

# Trapline foraging by bumble bees: V. Effects of experience and priority on competitive performance

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Animals collecting resources that are fixed in space but replenish over time, such as floral nectar and pollen, often establish small foraging areas to which they return faithfully. Some repeatedly visit a set of patches in a significantly predictable sequence (so-called “trapline foraging”), which may allow them to focus on more profitable patches in their foraging areas. The functional significance of trapline foraging itself, however, has not been empirically demonstrated, especially in competitive situations. We conducted laboratory experiments with artificial flowers to test whether and how accumulated foraging experience in bumble bees affects their movement patterns and foraging performance in the presence of competition. Experienced bees with prior access to flowers achieved higher rates of nectar intake than did later arrivals because they traveled faster between flowers and returned to flowers at more regular intervals. These behavioral skills improved foraging performance in competitive situations in 2 ways: nectar that accumulated in flowers could be harvested before its replenishment rate slowed down, and nectar could be taken before the arrival of a competitor. In each foraging trip, however, bees traveled more slowly as they followed more repeatable routes. Despite this trade-off between speed and accuracy in traplining, bees constantly upgraded both skills as they gained experience from trip to trip. This upgrading still occurred in the absence of a competitor. Foraging area fidelity thus allowed bumble bees to establish long-term spatial memory required for fast movements and accurate traplining and, in turn, increased their foraging performance in competition with less experienced individuals. *Key words:* area fidelity, *Bombus*, competition, foraging experience, long-term spatial memory, trapline foraging, travel speed. [*Behav Ecol* 19:936–948 (2008)]

Animals collecting foods 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; Singh 1950; 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). If such area fidelity allows animals to accumulate local knowledge and choose more profitable patches, experienced individuals may enjoy greater foraging success than newly arrived ones within a particular area (Makino and Sakai 2007).

In addition to this obvious advantage, area fidelity may provide foragers with some other advantages by affecting their movement patterns. It has been known that certain animals are not only faithful to an area but also repeatedly make circuits through a particular set of patches in a predictably nonrandom order, referred to as “trapline foraging” (Manning 1956; Janzen 1971; Heinrich 1976; Davies and Houston 1981; Janson et al. 1981; Ackerman et al. 1982; Dressler 1982; Thomson et al. 1982, 1987; Lemke 1984; Racey and Swift 1985; Garber 1988; Gill 1988; Tiebout 1991; Thomson 1996; Janson 1998; Watts 1998; Comba 1999; Garrison and Gass 1999; Ohashi et al. 2007; Saleh and Chittka 2007). Previous studies have suggested that trapline foraging is based on a long-term spatial memory

of locations, layout, reward values, or a sequence of resource patches along a route. For example, several field experiments found that traplining animals responded to changes in profitability of particular patches by adjusting visitation rate (Thomson et al. 1982, 1987; Lemke 1984; Gill 1988; Garrison and Gass 1999; Temeles et al. 2006), and also that they persistently searched the locations and paths from which traplined patches had been removed (“trapline holdover”; Manning 1956; Thomson 1988; Thomson et al. 1997). Moreover, 2 laboratory studies have recently examined how naive bumble bees develop their own traplines while collecting nectar in a floral array. Both studies have found that naive bees started out sampling flowers along a variety of routes, but that, as they gained experience, their foraging routes became more repeatable and more efficient than would be expected from a combination of simple movement rules (Ohashi et al. 2007; Saleh and Chittka 2007).

When an animal is foraging alone, traplining may increase its foraging performance in 3 ways. First, by producing periodical returns, traplining significantly reduces variation in elapsed time between visits on each patch (Thomson et al. 1997; Ohashi et al. 2007). Theoretical studies have shown that reducing variation in return intervals brings several advantages: a reduction of mean resource standing crop or mean reward crop encountered by other, random visitors (“defense by exploitation”; Garrison and Gass 1999); an increase of the mean reward crop encountered when resource renews in a decelerating way, caused by returning to patches before the refilling rate diminishes too much; and reduction of variation in reward crop at each visit, which will be preferred by risk-averse foragers (Possingham 1989; Ohashi and Thomson 2005). Second, empirical studies with bumble bees have

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Received 22 November 2007; revised 28 March 2008; accepted 28 March 2008.

suggested that traplining animals often enlarge their foraging circuits as they gain experience (Ohashi et al. 2007; Saleh and Chittka 2007). Foragers with longer circuits may encounter more reward on average when they arrive at patches because larger amount of nectar would be accumulated in flowers before their returns (Ohashi and Thomson 2005). Third, trapliners may travel faster between patches because, having learned the patches' locations, they spend less time searching (Saleh and Chittka 2007). Faster movements may reduce net time cost when resource renewal decelerates with time because the cost of increased travel time cannot be fully counterbalanced by the increase in reward crop.

In competitive situations, additional benefits and costs may develop. First, simulations show that foragers with less variable return intervals will more often preempt resources in patches ahead of competitors in moderately competitive situations, even if their average return interval stays constant (Ohashi and Thomson 2005). Second, trapliners with longer foraging circuits will tend to share more patches with others and will tend to benefit less from reduced variation in elapsed time between visits, but they may still encounter more reward per visit when they arrive at patches ahead of competitors (Ohashi and Thomson 2005). Third, traplining may increase the chance of preemption through fast returns to individual patches. To understand the evolution of area fidelity and traplining, therefore, we have to know whether these effects provide net benefits, especially in animals that forage in competition.

Quantifying the possible benefits and costs of area fidelity, however, encounters considerable difficulties. In the only field study that has examined relationships between visitation patterns and reward crops encountered by bumble bees (Williams and Thomson 1998), more periodic visitors did not encounter higher standing crops of reward. The most plausible reason for this is that the single *Penstemon strictus* plant observed by those authors was visited too frequently. As Ohashi and Thomson (2005) have shown, the differences in foraging performance among individuals with different movement patterns break down as competitors visit more frequently. Also, Williams and Thomson (1998) could have missed some true advantages of traplining because they observed only one focal plant and could not compare performance of competitors across all the patches they visited. Even if we could solve these problems by experimental manipulation, it may still be difficult to determine how accumulated experience could affect foraging performance. Foraging performance of an animal appears to be determined by a number of factors such as foraging speed, route geometry, spatial overlap with others, body size, and parasitic infection (Pyke 1978; Possingham 1989; Goulson et al. 2002; Spaethe and Weidenmüller 2002; Ohashi and Thomson 2005; Otterstatter et al. 2005; Ohashi et al. 2007; Saleh and Chittka 2007). These factors often covary with one another via multiple pathways, which would make it difficult to partition the variance in foraging performance explained by each factor. For example, larger animals might tend to forage better because they can fly faster, but if they are also more susceptible to infection, their intrinsic advantage of speed may be negated by their propensity to disease. With such complicated causal relationships, traditional statistical techniques assuming no correlation among independent variables (such as multiple regression and analysis of variance) are poorly suited for estimating the relative importance of each factor in determining an animal's foraging performance. Rather, we need to hypothesize a model describing complex relationships among a set of factors and subject it to rigorous statistical testing.

We therefore conducted laboratory experiments on the patterns of spatial use by bumble bees (*Bombus impatiens*) com-

peting to exploit controlled nectar sources in a large flight cage. We were particularly concerned with possible advantages of priority, so we paired experienced bees (which had already had an opportunity to establish their own foraging routes) with inexperienced bees that entered the competition later. We used an array of artificial feeders ("flowers") that secreted sugar solution ("nectar") at a uniform rate. The flowers were equipped with an automatic data acquisition system that combined radio frequency identification (RFID) of bees and light-emitting diode (LED) recording of visit times and durations. We monitored the timing and sequence of all flower visits as the bees foraged in the presence or absence of competition at different resource levels (low or high nectar secretion rate), and then we calculated the amount of nectar obtained by the bees at each visit. To identify the factors and effects that are most critical to foraging performance of animals in competition, we adopted path analysis with structural equation modeling (SEM). Here we addressed the following specific questions: 1) Does foraging experience affect a bee's performance in competitive situations? 2) Which behavioral aspects or traits are most critical to the foraging performance of a bee in competition? 3) How do behavioral aspects or traits of a bee affect its foraging performance in competition? 4) How does the presence or absence of competition and resource levels affect a bee's foraging behavior?

## MATERIALS AND 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 from 0900 to 1900 h with normal fluorescent bulbs. 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, which allowed individual bees to be tested by restricting access of other bees. Pollen was supplied ad lib every day, directly to the colony. Sucrose solution was dispensed by electric artificial flowers and by a training flower, as detailed below. We continued to use one colony for the experiment until it started producing males and new queens. We used 2, 20, 4, and 24 workers from each of 4 colonies, respectively.

### Artificial flowers and monitoring system

We used 16 identical electric artificial flowers for experiments. A small electric clock motor, mounted at the top of a vertical box made of clear Plexiglas, turns an axle (2.4 or 3.2 mm in diameter, depending on the secretion rate desired) at 1/30 r.p.m. The turning axle winds 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% sucrose solution (hereafter, "nectar"). The other end of the tube terminates in a steel needle inserted into a "flower," comprising a "nectar bucket" (a hole 5.5 mm in diameter and 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 (1.8 or 2.3 μL/min). Each nectar bucket was topped with a U-shaped block of plastic painted in blue, so that bees could easily find and learn to extract nectar from it. The block was further covered with a plastic roof, creating a short tunnel into which a bee had to crawl to reach the nectar bucket.

For automatic tracking and identification of individual foragers, we used infrared LEDs and phototransistors in combination with a RFID system (Pettit et al. 1996; Chittka and

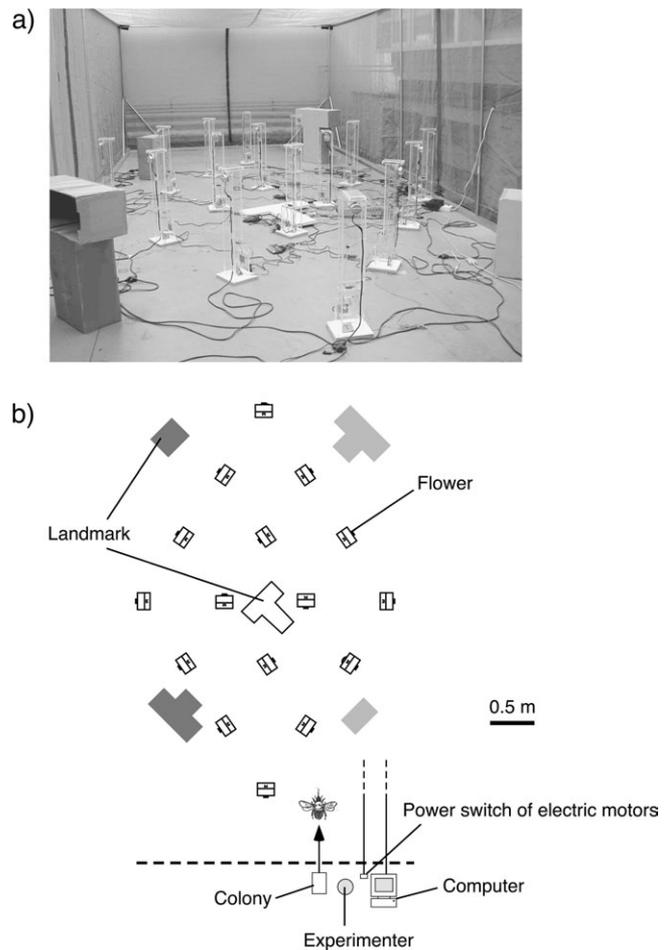
Thomson 1997; Streit et al. 2003; Sumner et al. 2007). By wiring phototransistors and RFID readers on flowers to an interface board in a personal computer, we built a data acquisition system that automatically wrote timing (arrival and departure) to 0.1 s, flower ID, and bee ID data to one disk file. At the opening of each flower, an infrared LED produced a beam that was sensed by a phototransistor. When a bee crawled through the tunnel, 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 flower's overhead RFID reader and interrogated a passive 2.5-mm square 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. Outside the cage, we used an additional U-shaped block with an LED and a phototransistor to record on/off timing of the electric motors for the artificial flowers by interrupting the beam while we turned the motors on. We could also 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 are described elsewhere (Ohashi et al. 2007; Ohashi K, D'Souza D, Thomson JD in preparation).

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 automated flowers, but the "bucket" communicated to a 3-cm wick made from a cotton dental roll, the other end of which was dipped in 20% sucrose solution 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 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 allowed bees to see through it. To minimize such effects, therefore, we arranged the peripheral flowers so that their backs faced outside of the array where there was no other flower. We also rotated the 2 middle flowers every 10 trips in random directions, so that their backs faced any of the 3 closest corners. 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 1). 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.

Before running an experiment, we connected the colony to the cage and let bees forage freely on the training flower. During the training phase, the 16 electric artificial flowers were turned off and individually covered with dark brown cloth bags to prevent the bees' access. The training flower was located away from any locations of artificial flowers used in the experiments. On nonexperiment days, we left the colony open between 1000 and 1700 h. 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



**Figure 1**  
Experimental setup. (a) The diamond-shaped array of 16 electric artificial flowers with 5 artificial landmarks in the flight cage and (b) its schematic view from above.

their nectar loads, and repeating the same process), we glued a 2.5-mm square RFID chip onto the thorax of each of several foragers.

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 while they remained naive to the array of flowers. 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 electric 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 set the nectar amount to 0, after which it accumulated with time while the motors were turned on.

We then performed the experiment in each of low- and high-resource conditions (low resource: 1.8  $\mu\text{L}/\text{min}$ , high resource: 2.3  $\mu\text{L}/\text{min}$ ), according to any of the following 3 types of treatments. These combinations of treatment and resource condition were randomly assigned to 26 trials to reduce the

bias in data due to the date of experiment and to the state of colonies.

### 1–2–1 Competition

This design simulated a situation in which an experienced and a newly arrived bee competed for nectar within a food site, and then either of them went away on the next day. After the warming-up phase, we released the first bee (B1) only. Upon release, a bee 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 in vain, 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. Therefore, we were simulating a situation in which foragers quickly deposited their collections in the nest and returned to foraging immediately. Such behavior is commonly, if not universally, shown by motivated bumble bee workers (Thomson et al. 1987). While B1 was making 30 foraging trips (“solo phase 1”), 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 solo phase 1. After the solo phase 1, we subsequently let the second bee (B2) into the main cage to compete with B1. Thus, B1 had accumulated experience for several hours (low resource:  $n = 8$  bees, mean  $\pm$  standard error [SE] = 3.51  $\pm$  0.33 h; high resource:  $n = 8$  bees, mean  $\pm$  SE = 2.78  $\pm$  0.21 h) when B2 started foraging. The trial was continued (“competition phase”) until B2 made 30 trips. On the following day, we arbitrarily chose one of the 2 bees and let it forage alone until it made 30 trips (“solo phase 2”). In this way, we observed 8 pairs of bees in each of the low- and the high-resource conditions.

### 2–2 Competition

In this treatment, we simulated a situation where 2 equally experienced bees competed within a food site. After the warming-up phase, we let 2 bees out to start foraging simultaneously. The trial was continued until both bees made at least 60 trips. In this way, we observed 4 pairs of bees in each of the low- and the high-resource conditions.

### Solo

As the control, we let a bee make 60 solo trips in the array. We performed this treatment for 1 bee in the low- and the high-resource conditions, respectively.

Note that the design of the flowers was intended to create a continuous and uniform supply rate while the motors were turned on, but that in practice we turned off the motors while the bees were not foraging in the experiments. 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 (low resource: Kendall’s tau =  $-0.50$ ,  $n = 433$  visits,  $P < 0.0001$ ; high resource: Kendall’s tau =  $-0.44$ ,  $n = 851$  visits,  $P < 0.0001$ ).

After each trial, we immediately placed each focal bee in a clean plastic vial and froze it at  $-20$  °C. We measured the length of the radial cell on the right forewing of each bee as an index of body size. We also inspected the hindgut contents under a microscope at  $\times 400$  for the intestinal trypanosome *Crithidia bombi* Lipa and Triggiani. *Crithidia* infections

sometimes occur in commercial stocks and can affect behavior (Gegeer et al. 2005, 2006; Otterstatter et al. 2005).

### Data analysis

#### Characterizing behavior and performance of individuals

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 (distance per second from the previous flower to the current flower), probing time (difference between the arrival time and the departure time at the flower), return interval (elapsed time since last visit to the flower by the same bee), return cycle (number of flower visits a bee made before returning to the flower), and turning angle (difference between the arrival direction and the departure direction at the flower). Previous studies in bumble bees (*B. impatiens*) have shown that return cycle increases with developing traplines (Ohashi et al. 2007; Saleh and Chittka 2007), and that this comes about because bees develop larger foraging circuits comprising straighter movements between flowers (Ohashi et al. 2007).

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 (1.8 or 2.3  $\mu\text{L}/\text{min}$ ) as long as the motors were running, 2) all the accumulated nectar was taken by a bee at one 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 each foraging trip made by a bee. We also calculated the coefficient of variation (CV) of return cycle (the number of flowers visited before returning) and CV of return interval (the elapsed time before returning) for each trip. Our algorithm counted all returns to all flowers that fell within a single trip from the hive and calculated these 2 types of CVs if the trip contained more than 2 returns. The CV of return cycle was suggested by Thomson et al. (1997) as the best practical measure of repeatable foraging routes or traplines. In this paper, we used the CV of return cycle multiplied by minus one as the index of repeatability (hereafter, “route repeatability”). 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 the currency of a bee’s foraging performance.

For each trip made during the competition phase, we calculated the proportion of revisits made by a bee before another bee’s arrival (hereafter, “preemption rate”). For the former and the latter halves (15 trips each) of the competition phase, we also measured the extent of spatial overlap (i.e., flower sharing) between B1 and B2 using Pianka’s (1973) symmetrical index of niche overlap:

$$\frac{\sum_i^{16} p_{i1} p_{i2}}{\sqrt{\sum_i^{16} p_{i1}^2 \sum_i^{16} p_{i2}^2}} \quad (1)$$

where  $p_{i1}$  and  $p_{i2}$  represent the relative visitation rates to the  $i$ th flower by B1 and B2, respectively. This index ranges between 0 and 1 with greater values indicating higher levels of spatial overlap.

#### Statistical analysis

We compared foraging behavior and performance during the competition phase between B1 and B2 in the 1–2–1 treatment,

or between 2 bees during 31st to 60th trips in the 2–2 treatment (corresponding to the competition phase in the 1–2–1 treatment). We calculated a median of each variable for each of paired bees and compared them with Wilcoxon's signed-ranks tests (Sokal and Rohlf 1995), treating the trials as pairs. We also compared certain behavioral variables between resource conditions or treatments with Mann–Whitney *U*-tests. When variances significantly differed between resource conditions, we alternatively used tests for equality of medians (Sokal and Rohlf 1995) to avoid a type I and/or type II error due to heterogeneity of variances (Kasuya 2001). Changes in these variables from trip to trip were tested with Kendall's tau with a third blocking variable (Korn 1984), treating the bees as blocks.

To examine whether and how bees change their behavior in response to an addition or a removal of a competitor, moreover, we fitted general linear models (GLMs), with the response variable being one of 3 measures of bee behavior (medians of *average travel speed*, *route repeatability*, and *average return cycle* within each phase of each bee), and the explanatory variables being “competitor” (absent or present), “experience” (accumulated number of foraging trips at the beginning of each phase), and “resource condition” (low or high) (Grafen and Hails 2002). Data from all the test bees ( $n = 50$ ) were used for these analyses; comparisons were made between the 1st to 30th trips and 31st to 60th trips, and between the 31st to 60th trips and the 61st to 90th trips.

To understand what factors determined bees' foraging performance in each trip during the competition phase in the 1–2–1 treatment, we performed path analysis with SEM using the software program AMOS 7.0 (Arbuckle 2006). We adopted SEM in path analysis because it allows simultaneous significance testing for the set of individual path coefficients (for more details, see Iriondo et al. 2003; Pugsek et al. 2003). We built a path model hypothesizing the causal relationships among variables, based on a priori knowledge from studies with bumble bees and theoretical considerations (Pyke 1978; Possingham 1989; Goulson et al. 2002; Spaethe and Weidenmüller 2002; Ohashi and Thomson 2005; Otterstatter et al. 2005; Ohashi et al. 2007; Saleh and Chittka 2007). We hypothesized that B1's gross rate of nectar intake per trip is determined by 3 major factors: 1) average and variance of B1's return interval at flowers, 2) average time spent on each visit (i.e., travel time plus probing time), and 3) proportion of revisits made by B1 before B2's arrival (i.e., preemption rate). B1's behavioral patterns, characterized by travel distance, travel speed, flower probing speed, route repeatability, turning angle, return cycle, and return interval, would directly or indirectly affect B1's gross rate of nectar intake per trip through their effects on the above 3 factors. In contrast, B2's behavioral patterns would only indirectly affect B1's performance through their effects on the third factor, that is, B1's preemption rate. Traits of test bees, such as body size and *Crithidia* infection, may also indirectly affect B1's performance through their effects on the behavioral patterns. To include B2's behavioral aspects into the model, we used the concurrent trip made by B2 for each B1's trip. Because B2 tended to be slower than B1 in making trips, they usually made only one trip while B1 was making 1–2 trips. In rare cases (<10%) where B2 made 2 trips during a single B1's trip, we chose the earlier one as the concurrent trip.

We fitted the same path model to the 2 data sets obtained in low- and high-resource conditions. The maximum likelihood method was used to estimate standardized path coefficients, which are equivalent to standardized partial regression coefficients. We set the means of errors in the observed variables to 0 and set the path coefficients from these errors to 1 to avoid the identification problem (Arbuckle 2006). We handled missing values in the data (<0.4% of total) with the “full in-

formation maximum likelihood” option that could analyze incomplete data sets directly by estimating paths and covariances from the raw data (Myrteit et al. 2001; Arbuckle 2006). We used multivariate Wald tests to assess the significance of individual path coefficients. To assess the degree of fit between the observed and expected covariance structures, we used chi-squared ( $\chi^2$ ) and the root-mean-square error of approximation (RMSEA). A significant chi-squared statistic indicates lack of satisfactory model fit, but Arbuckle (2006) cautions that this test is more likely to result in a type I error when sample size is larger than few hundred. RMSEA is also a goodness-of-fit index based on predicted versus observed covariances, but it is less affected by sample size, and it corrects for model complexity. RMSEA is less than 0.05 for very good models (close fit), less than 0.1 for models that fit adequately, and larger than 0.1 for poor models. When the fit was poor, we modified the model by deleting or adding variables and paths, based on the significance tests for path coefficients, and redid the analysis. We repeated such model trimming or building procedures until the model gave a satisfactory fit to the data without losing its biological relevance. It should be stressed that we carefully avoided any drastic change of the basic model structure that we initially predicted, because our primary interest was to quantify the contribution of each variable within the overall relationship, not to find a very accurate model to predict foraging performance of bees in a specific circumstance. Finally, we tested whether path coefficients differed between the low- and the high-resource conditions based on the critical ratio for the difference between coefficients (the difference between the estimates divided by the estimate of the SE of the difference) (Arbuckle 2006). The critical ratio (or *Z* statistic) has a standard normal distribution; the probability of getting a critical ratio as large as 1.96 in absolute value is less than 0.05 (2 sided).

## RESULTS

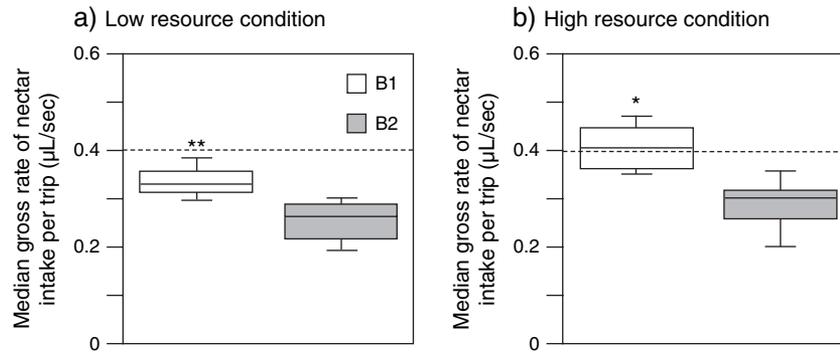
### Foraging performance of competitors

In each trip during the competition phase of the 1–2–1 treatment, the experienced bees (B1) collected significantly more nectar per unit time than the newly arrived bees (B2) (Figure 2). The difference in the median gross rate of nectar intake between competitors was statistically significant in both resource conditions (low resource:  $n = 8$  pairs,  $P = 0.0078$ ; high resource:  $n = 8$  pairs,  $P = 0.016$ ; Wilcoxon's signed-ranks test). We also found that foraging performance differed between paired bees during trips 31–60 in the 2–2 treatment (corresponding to the competition phase in the 1–2–1 treatment) and categorized the members of the pair as the “winner” and the “loser.” To determine whether prior experience aided a bee in pairwise competition, we compared the difference in performance between winner and loser in the 2–2 treatment (low resource:  $n = 4$  pairs, mean  $\pm$  SE =  $0.03 \pm 0.01$   $\mu$ L/s; high resource:  $n = 4$  pairs, mean  $\pm$  SE =  $0.05 \pm 0.03$   $\mu$ L/s) to the difference between B1 and B2 in the 1–2–1 treatment (low resource:  $n = 8$  pairs, mean  $\pm$  SE =  $0.08 \pm 0.02$   $\mu$ L/s; high resource:  $n = 8$  pairs, mean  $\pm$  SE =  $0.12 \pm 0.03$   $\mu$ L/s); the former was smaller than the latter, indicating that priority confers an advantage (low resource: 2-sided Fisher's exact  $P = 0.061$ ; high resource: 2-sided Fisher's exact  $P = 0.55$ ; pooled data: 2-sided Fisher's exact  $P = 0.027$ , test for equality of medians).

### Path analysis

#### Model fit

To determine which variables increased or decreased the competitive performance of B1 and to what degree, we turned to



**Figure 2**

Foraging performance of experienced (B1) and newly arrived (B2) bees in (a) the low-resource condition and (b) the high-resource condition. The gross rate of nectar intake was calculated for each trip, and each box-whisker plot was drawn using medians from 8 bees. Asterisks (\* $P < 0.05$ , \*\* $P < 0.01$ , and \*\*\* $P < 0.0001$ ) denote significant differences between B1 and B2, as assessed by Wilcoxon's signed-ranks tests. Dashed lines indicate median gross nectar intake rate per trip, calculated from 30th to 60th trips in solo treatment (low resource: median =  $0.40 \mu\text{L/s}$ ; high resource: median =  $0.39 \mu\text{L/s}$ ).

path analyses. After testing 90 or more possible path models, we eventually obtained a reasonably well-fitting, biologically meaningful model for describing the effects of variables on B1's foraging performance in each trip during the competition phase of the 1–2–1 treatment (Figure 3). This model had a significant chi-squared statistic ( $\chi^2 = 394.6$ , degrees of freedom [df] = 116,  $P < 0.0001$ ), but the  $\chi^2/\text{df}$  ratio (=3.4) was lower than 5, the threshold value suggested by Wheaton et al. (1977) for accepting a model. Moreover, the RMSEA (=0.061) was lower than 0.08, the threshold value suggested by Browne and Cudeck (1993). We therefore considered the model a satisfactory depiction of the overall relationship among variables. The model explained 24% and 9% of variance among trips in B1's gross rate of nectar intake per trip in the low- and the high-resource conditions, respectively.

The direct paths to B1's gross rate of nectar intake in the model indicate that B1 could increase its mean nectar crop per flower in 3 different ways (Figure 3). First, bees would obtain more nectar crops if they had higher preemption rates. Second, bees with larger return cycles would encounter larger crops when they returned to flowers. Third, because the nectar in our flowers replenished in a nonlinear, decelerating way (see Materials and methods), bees could increase mean crop by returning to flowers before the refilling rate diminishes too much. This could be done either by reducing the variance of return interval or by increasing the travel speed (Ohashi and Thomson 2005). Note that a reduction of nectar crop per flower due to fast returns, if any, would not decrease the rate of nectar intake because it would be fully counterbalanced by a shortened return interval. All the other indirect paths illustrate how changes in behavioral variables or traits of bees were reflected in B1's performance by affecting these aspects of foraging. We deleted several nonsignificant variables and paths from the model, such as travel distance between flowers, flower probing speed, *Crithidia* infection, B2's turning angle, B2's mean return cycle, paths from body size to route repeatability, and paths from return cycle to spatial overlap, because they significantly decreased the overall model fit. We also avoided including mean return interval and mean nectar crop into the model as independent variables because these variables united the effects of return cycle and travel speed and made their separate effects difficult to separate.

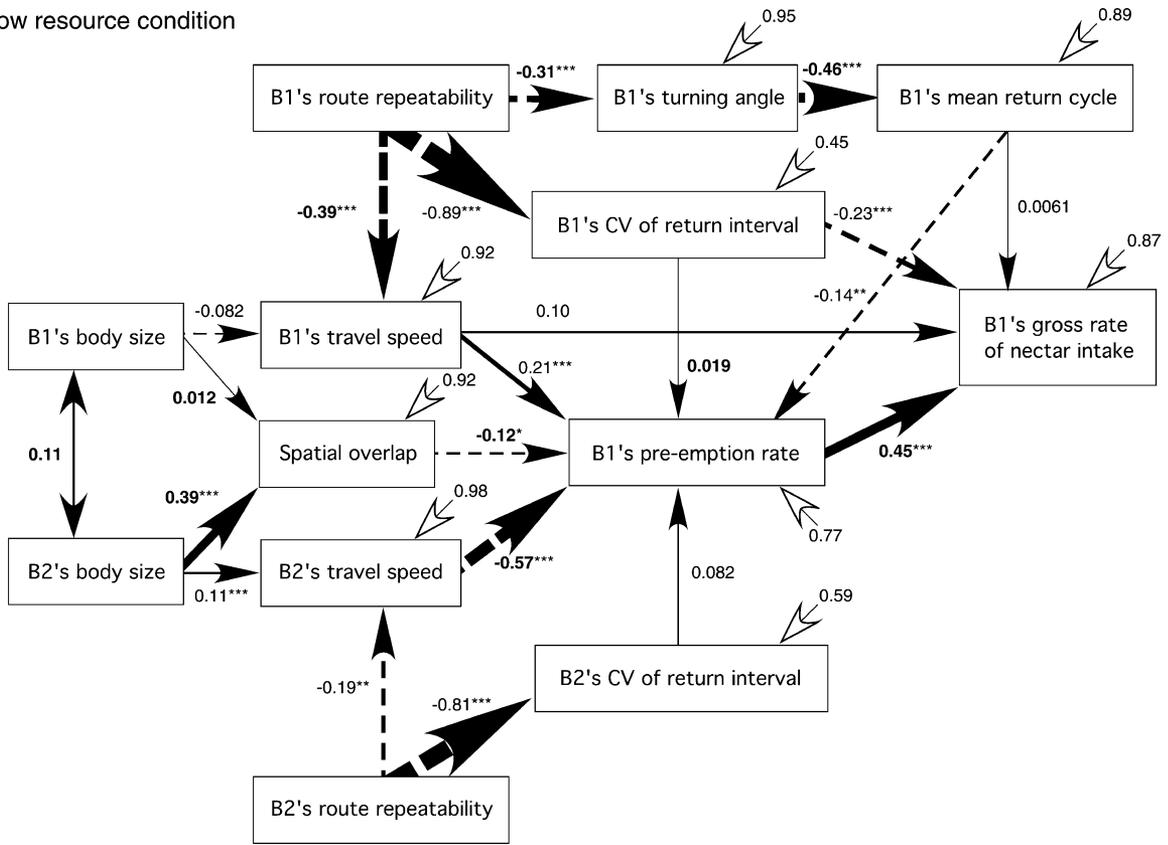
#### Effects of behavioral aspects

Bees collected more nectar per unit of time as they traveled faster between flowers; the total effect of B1's travel speed

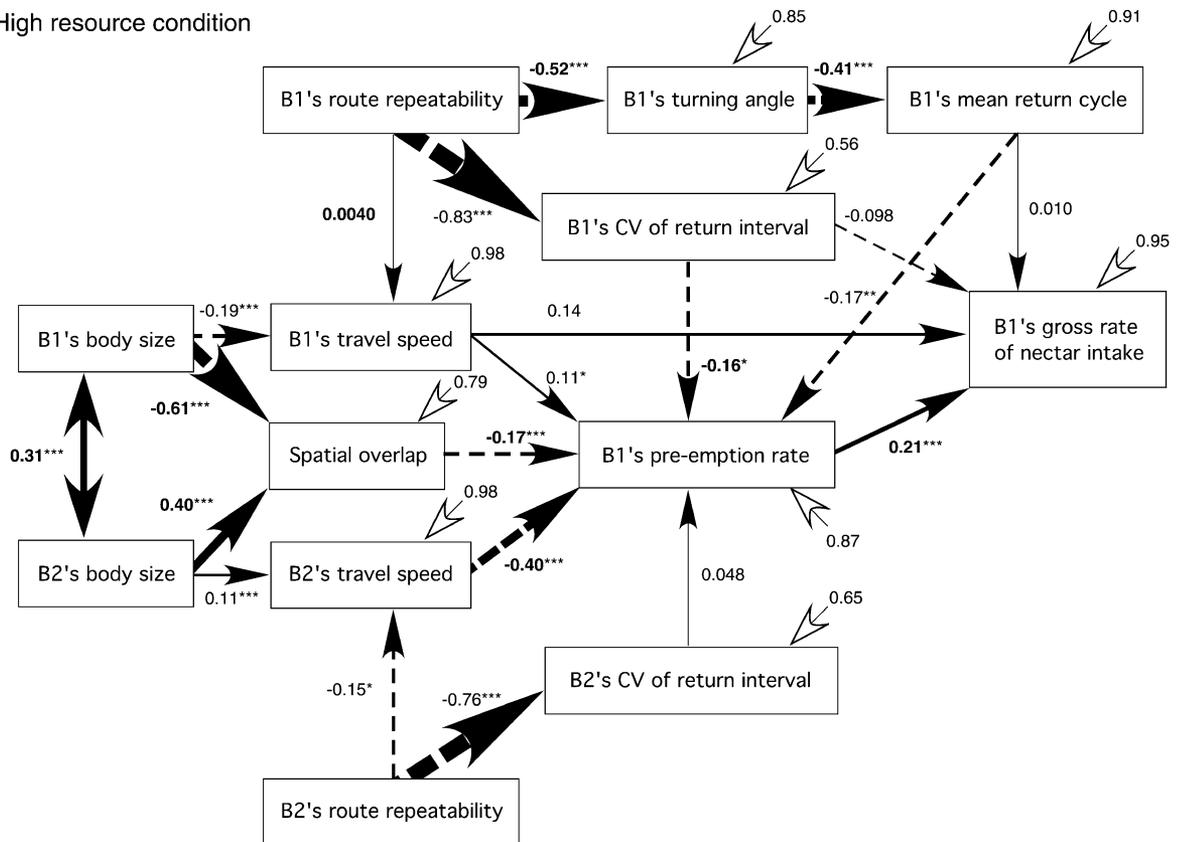
on its foraging performance was strong and positive in both the low- and the high-resource conditions (Figure 3 and Table 1). Fast movements between flowers improved B1's performance in 2 ways. First, fast returns directly increased the rate of nectar intake by returning to flowers before the refilling rate diminished too much. Second, fast returns increased chances of taking accumulated nectar in flowers before B2's arrival (i.e., increased B1's preemption rate), which also indirectly increased the rate of nectar intake. The indirect effect of B1's travel speed through this pathway was stronger in the low-resource ( $0.21 \times 0.45 = 0.095$ ) than in the high-resource conditions ( $0.11 \times 0.21 = 0.023$ ).

The total effect of B1's route repeatability or traplining on its foraging performance was also strong and positive in both resource conditions (Table 1). Route repeatability indirectly affected the bees' foraging performance in 3 ways. First, an increased repeatability in foraging route significantly reduced the CV of return intervals. Such periodic returns directly increased the rate of nectar intake by producing returns to flowers before the refilling rate diminished too much, as well as by increasing the preemption rate. The indirect effect of route repeatability on B1's performance through the former pathway was strong and positive (low resource: 0.20, high resource: 0.081), whereas through the latter pathway it was weak and positive only in the high-resource condition (low resource:  $-0.0076$ , high resource: 0.028). Second, travel speed was slower in trips where foragers had more repeatable routes. This trend was significant for both B1 and B2 in the low-resource condition but nearly disappeared for B1 in the high-resource condition. Overall, the reduction of B1's travel speed with increased route repeatability had a negative effect on B1's performance ( $-0.076$ ), but this effect was negligible in the high-resource condition (0.00065). Third, the establishment of route repeatability increased directionality in B1's movement and thereby increased the mean return cycle. The observed lengthening of the mean return cycle increased the amount of nectar accumulated in flowers but decreased the preemption rate, although both effects were negligible: the indirect effect of route repeatability on B1's performance through the former pathway was 0.00087 (low resource) and 0.0021 (high resource), whereas the effect through the latter pathway was  $-0.0090$  (low resource) and  $-0.0076$  (high resource). Therefore, the effects of route repeatability on travel speed or mean return cycle impaired B1's foraging performance, but the positive effects exerted by periodical returns outweighed such negative effects in both resource conditions.

a) Low resource condition



b) High resource condition



**Table 1**  
**Direct and total effects on B1’s foraging performance in the path model**

Independent variables	Low resource		High resource	
	DE	TE	DE	TE
B1’s preemption rate	0.45***	0.45	0.21***	0.21
B1’s travel speed	0.10	0.19	0.14	0.16
B1’s route repeatability	—	0.11	—	0.12
B1’s CV of return interval	−0.23***	−0.22	−0.098	−0.13
B1’s turning angle	—	0.025	—	−0.027
B1’s mean return cycle	0.061	−0.055	0.10	0.066
B1’s body size	—	−0.017	—	−0.0085
B2’s travel speed	—	−0.25	—	−0.085
B2’s route repeatability	—	0.018	—	−0.0052
B2’s CV of return interval	—	0.036	—	0.010
B2’s body size	—	−0.048	—	−0.024
Spatial overlap (Pianka’s index)	—	−0.052	—	−0.035

Significant direct effects are marked with asterisks (\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.0001$ ). Total effects cannot be evaluated as significant or not as they include all the pathways, both those statistically significant and those not. DE, direct effects; TE, total effects.

*Effects of body size*

As we intended, the paired bees in each trial were similar in their size (Figure 3). No significant size difference was found between B1 and B2 (low resource:  $n = 8$  pairs,  $P = 0.81$ ; high resource:  $n = 8$  pairs,  $P = 0.30$ ; Wilcoxon’s signed-ranks test). Although the total effect of body size on B1’s performance was negligible for this reason (Table 1), we found notable asymmetric trends between B1 and B2 in the effects of body size on travel speed and spatial overlap (Figure 3). First, larger bees traveled faster when they were newly arrived (B2), but this trend entirely disappeared or even reversed when they had gained foraging experience (B1). Second, B2’s body size had a strong, positive effect on spatial overlap with B1, whereas B1’s body size had a small or negative effect on spatial overlap with B2. In the 2–2 treatment, the winner tended to be larger than the loser, although this trend was not significant due to the scarcity of data (low resource:  $n = 4$  pairs,  $P = 0.13$ ; high resource:  $n = 4$  pairs,  $P = 0.75$ ; pooled data:  $n = 8$  pairs,  $P = 0.30$ ; Wilcoxon’s signed-ranks test).

**Behavioral aspects of competitors and their changes with experience and competition**

First, we compared the 2 most influential bee behaviors, travel speed and route repeatability, for B1 and B2 during the first day in the 1–2–1 treatment. During the solo phase 1, travel speed between flowers significantly increased with experience in a nonlinear, decelerating fashion (Figure 4a; low resource:

Kendall’s blocked tau = 0.55,  $n = 9$  bees as blocks,  $P < 0.0001$ ; high resource: Kendall’s blocked tau = 0.43,  $n = 9$  bees as blocks,  $P < 0.0001$ , Kendall’s rank correlation with a third blocking variable). By the time B2 started foraging, therefore, B1 had already reached high levels of travel speed. B1’s priority had a lasting effect for the following 30 trips, and B1 traveled significantly faster than B2 during the competition phase, regardless of the resource condition (Figure 5a; low resource:  $n = 8$  pairs,  $P = 0.039$ ; high resource:  $n = 8$  pairs,  $P = 0.0078$ ; Wilcoxon’s signed-ranks test). Both bees traveled significantly faster in the low-resource condition than in the high-resource condition, both during the solo phase 1 (low resource: pooled mean for 9 bees = 0.38 m/s, SE = 0.02; high resource: pooled mean for 9 bees = 0.36 m/s, SE = 0.02;  $U = 36.0$ ,  $P = 0.73$ , Mann–Whitney  $U$ -test) and the competition phase (low resource: pooled mean for 24 bees = 0.43 m/s, SE = 0.01; high resource: pooled mean for 24 bees = 0.39 m/s, SE = 0.01;  $U = 171.0$ ,  $P = 0.015$ , Mann–Whitney  $U$ -test). Route repeatability also increased with experience during the solo phase 1, although this trend was significant only in the low-resource condition (Figure 4b; low resource: Kendall’s blocked tau = 0.13,  $n = 9$  bees as blocks,  $P = 0.039$ ; high resource: Kendall’s blocked tau = 0.10,  $n = 9$  bees as blocks,  $P = 0.23$ ; Kendall’s rank correlation with a third blocking variable). As a result of this small improvement, median route repeatability was higher in B1 than in B2 during the competition phase, although it was not significant (Figure 5b; low resource:  $n = 8$  pairs,  $P = 0.055$ ; high resource:  $n = 8$  pairs,  $P = 0.078$ ; Wilcoxon’s signed-ranks test). Route repeatability tended to be higher under low resources than under high, but this tendency was not significant either in the solo phase 1 (low resource: pooled mean for 9 bees = −0.65, SE = 0.02; high resource: pooled mean for 9 bees = −0.69, SE = 0.02;  $U = 26.0$ ,  $P = 0.22$ , Mann–Whitney  $U$ -test) or in the competition phase (low resource: pooled mean for 24 bees = −0.73, SE = 0.02; high resource: pooled mean for 24 bees = −0.74, SE = 0.02;  $U = 281.0$ ,  $P = 0.89$ , Mann–Whitney  $U$ -test).

For comparison, we tested whether winners and losers in the 2–2 treatment differed from one another in terms of travel speed and route repeatability during trips 31–60 (corresponding to the competition phase in the 1–2–1 treatment). In contrast to the results from the 1–2–1 treatment, we found no significant difference in either of these behavioral variables between competitors in the low-resource (travel speed:  $n = 4$  pairs,  $P > 0.99$ ,  $n = 8$  bees, mean  $\pm$  SE = 0.44  $\pm$  0.01 m/s; route repeatability:  $n = 4$  pairs,  $P = 0.63$ ,  $n = 8$  bees, mean  $\pm$  SE = −0.72  $\pm$  0.03; Wilcoxon’s signed-ranks test) or the high-resource conditions (travel speed:  $n = 4$  pairs,  $P = 0.63$ ,  $n = 8$  bees, mean  $\pm$  SE = 0.43  $\pm$  0.01 m/s; route repeatability:  $n = 4$  pairs,  $P = 0.38$ ,  $n = 8$  bees, mean  $\pm$  SE = −0.77  $\pm$  0.04; Wilcoxon’s signed-ranks test).

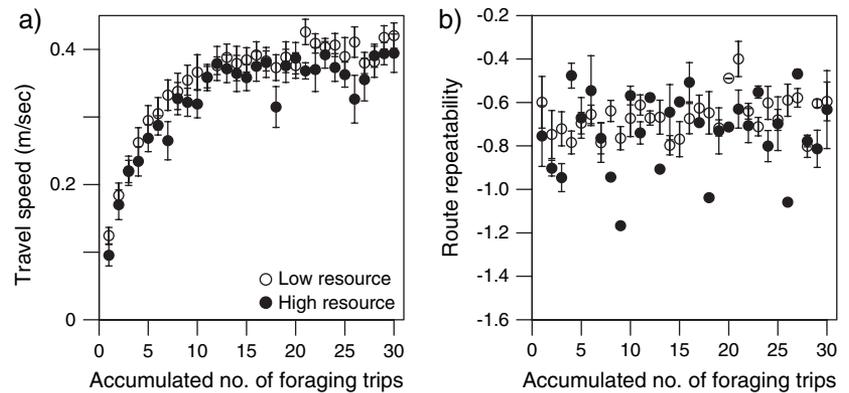
Second, we compared lengths of return cycles between B1 and B2 during the competition phase in the 1–2–1 treatment. B1 had significantly longer return cycles ( $n = 8$  bees, mean  $\pm$

**Figure 3**

Path diagrams for determinants of foraging performance of experienced bumble bees (B1’s gross rate of nectar intake) during the competition phase of the 1–2–1 treatment in (a) the low-resource condition ( $n = 296$  trips) and (b) the high-resource condition ( $n = 345$  trips). One-headed arrows represent the hypothesized effects of one variable on another and 2-headed arrows represent unanalyzed correlations between 2 variables, that is, shared variation that is not explained within the model. Continuous lines indicate positive effects and dashed lines negative effects, with the magnitude of the coefficient determining their width. Numbers near the paths indicate standardized path coefficients. Asterisks (\* $P < 0.05$ , \*\* $P < 0.01$ , and \*\*\* $P < 0.0001$ ) denote standardized path coefficients that are significantly different from 0, as assessed by multivariate Wald tests. Coefficients in bold type differed between the low- and the high-resource conditions at significance level 0.05. Residual variances of endogenous variables (those being affected by other variables) are also indicated with outline arrows. Chi square = 394.6, df = 116,  $P < 0.00001$ ; RMSEA = 0.061.

**Figure 4**

Changes in bee behavior with accumulated foraging experience during the first 30 trips in the 1–2–1 and the solo treatments. (a) Travel speed and (b) route repeatability. Mean and SE were calculated for each trip using data on 9 bees. Open circles represent the low-resource condition and closed circles represent the high-resource condition, respectively.



SE =  $7.84 \pm 0.59$ ) than B2 ( $n = 8$  bees, mean  $\pm$  SE =  $6.49 \pm 0.60$ ) in the low-resource condition ( $n = 8$  pairs,  $P = 0.023$ , Wilcoxon's signed-ranks test), whereas there was no significant difference in the high-resource condition ( $n = 8$  pairs,  $P = 0.46$ , Wilcoxon's signed-ranks test;  $n = 16$  bees, mean  $\pm$  SE =  $5.22 \pm 0.33$ ). Return cycles were longer under low than under high resources ( $U = 48.5$ ,  $P = 0.0021$ , Mann–Whitney  $U$  test with data pooled for B1 and B2). During trips 31–60 in the 2–2 treatment, on the other hand, winners and losers had equivalent return cycles in either resource condition (low resource:  $n = 4$  pairs,  $P = 0.38$ ,  $n = 8$  bees, mean  $\pm$  SE =  $6.98 \pm 0.59$ ; high resource:  $n = 4$  pairs,  $P = 0.88$ ,  $n = 8$  bees, mean  $\pm$  SE =  $6.68 \pm 0.48$ ; pooled data:  $n = 8$  pairs,  $P = 0.38$ ; Wilcoxon's signed-ranks test).

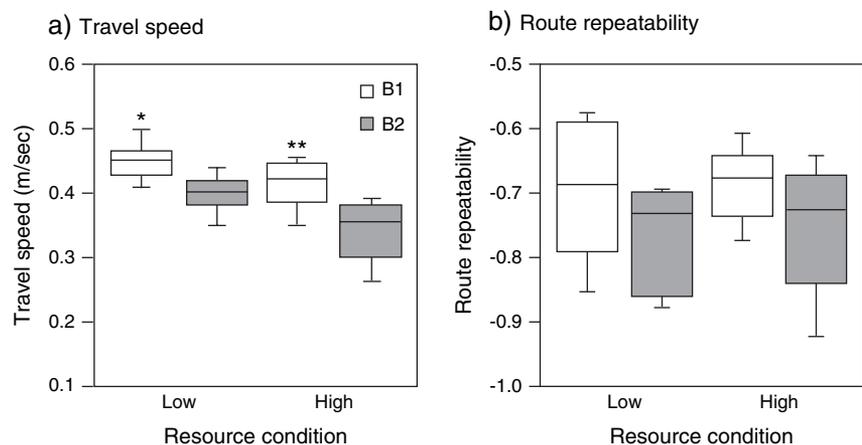
We also examined whether and how the bees altered the length of return cycle and spatial overlap during the competition phase in the 1–2–1 treatment. We found that the average return cycle per trip increased with the accumulated number of trips, although this trend was significant only for B2 in the low-resource condition (low resource: Kendall's blocked tau for B1 = 0.084,  $P = 0.054$ , tau for B2 = 0.17,  $P = 0.0004$ ; high resource: Kendall's blocked tau for B1 = 0.076,  $P = 0.12$ , tau for B2 =  $-0.0076$ ,  $P = 0.90$ ; Kendall's tau with a third blocking variable). In contrast to the increase in return cycle, we found that Pianka's index was smaller in the latter half than in the former half of the competition phase, although this trend also was significant only in the low-resource condition (Figure 6; low resource:  $n = 8$  pairs,  $P = 0.0078$ ; high resource:  $n = 8$  pairs,  $P = 0.11$ ; Wilcoxon's signed-ranks test). Pianka's index tended to be larger in the low-resource condition, although

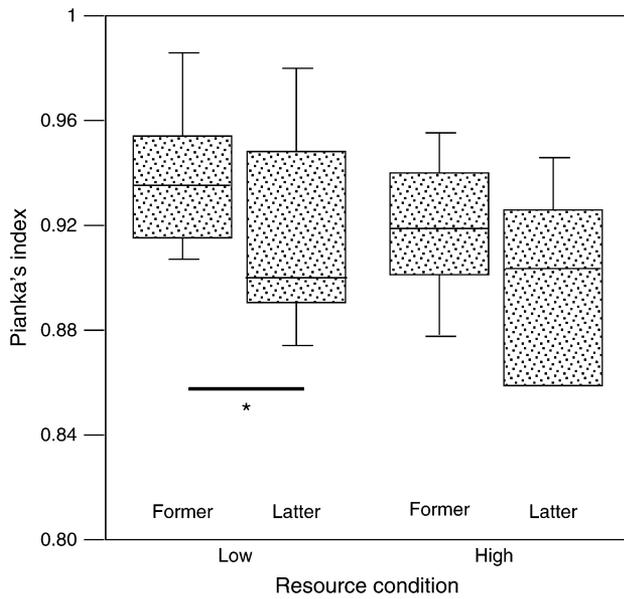
this trend did not reach significance ( $U = 80.0$ ,  $P = 0.073$ , Mann–Whitney  $U$ -test with data pooled for B1 and B2). This indicates that spatial overlap between bees tended to decrease as the competition progressed.

Finally, we performed GLMs to examine whether and how bees changed their travel speeds, route repeatability, and return cycle in response to an addition or a removal of a competitor, using data from all the test bees from the 3 treatments. Comparisons of bee behavior between 1st to 30th trips and 31st to 60th trips (before and after the competitor addition) were summarized in Table 2(a), and comparisons between 31st to 60th trips and 61st to 90th trips (before and after the competitor removal) were summarized in Table 2(b). Bees traveled faster in the low-resource condition, although this trend was significant only in Table 2(a). The effect of competition on travel speed was not significant in either case, but the interaction term between competition and experience was significant and negative in Table 2(a). As the effect of experience was positive, a negative interaction means that the increase in travel speed with experience dropped when a competitor was added. Route repeatability was unaffected when a competitor was added or removed. The effect of competition on route repeatability was negative, although this was significant only when a competitor was added (Table 2a). Bees did not significantly decrease their travel speed or route repeatability when a competitor was removed (Table 2b). In contrast to these results, bees increased the average return cycle when a competitor was added (Table 2a) and then decreased it again when a competitor was removed (Table 2b). In both cases, moreover, bees had longer return cycles when resources were low.

**Figure 5**

Comparisons between experienced (B1) and newly arrived (B2) bees in (a) travel speed and (b) route repeatability during the competition phase in the 1–2–1 treatment. Medians of average travel speed between flowers and route repeatability (=CV of return cycle multiplied by minus one) from 8 bees were used to draw each box–whisker plot. Asterisks (\* $P < 0.05$ , \*\* $P < 0.01$ , and \*\*\* $P < 0.0001$ ) denote differences between B1 and B2 were significant, assessed by Wilcoxon's signed-ranks tests.





**Figure 6**  
Changes in spatial overlap between B1 and B2 (Piánka's symmetrical index, Equation 1) during the competition phase in the 1–2–1 competition. Asterisks (\* $P < 0.05$ , \*\* $P < 0.01$ , and \*\*\* $P < 0.0001$ ) denote differences between the former and the latter halves (15 trips each) were significant, assessed by Wilcoxon's signed-ranks tests.

**Table 2**  
Analysis of variance tables for bee behavior within 30 successive trips

Source	df	SS	F	P	$\beta$
a) 1st to 30th trips and 31st to 60th trips					
Travel speed ( $R^2 = 0.39$ , $F_{4,76} = 13.6$ , $P < 0.0001$ )					
Resource condition (low $\rightarrow$ high)	1	0.014	6.95	0.010	-0.013
Competitor (absent $\rightarrow$ present)	1	0.0047	2.42	0.12	-0.024
Experience (accumulated no. of trips)	1	0.078	40.1	<0.0001	0.0024
(Competitor) $\times$ (Experience)	1	0.015	7.57	0.0074	-0.0032
Residuals	76	0.15			
Route repeatability ( $R^2 = 0.11$ , $F_{3,77} = 4.16$ , $P = 0.087$ )					
Resource condition (low $\rightarrow$ high)	1	0.014	1.75	0.19	-0.013
Competitor (absent $\rightarrow$ present)	1	0.081	10.4	0.0019	-0.078
Experience (accumulated no. of trips)	1	0.016	2.07	0.15	0.00098
Residuals	77	0.60			
Mean return cycle ( $R^2 = 0.28$ , $F_{3,77} = 11.4$ , $P < 0.0001$ )					
Resource condition (low $\rightarrow$ high)	1	39.8	17.3	<0.0001	-0.70
Competitor (absent $\rightarrow$ present)	1	28.9	12.6	0.0007	1.48
Experience (accumulated no. of trips)	1	2.80	1.21	0.27	0.013
Residuals	77	177.5			
b) 31st to 60th trips and 61st to 90th trips					
Travel speed ( $R^2 = 0.23$ , $F_{4,73} = 6.67$ , $P < 0.0001$ )					
Resource condition (low $\rightarrow$ high)	1	0.0020	0.52	0.47	-0.00051
Competitor (absent $\rightarrow$ present)	1	0.00015	0.039	0.84	-0.0035
Experience (accumulated no. of trips)	1	0.066	17.1	<0.0001	0.0014
(Resource condition) $\times$ (Experience)	1	0.019	4.87	0.030	-0.00070
Residuals	73	0.28			
Route repeatability ( $R^2 = 0.28$ , $F_{3,74} = 1.75$ , $P = 0.16$ )					
Resource condition (low $\rightarrow$ high)	1	0.0026	0.28	0.60	0.0057
Competitor (absent $\rightarrow$ present)	1	0.011	1.14	0.29	0.029
Experience (accumulated no. of trips)	1	0.017	1.79	0.18	-0.00072
Residuals	74	0.68			
Mean return cycle ( $R^2 = 0.26$ , $F_{3,74} = 10.2$ , $P < 0.0001$ )					
Resource condition (low $\rightarrow$ high)	1	42.1	16.4	0.0001	-0.74
Competitor (absent $\rightarrow$ present)	1	33.7	13.1	0.0005	1.65
Experience (accumulated no. of trips)	1	5.00	1.95	0.17	0.012
Residuals	74	190.1			

Data from (a) 1st to 30th trips and 31st to 60th trips and (b) 31st to 60th trips and 61st to 90th trips in all treatments ( $n = 50$  bees). Values of  $\beta$  represent coefficients in GLMs.

**DISCUSSION**

The foraging performances of bumble bees depended on the amount of prior experience they had accumulated in a habitat. In both resource conditions, experienced foragers (B1) consistently achieved higher rates of nectar intake than the less experienced ones (B2). Although differences in competitive performance emerged even when the 2 bees started foraging at the same time (the 2–2 treatment), those differences were much smaller than in the 1–2–1 treatment. To our knowledge, this is the first empirical evidence that area fidelity could benefit animals by increasing their foraging performance in competitive situations without spatial heterogeneity of resources.

The superiority of experienced foragers in competition arose from advantages conferred by 2 aspects of behavior: faster travel speeds between flowers and greater repeatability of routes (Table 1 and Figure 3). Faster bees increased their rates of nectar intake by increasing their chances of encountering accumulated nectar before their competitors did (pre-emption rate) and by returning to flowers before the refilling rate diminished too much. The positive effect of travel speed was higher when nectar flow was slower, that is, when resources were scarce. Bees with more repeatable routes also increased their rates of nectar intake, mainly by reducing variation in elapsed time between visits (return intervals) on flowers. In both resource conditions, reduction of variation in return intervals increased the rate of nectar intake mostly by returning to flowers before the refilling rate diminished.

Reducing variation in return intervals also increased the pre-emption rate, but this effect was significant only in the high-resource condition where competition was moderate. These results agree well with the theoretical predictions made by Ohashi and Thomson (2005) on how and when trapline foraging benefits animals.

On the other hand, route repeatability also had a negative effect on a bee's rate of nectar intake via a reduction of its travel speed, although this effect was not significant for B1 in the high-resource condition where the overall travel speed was low (Figure 3). Such a "trade-off" between speed and accuracy in traplining appears to contradict the fact that bees spend less time moving between flowers as they developed more repeatable foraging routes, and that both fast movements and traplining rely on long-term spatial memory (Ohashi et al. 2007; Saleh and Chittka 2007; Figure 4 in this study). One probable reason for this discrepancy is that traplining requires some additional information, such as the memory of sequential order of flowers along a route (Chameron et al. 1998), whereas fast movement only requires the memory of flower locations or spatial layout. If these were the case, the time cost needed for memory retrieval would have increased as bees followed more accurate traplining. Although the above explanation is purely hypothetical and needs empirical explorations, we suggest that an increase of travel speed between flowers or patches is not the primary advantage of trapline foraging in bumble bees. Burns (2005) discusses another aspect of speed-accuracy trade-offs in bumble bee foraging; in that particular case, where bees were challenged to discriminate between flowers with different values, the benefits of higher speed outweighed the costs of more accurate discrimination.

Even if there was a trade-off between travel speed and route repeatability in individual foraging trips, bees upgraded these skills as they accumulated experience during the first 30 trips (solo phase 1, Figure 4). As a consequence of this, B1 traveled significantly faster and repeated significantly more consistent routes than B2 throughout the competition phase (Figure 5). Strikingly, the route repeatability of B2 during the competition phase was much lower than the route repeatability of B1 during the first 30 trips, whereas the decrease was not so large between the solo phase 1 and the competition phase in B1 (Figures 4b and 5b). Such a stability of B1's route repeatability further emphasized the difference between B1 and B2 during the competition phase. Because no such behavioral differences were observed between winners and losers in the 2-2 treatment, the observed difference in the rate of nectar intake between B1 and B2 (Figure 2) can be attributed to B1's priority in foraging experience. These results strongly suggest that establishing a long-term spatial memory can improve a bee's foraging performance in competitive situations by increasing its travel speed and route repeatability.

In this study, we did not find any evidence that bees adjusted their travel speed (or its acceleration) and route repeatability in response to the presence or absence of competition. Instead, travel speed (or its acceleration) and route repeatability decreased when a competitor was added (Table 2a). Perhaps the bees were prevented from improving these skills because they did not experience continuous reinforcement due to the presence of the competitor. Alternatively, the bees might be responding to their past reward experience in a "win-stay, lose-shift" manner (Thomson 1988), which would tend to increase 1) their time spent in sampling and 2) their variation in return intervals (Ohashi and Thomson 2005). Also, bees did not decrease their travel speed and route repeatability when a competitor was removed (Table 2b); instead, they continued to upgrade these aspects of performance. Considering that bumble bees in most field conditions compete with others for limited amounts of floral rewards and it often takes hours

for spatial learning (Makino and Sakai 2007; Ohashi et al. 2007), consistent upgrading may be as good a strategy as a conditional adoption of competitive skills. Even in the absence of competition, moreover, fast movements and traplining will tend to improve a bee's foraging performance on flowers with a decreasing renewal rate, by making revisits happen before the refilling rate has decelerated very much (Possingham 1989; Ohashi and Thomson 2005).

In contrast to the insensitivity of speed and repeatability to competition, bees did adjust the average number of visits made before returning (return cycle) in response to the presence or absence of competition, as well as to the resource level. Bees increased the average return cycle when a competitor was added (Table 2a) and decreased it again when the competitor was removed (Table 2b). Also, bees consistently had larger return cycles in the low- than in the high-resource condition (Table 2). Large return cycles could have a negative effect on a bee's foraging performance due to an increase in spatial overlap (Ohashi and Thomson 2005). In both resource conditions, however, Pianka's index for spatial overlap did not increase with the average return cycle (Figure 3). Instead, this measure of overlap declined over time during the competition phase while the average return cycle was increasing (Figure 6). This may indicate that bees were increasing their return cycles while minimizing an increase in spatial overlap by optimizing route geometry (Ohashi et al. 2007) or by shifting their foraging routes away from others (Thomson et al. 1987; Ohashi and Thomson 2005). Moreover, the increased reward crop per flower was counterbalanced by the reduction in preemption rate (Figure 3). Thus, an increase in the average return cycles will barely affect a bee's competitive performance, whereas it will have an obvious advantage of increasing nectar crop per visit when no competitor exists. In that it would incur no costs, therefore, it seems a reasonable strategy for bees to increase their return cycles in response to any reduction in resource levels.

Because we minimized the difference in body size between competitors to focus on the effects of experience, we did not detect a large effect of a bee's body size on its rate of nectar intake (Table 1). Nevertheless, body size did influence foraging behavior in 2 ways. First, travel speed increased with body size in B2 (Figure 3). It is known that the flight speed of a bumble bee increases with body temperature (Heinrich 1979). Because the ratio of surface area to volume decreases with body size, our result may partially reflect the ability of larger bees to keep their body temperature more constant than smaller ones (Stone and Willmer 1989). Small bees may have suffered from significant heat loss earlier in their foraging careers, when they often stayed longer on flowers. It is also possible that larger bees with greater visual acuity could have saved time searching for flowers when they were naive to the habitat (Spaethe and Chittka 2003). Yet another possibility is that smaller B2 may have taken longer in choosing next flowers to visit while avoiding B1's paths at the same time (as suggested below). Second, spatial overlap decreased as B2 was smaller, and also as B1 was larger (Figure 3). Such a pattern would have emerged if B2 avoided using the same flowers as B1, and if that avoidance were magnified by a size advantage of B1. It seems reasonable that B2 would avoid sharing flowers with B1, considering that trapliners could effectively reduce the average reward crop encountered by random samplers (Possingham 1989). Such an asymmetric relationship may also have contributed to the difference in route repeatability between B1 and B2 during the competition phase (Figures 4b and 5b) because spatial avoidance of competitors would increase the variation in return intervals due to sampling and shifting behavior (Ohashi and Thomson 2005). On the other hand, it is unclear why (and how) the

avoidance of B1 by B2 depended on the size difference between the individuals. This may suggest that small bees were intimidated by the presence of larger bees through visual perception or physical interference, although we rarely observed bee-bee encounters on flowers during the competition phase in the 1–2–1 treatment (1–17 encounters out of 802–3032 visits). It is conceivable that scent marking might have provided cues to the body size of an unseen competitor. Morse (1977, 1982) has observed similar patterns among bumble bee species with no overt hostile interactions, in which small bees shifted their foraging areas to peripheral parts of *Solidago* inflorescences when larger ones were present. Whatever the mechanism is, small bees may encounter difficulty in establishing stable traplines when they are naive with little foraging experience or when they are experienced foragers but naive to a habitat. This effect would tend to reward fidelity to small, familiar foraging areas.

### Conclusions

By comparing movement paths and resultant nectar gain of bumble bees for complete sequences of the resources they visited, this work provides the first experimental demonstration of the functional significance of trapline foraging in the presence of competition. The path analysis with SEM allowed us to assess how multiple bee traits and behavioral aspects interacted with one another and how each factor or pathway determined the foraging performance of competitors. The path model strongly supported our initial hypothesis that traplining would increase a forager's competitive performance in moderately competitive situations, and that it would increase the average reward per visit on patches with a decreasing renewal rate. The model also revealed that trapline foraging decreased travel speed between flowers, which by itself would tend to decrease a bee's nectar gain and its competitive performance, but in our situation, the advantages of traplining outweighed the costs. When circumstances make traplining cognitively difficult, as is probably the case when plants grow in dense homogeneous stands, when landmarks are absent, or when plants are arranged in confusing patterns such as zigzags (Ohashi et al. 2007), therefore, it may become a better strategy for a bee to increase its travel speed without following an accurate trapline.

Our results thus clarified that foragers exhibiting area fidelity can collect renewing resources from isolated patches more efficiently and competitively by establishing long-term spatial memory of locations, configurations, or visit sequences of patches. Although our flowers were uniform in terms of nectar renewal rate, foraging experience may have additional advantages when bees could choose among flowers with different nectar renewal rates (Cartar 2004; Makino and Sakai 2007). In future studies, we plan to examine how resource heterogeneity in space influences a bee's foraging behavior and performance in the presence or absence of competition.

### FUNDING

Japan Society for the Promotion of Science for Research Abroad to K.O. (no. 1597); Natural Sciences and Engineering Research Council of Canada; Canada Foundation for Innovation; Ontario Innovation Trust to J.D.T.

Biobest provided commercial colonies of *Bombus impatiens*. Daniel D'Souza designed and constructed the monitoring system. Alex Fujiwara and Toshiyuki Kaneko (Hitachi Maxell Corporation) provided the product specifications of the Coil-on-Chip RFID system®. Useful discussion has been contributed by James Burns, Jonathan Cnaani, Robert Gegear, Crispin Jordan, and Michael Otterstatter.

Takashi Makino, Hugh Possingham, and an anonymous reviewer made useful comments on the manuscript.

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