Bees significantly increased the gross rate of nectar intake during the postremoval phase in the removal treatment, but not during the latter phase in the solo treatment (Figure 2b and Table 1). A significant increase in performance was achieved by the gradual improvement that occurred between the transitional and the stabilized periods of the postremoval phase in the clumped array, and this was also true when we pooled the data from both the intermingled and the clumped arrays (Table 1). This gradual increase, together with the immediate increase after the removal, eventually allowed the bees to achieve the same performance level as those in the solo treatment (Figure 2b).

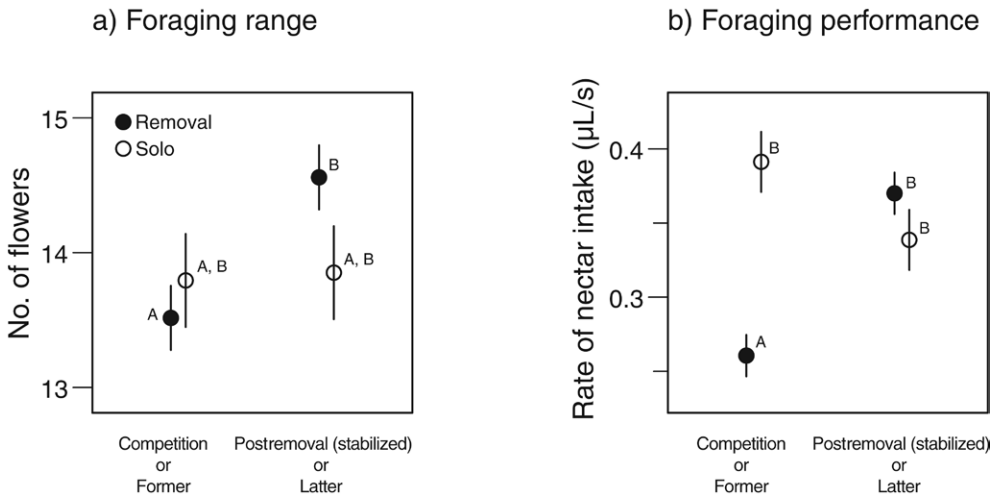

Figure 2
Changes in (a) foraging range and (b) performance between different phases of foraging. Data only from the stabilized period are used for representing the postremoval phase. Closed and open circles indicate means for the removal and the solo treatment, respectively. Bars indicate ±1 SEs. These values were calculated from multiple bees tested in each treatment. In each graph, the mean values significantly differ from one another at $P < 0.05$ are labeled with different alphabets (the adjusted Tukey–Kramer comparison, where repeated measures for individual bees are considered).

Table 1
Changes in spatial-use patterns and foraging performance in different periods in the removal and the solo treatements

	Removal treatment			Solo treatment	
	Competition phase	Transitional period	Stablized period	Former phase	Latter phase
Foraging range (flowers)					
Intermingled	13.1 ± 0.38^{A}	13.8 ± 0.34^{A}	14.5 ± 0.24^{B}	14.2 ± 0.33^{a}	13.8 ± 0.75^{a}
Clumped	13.8 ± 0.38^{A}	13.8 ± 0.28^{A}	14.6 ± 0.13^{A}	13.6 ± 0.86^{a}	13.9 ± 0.20^{a}
Pooled	13.5 ± 0.28^{A}	13.8 ± 0.21^{B}	14.6 ± 0.13^{C}	13.8 ± 0.44^{a}	13.9 ± 0.37^{a}
Route repeatability (−CV of return cycle)					
Intermingled	-0.89 ± 0.07^{A}	-0.76 ± 0.03^{A}	-0.82 ± 0.05^{A}	-0.74 ± 0.11^{a}	-0.75 ± 0.05^{a}
Clumped	-0.87 ± 0.08^{A}	-0.78 ± 0.06^{A}	-0.77 ± 0.10^{A}	-0.73 ± 0.10^{a}	-0.94 ± 0.13^{a}
Pooled	-0.87 ± 0.05^{A}	-0.77 ± 0.03^{A}	-0.79 ± 0.06^{A}	-0.73 ± 0.07^{a}	-0.85 ± 0.07^{a}
Centroid distance to competitor (CDC) (m)					
Intermingled	0.49 ± 0.09^{A}	0.44 ± 0.09^{A}	0.34 ± 0.06^{A}	—	—
Clumped	0.45 ± 0.07^{A}	0.37 ± 0.08^{A}	0.36 ± 0.04^{A}	—	—
Pooled	0.47 ± 0.06^{A}	0.40 ± 0.06^{A}	0.35 ± 0.03^{A}	—	—
Centroid distance to rich flowers (CDC) (m)					
Intermingled	2.51 ± 0.08^{A}	2.47 ± 0.08^{A}	2.41 ± 0.06^{A}	2.52 ± 0.19^{a}	2.43 ± 0.15^{a}
Clumped	2.53 ± 0.09^{A}	2.67 ± 0.08^{B}	2.40 ± 0.05^{A}	2.57 ± 0.21^{a}	2.43 ± 0.20^{a}
Pooled	2.52 ± 0.06^{A}	2.58 ± 0.06^{A}	2.40 ± 0.04^{A}	2.54 ± 0.14^{a}	2.43 ± 0.12^{a}
Preference for rich flowers					
Intermingled	1.20 ± 0.10^{A}	1.05 ± 0.13^{A}	1.00 ± 0.11^{A}	1.07 ± 0.08^{a}	1.14 ± 0.14^{a}
Clumped	1.17 ± 0.18^{A}	1.33 ± 0.19^{A}	0.89 ± 0.06^{A}	1.31 ± 0.46^{a}	1.24 ± 0.48^{a}
Pooled	1.19 ± 0.10^{A}	1.20 ± 0.12^{A}	0.95 ± 0.06^{A}	1.19 ± 0.22^{a}	1.19 ± 0.24^{a}
Turning angle (relative rank)					
Intermingled	0.39 ± 0.03^{A}	0.37 ± 0.02^{A}	0.35 ± 0.02^{A}	0.39 ± 0.03^{a}	0.36 ± 0.02^{a}
Clumped	0.37 ± 0.03^{A}	0.36 ± 0.02^{A}	0.33 ± 0.02^{A}	0.34 ± 0.05^{a}	0.36 ± 0.03^{a}
Pooled	0.38 ± 0.02^{A}	0.36 ± 0.01^{A}	0.34 ± 0.01^{A}	0.36 ± 0.03^{a}	0.36 ± 0.02^{a}
Travel speed between flowers (m/s)					
Intermingled	0.47 ± 0.02^{A}	0.46 ± 0.01^{A}	0.45 ± 0.02^{A}	0.41 ± 0.02^{a}	0.46 ± 0.02^{a}
Clumped	0.46 ± 0.02^{A}	0.46 ± 0.02^{A}	0.44 ± 0.02^{A}	0.46 ± 0.03^{a}	0.42 ± 0.02^{a}
Pooled	0.46 ± 0.01^{A}	0.46 ± 0.01^{A}	0.45 ± 0.01^{A}	0.44 ± 0.02^{a}	0.44 ± 0.02^{a}
Gross rate of nectar intake (μL/s)					
Intermingled	0.25 ± 0.01^{A}	0.35 ± 0.02^{B}	0.37 ± 0.02^{B}	0.44 ± 0.04^{a}	0.34 ± 0.02^{a}
Clumped	0.27 ± 0.02^{A}	0.32 ± 0.02^{A}	0.37 ± 0.02^{B}	0.35 ± 0.03^{a}	0.34 ± 0.03^{a}
Pooled	0.26 ± 0.01^{A}	0.34 ± 0.02^{A}	0.37 ± 0.01^{B}	0.39 ± 0.03^{a}	0.34 ± 0.02^{a}

Means ± SEs were calculated for each variable, using results from multiple bees. Values with different superscripts in each row (upper case alphabets for removal treatment, and lower case alphabets for solo treatment) were significantly different from each other at the 0.05 level. Statistical significance was evaluated with Wilcoxon singed-rank test, corrected for 3 nonindependent comparisons in the removal treatment using Benjamini and Hochberg's (1995) false discovery control.

Determinants of foraging performance after the removal

We retained the variables foraging range, turning angle, travel speed between flowers, and *Crithidia* infection as important influences on foraging performance (average nectar crop encountered per flower) during the stabilized period of the postremoval phase, as they had independent effects on the response variable of greater than 10% in hierarchical partitioning. Note that the variable with the lowest independent effect on the response variable was array type (0.2%). We then used the 4 remaining variables as the candidates for a GLM analysis, and performed an exhaustive search of all possible models to find the most parsimonious one with the smallest AIC. The resultant model (Table 2) included only foraging range and travel speed between flowers. No other variable or interaction term improved the overall fit. The estimated parameter values suggest that slow bees with greater foraging ranges gained higher average nectar crop per flower after the competitor removal (Table 2).

Effects of spatial-use patterns on responses to competitor removal

Given that expanded foraging area was the only spatial-use aspect that could explain the improved performance of bees after the competitor removal (Figure 2, Tables 1 and 2), we then asked which aspects of spatial use employed by individuals during the competition phase contributed most to their foraging range during the stabilized period. Using hierarchical partitioning, we chose route repeatability during the competition phase and *Crithidia* infection as possible important variables influencing foraging range during the stabilized period. Note, again, that the variable with the lowest independent effect on the response variable was array type (1.6%). Also, foraging range during the competition phase had little effect on the size of rearranged areas after the removal (2.3%). We then used the 2 remaining variables as the candidates for a GLM analysis, and performed an exhaustive search of all possible models to find the most parsimonious one with the smallest AIC. The resultant model (Table 3) included both explanatory variables. The estimated parameter values suggest that less infected bees that had established more repeatable routes during the competition phase acquired larger foraging ranges after the competitor removal (Table 3).

DISCUSSION

Readjustment of spatial use in response to loss of neighboring competitors

Bumble bees included more flowers in their foraging areas after they had encountered a competitor removal (Figure 2a

Table 2

Factors influencing foraging performance (the average nectar crop per flower) during the stabilized period of the postremoval phase

Explanatory variable	Parameter estimate ± SE
Intercept	0.55±3.01
Foraging range (flowers)	0.52±0.23
Travel speed between flowers (m/s)	−9.06±2.50

GLM was performed with an identity link function and a gaussian (normal) distribution function. Explanatory variables were narrowed from all the candidates to those with independent effects of greater than 10% in hierarchical partitioning, and the most parsimonious model with the smallest AIC was selected by an exhaustive search.

Table 3

Factors influencing foraging range during the stabilized period of the postremoval phase

Explanatory variable	Parameter estimate ± SE
Intercept	15.4±0.31
Route repeatability during the competitive phase	0.77±0.36
Crithidia infection (cells/μL)	−0.0011±0.00025

GLM was performed with an identity link function and a gaussian (normal) distribution function. Explanatory variables were narrowed from all the candidates to those with independent effects of greater than 10% in hierarchical partitioning, and the most parsimonious model with the smallest AIC was selected by an exhaustive search.

and Table 1). This result is consistent with another experiment by Makino and Sakai (2005), where a bumble bee significantly increased its foraging repertoire when all the other competitors were removed from a flight arena. Because bees in the solo treatment showed no such trend during the latter phase, it seems unlikely that this expansion of foraging area arose simply through accumulated experience (Figure 2a and Table 1). None of the other aspects of spatial use significantly changed after the removal, although there were some weak tendencies (Table 1): 1) a shifting of the center of the foraging area to move toward the area that had been occupied by the removed competitor, as well as toward the center of rich flowers, 2) a decrease in preference for rich flowers, and 3) an increase in route repeatability. These aspects of spatial use did not significantly differ from those in the solo treatment, either (indicated by the adjusted Tukey–Kramer tests, see Results). In addition, spatial distribution of rich flowers did not have a significant effect on bees' spatial-use patterns and their responses to the competitor removal (indicated by GLMM, see Results).

Foraging performance significantly improved after the removal of the competitor (Table 1). Because a substantial portion of the increase occurred as a delayed response during the stabilized period of the postremoval phase, this increase cannot be attributed solely to the relaxation of competitive pressure—which took effect immediately during the transitional period—but also to behavioral changes in response to the competitor removal (Table 1). In fact, bees encountered more nectar at each flower as they increased their foraging ranges after the competitor removal (Table 2). As one can tell from the negative correlation between foraging range and turning angle (see Results), as well the absence of a reduction in shift in the CDR after the removal (Table 1), larger foraging ranges must have increased the average nectar crop primarily by allowing bees to make more visits before returning to the same flowers. The decrease in turning angles after the competitor removal fell short of significance, however (Table 1).

Clearly, bee foragers are able to quickly exploit the abrupt disappearances of neighboring competitors due to death, resignation, or emigration; they readjust their own foraging areas and routes so as to improve their performance. Although previous authors suggested that bees modify spatial-use patterns and concurrently increase their foraging performance after changes of surrounding competitive situations (Thomson et al. 1987; Makino and Sakai 2005; Ohashi et al. 2008), our experiments provide the first direct evidence that changes in spatial use improve the foraging performances of individuals (Table 2). Furthermore, our results differ from previous studies in that we have distinguished the effects of behavioral changes on foraging performance (delayed response) from those of competitive release (immediate response; Table 1).

Advantages of persistent traplining in flexible responses to changing environments

Bees acquired larger foraging ranges after the competitor removal if they had established more repeatable routes during the competition phase, and if they were heavily infected by *Crithidia* (Table 3). This result suggests that trapline foraging, or repeated sequential visits to a series of resource patches (in our case, flowers), allows bees to respond more effectively to resource patchiness in time. Given that traplining is intrinsically conservative, however, such a positive association with effective readjustment seems counterintuitive. As Thomson et al. (1987) pointed out, information gathering through occasional sampling of peripheral patches (in this case, shoots) will necessitate less repeatable foraging routes, from which one would expect a trade-off between persistence and flexibility in traplining.

A probable explanation for this discrepancy is that bees may not necessarily need to sample neighboring patches to monitor temporal changes in resource distribution, even though such a direct evaluation is necessary in the actual process of readjustment where bees make decisions to include or exclude individual patches. For example, it is probable that a trapliner has more chances of detecting the absence of competitor through visual cognition, because it is making periodical rounds of a widespread circuit that allows more exhaustive collection of information about surroundings. As Kawaguchi et al. (2006, 2007) suggested, bumble bees can visually recognize conspecifics on other flowers and use those observations to decide whether to sample. Similar advantages of traplining may apply for situations where bees monitor newly blooming flowers on neighboring plants or patches. Alternatively, periodical rounds made by a trapliner may allow it to build an accurate expectation for reward crop gained by returning to each patch. Because a bee's foraging area is not an exclusively held territory, it may quickly notice the absence of neighbors through the increased reward level on their patches formerly shared with those competitors. Once they detect changes in resource distribution, trapliners may also be able to expand their foraging areas more easily, by simply introducing newly opened patches into their established routes comprised patches with well-known qualities. Foragers with less regular routes, on the other hand, may have to reevaluate many "stop-off" patches with unfamiliar qualities together with newly opened patches, to decide which ones to recruit into their foraging areas.

Our experimental conditions may be less competitive and less cognitively challenging than those in nature, where bees may encounter more competitors on plants or smaller

volumes of nectar provided by more flowers. Traplining may not make much difference in such situations: if competitors are plentiful, the disappearance of one or a few may be inconsequential, and the nectar crops encountered at each flower may be too scarce and variable to build an accurate patch-level expectation. It should be noted, however, that a trapliner might still obtain more reliable information than random foragers because its route tends to spread widely in space and pass through areas that are not shared by competitors (Ohashi and Thomson 2005). To test these hypotheses, we need to learn more about how traplining bees monitor and detect changes in resource availability or competitive intensity at a food site, as well as how they realign their foraging routes when they detect any changes in circumstances.

Possible influences of spatial scales

As described above, we could not find any significant response to the competitor removal except the increase in foraging range. It should be noted, however, that changes in some aspects of spatial use were simply too small to be detected in a data set of this size. For example, foraging areas of the remaining bees shifted in ways that could increase the probabilities of encountering underused or rich flowers, although the shifts were not significant (i.e., CDC and CDR in Table 1). This seems consistent with another removal experiment by Thomson et al. (1987), where the remaining bumble bees shifted their foraging locations toward dense, rewarding flower patches in the removal area. Similarly, bees barely increased the repeatability of their foraging routes after the removal, which is consistent with the previous finding that bees built more repeatable routes in solo than in competitive situations (Ohashi et al. 2008). The relatively small changes in these aspects may be explained, at least partially, by the spatial scales considered in these experiments. Our flower setup attempted to simulate situations where a bee fills its crop by making multiple revisits to patches during 1 foraging trip, whereas only a fraction of high-reward patches is available inside and outside its foraging area. Similar situations may frequently be encountered by bumble bees whose foraging areas are squeezed by surrounding competitors (Thomson et al. 1982; Makino et al. 2007). At the small spatial scale of our experiments, disappearance of one or a few competitors may not cause significant changes in a bee's foraging location or route repeatability for 2 reasons.

First, reward crop encountered by a bee under these circumstances depends on both the elapsed time since the last visit and the resource renewal rate at each patch. If a bee restricts its visits to a few high-reward patches, therefore, its performance will inevitably drop because it will be revisiting patches too soon; in our case, visits restricted to 5 rich flowers will reduce average return intervals to one-third of those expected when 16 flowers are visited at equal probability, which cannot be surpassed by the contrast of average nectar productivity in flowers encountered by the discriminative and nondiscriminative foragers (2.3/1.48 = 1.6 times). If a bee could manage to visit more rewarding patches during a circuit of its foraging route, there may still be a chance that resource productivity and return intervals are well balanced across patches. Such adjustments, however, will inevitably produce many loops or detours along a foraging route, leading to increased costs of travel distance or irregular return intervals. The former cost could be considerable in our case, where a bee needed to make a number of foraging circuits before filling its crop. In experiments by Lihoreau et al. (2011), *Bombus terrestris* workers exhibited trade-offs between the 2 advantageous behaviors of 1) route shortening and 2) prioritizing visits to higher-reward patches (i.e., visiting them first). Even when Lihoreau et al. increased nectar so that a bee could fill its crop without making return visits, bees did not give priority to richer patches if doing so required excessively long flights. Such a trade-off between preference and distance may explain the low preference for rich flowers in the solo treatment, the nonsignificant changes in foraging locations, as well as the inconsistent trends between CDR and the preference index (Table 1).

Second, the loss of competitors at such a densely crowded food site will make only a limited number of patches newly available to the remaining bee. It is likely that this aspect of our setup made the shifts in bees' foraging locations too small to be detected. The centroid of a bee's foraging area did tend to move toward the area that had been occupied by its removed competitor (Table 1), although the effect was not significant. This suggests that bees have abilities to do such adjustments by recruiting flowers that had been frequented by the competitor while abandoning few of their previous favorites.

Although some natural situations will be similar to those simulated here, there are certainly other cases too. For example, bees may have larger foraging ranges with fewer overlaps at a food site if they can find many other plant species or populations in bloom. When competitors disappear from such situations, then, a number of patches will become newly available. This would provide the remaining bees with more chances of concentrating on high-reward patches while avoiding too frequent returns. As suggested by Thomson et al. (1987), this may allow bees to shift their foraging locations toward more rewarding patches in the competitive vacuums and, in turn, achieve greater levels of performance. More experiments will be needed to clarify effects of different spatial scales on flexible adjustments in bees' use of space.

CONCLUSIONS

By tracking movement paths of individuals and the resulting reward gain, this work provides the first demonstration that bumble bees respond to the loss of competitors by increasing their foraging repertoires, and that such expansion improves their foraging performance more than expected from a simple relaxation of competitive pressure. In plant populations where previously exploited foraging areas open up frequently, as plants start and stop flowering or as bees disappear, such a refined ability to locate and fill competitive vacuums would produce long-term competitive advantages. Our results further suggest that bees with better-established traplines have more chances of making proper adjustments of spatial-use patterns when previously exploited areas open up in their neighborhood. The primary advantages of traplining arise from its inherent conservatism and its consequent tendency to produce periodic returns (Ohashi et al. 2008). Nevertheless, the observed correlation between route repeatability and postremoval readjustment may indicate another indirect advantage of traplining: it eases the monitoring of temporal changes in resource distribution, and the use of previous knowledge to decide which patches to recruit. In further studies, we plan to examine how trapliners monitor surroundings while maintaining a certain level of route repeatability, and how they realign their routes when changes are detected. We also hope that our present results will encourage future work on spatial scales and flexibility of foraging areas in animals collecting renewable resources from isolated patches in the field.

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