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Original Article

Trapline foraging by bumble bees: VI. Behavioral alterations under speed–accuracy trade-offs

Kazuharu Ohashi[a] **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, Canada M5S 3G5

Trapline foraging (repeated sequential visits to a series of feeding locations) has often been observed in animals collecting floral resources. Past experiments have shown that bumble bees cannot always develop accurate (i.e., repeatable) traplines to a sufficient level, despite their economic advantages in many situations. The bees' preference for short flights works against developing accurate traplines when plants or patches are distributed in zigzag fashion. How should bees cope with such situations in nature? We conducted laboratory experiments with artificial flowers to test 2 nonexclusive hypotheses: bees may travel faster to compensate for low traplining accuracy, and when local landmarks are available, bees may be able to develop traplines by remembering external spatial information in addition to the locations of flowers. As predicted, foragers on a zigzag-shaped floral array traveled faster, with lower route repeatability, than those on a triangular lattice where distance and angle could be chosen independently, suggesting that bees trade-off accuracy for speed when it is more feasible. In contrast, bees traveled more slowly with unchanged traplining accuracy when landmarks were added into both arrays, possibly because the landmarks caused information load or visual distraction. Finally, bees on the zigzag array with additional landmarks made a quicker decision to switch from accurate traplining to fast traveling. If landmarks helped the bees to grasp the overall array geometry in our experiments, they may also permit bees in nature to select a distribution of plants or patches that aids accurate traplining. *Key words: Bombus*, foraging, landmark effect, route learning, spatial use, speed–accuracy trade-off, trapline, travel speed. *[Behav Ecol]*

INTRODUCTION

Patterns of movement or "spatial-use strategies" are considered key factors in the success of most animals collecting food that is unevenly scattered in space and time. Spatial-use strategies are especially interesting when foragers are pollinators because they also affect gene flow or reproductive success of plants (Levin and Kerster 1968; Waddington 1981; Schmid-Hempel 1986; Cartar and Real 1997; Cresswell 2000). Although researchers have often focused on simple movement rules as determinants of successive flights of pollinators (i.e., choices of distance and turning angle) as if the bees are "searching" for unknown locations in unfamiliar habitats, growing evidence suggests that other aspects of spatial use are important (reviewed by Ohashi and Thomson 2009). Specifically, certain pollinators return faithfully to small foraging areas (Ribbands 1949; Manning 1956; Gill and Wolf 1977). Within those areas, moreover, they sometimes visit a particular set of plants in repeatable sequences, referred to as "trapline foraging" (Manning 1956; Janzen 1971; Heinrich 1976; Ackerman et al. 1982; Dressler 1982; Lemke 1984; Gill 1988; Tiebout 1991; Thomson 1996; Thomson et al. 1997; Garrison and Gass 1999).

Recent laboratory experiments with nectar-collecting worker bumble bees have clarified several important aspects of trapline foraging. First, a bee tends to establish a trapline with geometric features that directly improve foraging performance, such as an increased return interval (Ohashi et al. 2007; Saleh and Chittka 2007), an approximation of the shortest possible route (Ohashi et al. 2007; Lihoreau et al. 2010, 2011, 2012), and priority for visits to higher-reward locations (i.e., visiting them first) (Lihoreau et al. 2011). Moreover, a bee increasingly repeats a particular sequence more accurately with each foraging circuit, producing periodical returns to each location with less variable intervals (Ohashi and Thomson 2005; Ohashi et al. 2007). Thus an increased repeatability or "accuracy" in traplining indirectly improves a bee's foraging by (1) increasing its chances of encountering accumulated nectar before its competitors (Ohashi and Thomson 2005; Ohashi et al. 2007), (2) discouraging others from intruding by keeping nectar standing crops low (Possingham 1989; Ohashi and Thomson 2005), and (3) getting to feeding locations before the slowing refilling rate diminishes too much (Ohashi and Thomson 2005; Ohashi et al. 2008).

Previous studies have also shown that the advantageous features of traplines develop over hours and cannot be reproduced by simple rules of movement between successive visits, such as choosing short distances and straight moves (Ohashi

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

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et al. 2007; Saleh and Chittka 2007; Ohashi et al. 2008; Lihoreau et al. 2010, 2011, 2012). This suggests that traplining requires a long-term spatial memory of locations, reward values, a sequence of locations, or a sequence of motor patterns. In addition, foragers tend to develop repeatable circuits with experience even in the absence of others, although most of the benefits associated with accurate traplining show up only in the presence of competitors or potential intruders (Ohashi and Thomson 2005; Ohashi et al. 2008). In fact, solo bees developed accurate traplines more readily than those gaining experience in competitive situations. Because bumble bees in most field conditions compete for limited resources and it often takes hours for spatial learning, it is probably advantageous for a forager to make such a "prior investment" in an accurate trapline even if it finds itself working alone (Ohashi et al. 2008).

Even if accurate traplining is an efficient foraging tactic and bumble bees have sufficient cognitive ability to employ it, bees in nature may not always enjoy the benefits of it. Past experiments have suggested that trapline foraging has at least 1 limitation in its implementation: route repeatability or traplining accuracy is reduced if the spatial configurations of plants or patches such as zigzags require sharp turns to make nearest-neighbor flights, although the realized visit sequences are still more repeatable than those generated by pure searching behavior (Ohashi et al. 2007). This is because bees prefer to choose short distances over straight moves and show little plasticity in this regard, unless circuitous routes involve heavy penalty costs (Ohashi et al. 2007; Lihoreau et al. 2010). If a difficult plant configuration does not permit a bee to select a set of plants where nearest neighbors are consistent with those of directional movements, therefore, the bees are likely to suffer from inaccurate traplining. Considering that bumble bees tend to avoid intensive overlap of their foraging areas with competitors (Thomson et al. 1987; Makino and Sakai 2005) and that this would limit available plant options for an individual, such geometrical difficulties in traplining may often prevail in nature.

One possible response to difficult configurations is to increase travel speeds to compensate for the inaccuracy in traplining. Ohashi et al. (2008) have shown that fast travel improves a bee's foraging performance through effects very similar to those of periodic returns, that is, by taking accumulated nectar in feeders more often than competitors, as well as by returning to feeders before the refilling rate tapers off. Pushing travel speed above a certain level, however, may sacrifice the accuracy of traplining; in an array of feeders where choices of nearest neighbors are consistent with those of directional movements, Ohashi et al. (2008) discovered that experienced bees followed less repeatable routes in foraging trips during which they traveled faster, while speed and accuracy both contributed to their competitive performance. When confronted with zigzag configurations, therefore, such a "speed–accuracy trade-off" in traplining may encourage bees to actively choose higher speeds at the cost of accurate traplining. Another solution may come from choosing habitats with rich visual landmarks close to focal plants or patches. It is well known that animals can learn more precise locations or routes when visual landmarks are available near the goal or intermediate goals (reviewed by Collett et al. 2003). Although bees were provided with a few potential cues such as the observer and the nest box in our previous studies (Ohashi et al. 2007), they might have been able to trapline with greater accuracy (i.e., repeatability) or speed if more or better landmarks had been available. Therefore, we revisited Ohashi et al.'s (2007) experiments, adding very salient landmarks and a system for measuring speed.

As before, we conducted laboratory experiments on the patterns of spatial use by bumble bees (*Bombus impatiens*) collecting nectar from multiple feeders ("flowers") in a flight cage. We allowed naive bees to accumulate foraging experience singly in different learning conditions, by crossing the 2 arrangements of flowers and the presence or absence of additional salient landmarks in a 2×2 design. Using a light-emitting diode-based monitoring system, we recorded all the flower visit sequences that each bee followed during foraging, as well as its travel speed between flowers. We asked these specific questions: (1) when flowers are distributed in ways that make accurate traplining difficult, do bees actively switch to fast traveling? (2) when bees can use visual landmarks to learn the locations and sequences of flowers, do they perform more accurate traplining? Or do they further increase their travel speed? (3) how do the effects of flower distribution and landmark availability on bees' spatial-use patterns interact with one another?

MATERIALS AND METHODS

We worked indoors in a mesh flight cage measuring 788 (length) × 330 (width) × 200 (height) cm. The same cage was used in Ohashi et al.'s (2007) experiments, except that it was then set up in a rooftop greenhouse. Temperature ranged from 26 to 30 °C. The room was illuminated during daylight hours with normal fluorescent bulbs, while the windows were covered with cardboard. Our subjects were workers from 2 commercial colonies of *B. impatiens* Cresson (supplied by Biobest, Leamington, Canada; Figure S1). 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 artificial flowers, as detailed below.

Artificial flowers

We used 10 morphologically identical artificial flowers for experiments. The design of the artificial flowers is described elsewhere (Ohashi et al. 2007, 2010; see also Figure S1). Briefly, each flower consists of a vertical box of clear Plexiglas (67 cm tall), equipped with a small electric clock motor on its top. As the motor turns a thin axle (diameter = 3 mm) at 1/30 rpm, the axle winds up a thread that is clipped to one end of a 50-cm of flexible tubing (internal diameter = 3 mm) that contains 30% sucrose (w/w) solution ("nectar"). The nectar oozes out through the needle at the other end of the tube into a "nectar bucket" (diameter = 5.5 mm and depth = 7 mm) on a horizontal platform halfway up the box, and accumulates in the bucket at a constant rate (2.2 µL/min). A thin plastic baffle prevents the bees from getting excess nectar directly from the steel needle hole. The depth of the nectar bucket is adjusted to the tongue length of *B. impatiens* workers so that they can empty the nectar accumulated at the bottom. Each nectar bucket is topped with a U-shaped block of plastic painted in blue, so that bees can easily find and learn to extract nectar from it. A piece of clear plastic canopy covers the block, so that a bee can approach the bucket only from the front opening through the tunnel.

An electronic monitoring system recorded all the visit sequences and the arrival/departure time at each flower. The opening of each U-shaped block houses an infrared detector: an infrared light-emitting diode produces a beam that is sensed by a phototransistor. When a bee crawls through the tunnel, it interrupts the beam and produces a signal on the phototransistor output. The infrared detectors are all connected to a central control box. The control box converts the analog signal received from the phototransistor to the appropriate electrical levels required for sending it to a personal computer through a digital input/output card.

When the change of the electrical level indicates that the bee has vacated the tunnel (i.e., the beam is reconnected), then the arrival and departure time (to 0.1 s) are logged to a data file. Similar infrared systems have been often used to record the presence and the timing of bee visits to artificial feeders (Keasar et al. 1996; Chittka and Thomson 1997; Cnaani et al. 2006).

Between experiments, we used 2 training flowers to let bees learn where to find nectar. One of the flowers is made of a plastic vial and the other is made of a plastic Petri dish (Figure S1). The vial is topped with a Plexiglas platform with a hole (diameter = 5.5 mm) and U-shaped blue plastic block. The lid (platform) of the Petri dish also has a hole, topped with a U-shaped blue plastic block. In either training flower, the hole on the platform was plugged with a 3-cm wick made from a cotton dental roll, the other end of which was dipped in 20% (w/w) sucrose solution in the container. Bees could extract nectar from the surface of the wick. We lowered the nectar concentration in the training flowers to 20%, so that bees could become more motivated for foraging when they encountered 30% nectar in the artificial flowers.

Spatial arrangements of flowers and additional landmarks

We tested 2 configurations of floral arrays to simulate variation in available spatial distribution of plants or patches in nature (Figure 1). These arrays varied with respect to 2 general preferences of bees: the preference to make short flights and the preference to continue moving in one direction. In the "independent" array, flowers always had 2–6 equidistant nearest neighbors in different directions, and bees could choose movement distance and turning angle independently. In the "negative" array, on the other hand, proximity and directionality were negatively linked, that is, a bee had to turn to choose the nearest neighbor. For the negative array, Ohashi et al. (2007) showed that *B. impatiens* foragers produced less repeatable circuits than those in the independent array, suggesting that the negative link between proximity and directionality hampered the establishment of more repeatable traplines. In both arrays, the interflower spacing of 0.95 m was chosen to be far enough that neighboring flowers would be distinguishable to bees as different "patches" or "plants" (Thomson et al. 1982; Burns and Thomson 2006).

The design of our flower, with its tower behind the platform, might limit bees' departure directions even though its transparency is likely to allow bees to see through it. To minimize such effects, therefore, we arranged all flowers so that their backs faced outside of the array where there was no other flower. In the independent array, moreover, we rotated the center flower every 10–12 trips in a clockwise direction, so that its back faced each of the 3 edges in turn.

We performed 2 types of experiments for each array to simulate variation in landmark availability among habitats. In the treatment experiment, we added 4 artificial landmarks with different combinations of color and shape; yellow and purple columns (50 cm tall and 32 cm wide), and yellow and purple T-shaped columns (71 cm tall and 32 cm wide). We set out each of them within 1 m from the array (Figure 1). Positions of these landmarks were kept constant throughout trials in each array. Considering that the maximum distance between a landmark and a flower is approximately 5.2 m (Figure 1), the minimum visual angle required for detecting a 50 cm tall landmark is 5.5°. We thus assume that *B. impatiens* on flowers could perceive all the 4 landmarks, as they possess a minimum resolvable angle of 1.39° (Macuda et al. 2001). In the control experiment, artificial landmarks were absent. Without additional landmarks, the only potential spatial cues for bees, except the feeders themselves, were the bees' entrance hole on the cage screen (1.2 m from the floor) visually emphasized with ivory-colored paper cut out into a star-shaped polygon, and other stationary objects external to the cage.

Experimental procedures

Before running an experiment, we opened the gate to the cage and let bees forage freely on the 2 training flowers. These flowers were placed within 1.5 m from the entrance, away from any locations of the artificial flowers. The vial flower was placed halfway up a Plexiglas box resembling the artificial flowers (Figure S1). The Petri dish flower was placed on the floor. During this training phase, the 10 electric artificial flowers were turned off and covered with dark brown cloth bags to prevent the bee's access. None of the 4 artificial landmarks was added in the cage. On nonexperiment days, we left the gate open typically between 10:00 and 17:00 hours. This procedure allowed bees to associate the U-shaped blue

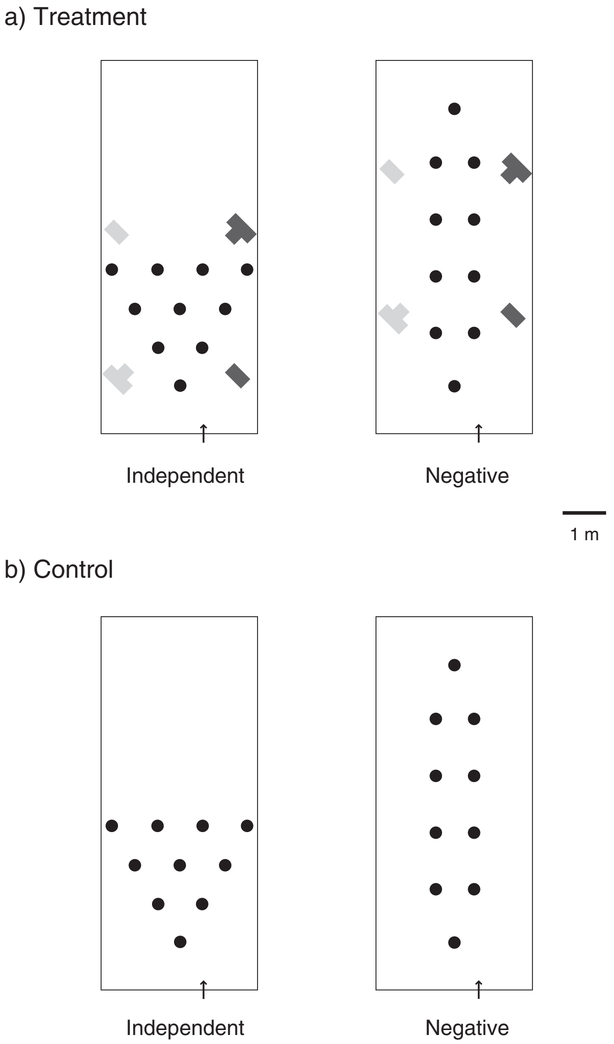


Figure 1
The spatial arrangement of flowers and the additional landmarks used in the (a) treatment and (b) the control experiments. Yellow and purple landmarks are shown in light and dark gray, respectively. Rectangle and arrow represents the cage screen and the gate of the colony, respectively.

plastic block with nectar reward, but they remained naive to the spatial array of flowers and additional landmarks.

On experiment days, we let bees forage on the training flowers for 30–60 min in the morning to refresh their experience of being rewarded on the flowers with the U-shaped block. 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 prevented the other bees from reentering the cage once they returned to the hive. Among these regular foragers, we picked one for the trial that had accumulated more than 2 trips and uniquely marked its thorax with an oil-based paint marker. The training flowers and the cloth bags on the 10 artificial flowers were then removed. The 4 artificial landmarks were added only in the treatment experiment. 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 a 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 nectar with time while the motors were turned on.

We then released the focal bee 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 not turning on the electric motors until the bee had visited the first 5–6 flowers. When the bee finished its first foraging trip and returned to the hive, we turned off the motors 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). The trial was continued until the bee made 64–73 foraging trips, which would usually take 5–6 h. We observed 23 bees in this way, assigning 5 bees to each of the 3 factorial combinations of landmark availability and array type (i.e., treatment-independent, control-independent, and treatment-negative experiments) and 8 bees to the control-negative experiment.

After each trial, we immediately placed the focal bee in a clean plastic vial and froze it at −20 °C. For all experimental bees, we measured the average radial cell length of the left and right forewings of each bee as an index of body size (Bertsch 1984; Owen 1988, 1989). We also checked all the experimental bees through dissection and fecal screening and confirmed that none of them had the tracheal mite *Locustacarus buchneri* (Husband and Sinha 1970) or the intestinal trypanosome *Crithidia bombi* (Lipa and Triggiani 1988). Infections by these parasites sometimes occur in commercial stocks and can affect behavior (Otterstatter et al. 2005).

Data analysis

Using the flower visitation sequences (Table S1) and timing data recorded in the personal computer, we characterized 2 aspects of behavior for each bee: repeatability of foraging routes (i.e., traplining accuracy) and travel speed between flowers. For an index of foraging-route repeatability or traplining accuracy, we calculated the coefficient of variation of the "return cycle" (= number of flower visits a bee made before returning to any particular flower) for each trip made by a bee, multiplied by minus 1. Larger (i.e., closer to zero) values of this "route repeatability" indicate more accurate traplining, because variation in return cycles would be small if a bee repeated a fixed circuit (Thomson et al. 1997; Ohashi et al. 2007). We also calculated the travel speed between flowers for each trip as the sum of all distances between successively visited flowers divided by the total time spent traveling the distance (hereafter, "travel speed"). For each bee, we computed an average of each behavioral measure during the initial 30 foraging trips (former half) and during all the remaining trips (latter half), respectively.

To examine whether and how bees changed their travel speed and route repeatability in response to varying learning conditions, we fitted general linear models (Grafen and Hails 2002) with "array type" (independent or negative), "landmark availability" (treatment or control), and "body size" (radial cell length) as the explanatory variables and "array type × landmark availability" as the interaction term. We included body size as a potential covariate to adjust for its possible effects on bee behavior through correlations with physiological and cognitive abilities (Goulson et al. 2002; Spaethe and Weidenmüller 2002; Worden et al. 2005; Spaethe et al. 2007; Ohashi et al. 2008; Riveros and Gronenberg 2010).

To illustrate how quickly bees responded to differences of learning conditions, we also calculated least-squares means for route repeatability and travel speed, i.e. the expected values of an observed marginal mean if body size were fixed to the sample mean (Searle et al. 1980), in each of the 4 combinations of array type and landmark availability. To control for the repeated measurements from individual bees in calculating the least-squares means and their standard errors, we used a generalized linear mixed model (Crawley 2002) with "learning condition" (either of 4 combinations of array type and landmark availability), "phase" (former or latter), and "body size" as the fixed effects, the individual bees as the random effect, and "learning conditions × period" as the interaction term.

RESULTS

The GLMs (general linear models) fitted to the data explained significant portions (43–58%) of the variance in route repeatability or travel speed (Table 1). We found 3 major trends in these analyses. First, there was a consistent effect of spatial arrangement of flowers throughout the experiments, such that bees followed more repeatable or accurate traplines at lower travel speed in the independent than in the negative array (Table 1, Figure 2).

Next, addition of artificial landmarks did not change the above trend; route repeatability in the negative array never surpassed that in the independent array (Figure 2a), while travel speed was consistently higher in the negative than in the independent array (Figure 2b). On the other hand, the additional landmarks significantly reduced travel speed between flowers in both the independent and the negative arrays (Table 1, Figure 2). This trend became more apparent during the latter half, where control-experiment bees in the negative array traveled faster than those in the independent array (Figure 2b).

Finally, the interaction between array type and landmark availability was significant during the former half of the experiments, although this effect dissipated during the latter phase where bees had accumulated more experience (Table 1). This is because the differences in the bee behavior between the array types became evident more quickly when additional landmarks were available (Figure 2). In contrast, bees shifted their priority from traplining to fast traveling after they gained experience in the control experiment (Figure 2).

Table 1

Effects of array type, landmark availability, and their interaction on route repeatability and travel speed between flowers for the former and the latter half, respectively (GLM with body size as the covariate)

Source	df	SS	F	P	β
Former half					
Route repeatability ($R^2 = 0.52$, $F_{4,15} = 6.10$, $P = 0.0041$)					
Array type (independent → negative)	1	0.026	9.77	0.0070	−0.53
Landmark availability (control → treatment)	1	0.0010	0.37	0.55	−0.11
Body size	1	0.0032	1.16	0.30	0.21
(Array type) × (landmark availability)	1	0.015	5.58	0.032	−0.41
Residuals	15				
Travel speed ($R^2 = 0.43$, $F_{4,15} = 4.66$, $P = 0.012$)					
Array type (independent → negative)	1	0.016	13.7	0.0021	0.68
Landmark availability (control → treatment)	1	0.0057	4.96	0.042	−0.42
Body size	1	0.0040	3.45	0.083	0.39
(Array type) × (landmark availability)	1	0.0046	3.96	0.065	0.37
Residuals	15				
Latter half					
Route repeatability ($R^2 = 0.45$, $F_{4,15} = 4.93$, $P = 0.009$)					
Array type (independent → negative)	1	0.067	8.18	0.012	−0.52
Landmark availability (control → treatment)	1	0.00010	0.012	0.91	−0.020
Body size	1	0.034	4.19	0.059	0.43
(Array type) × (landmark availability)	1	0.00091	0.11	0.74	0.062
Residuals	15				
Travel speed ($R^2 = 0.59$, $F_{4,15} = 7.75$, $P = 0.0014$)					
Array type (independent → negative)	1	0.012	19.1	0.00055	0.69
Landmark availability (control → treatment)	1	0.0091	14.0	0.0020	−0.60
Body size	1	0.0014	2.11	0.17	0.26
(Array type) × (landmark availability)	1	0.00019	0.30	0.59	0.087
Residuals	15				

Values of β represent standardized partial regression coefficient in GLMs, that is, the change in response variable in standard deviation unit when all variables are standardized, which results from an increase of 1 SD or a shift to the direction of the arrow in each explanatory variable.

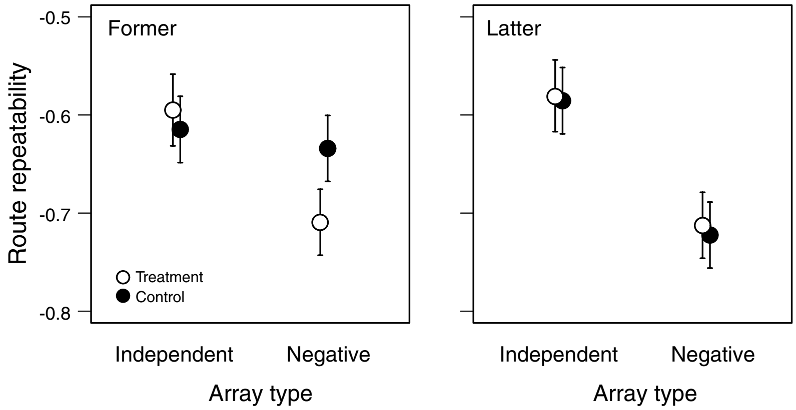
DISCUSSION

Behavioral alterations under speed–accuracy trade-off in traplining

Foraging bumble bees adopted different movement tactics depending on the spatial arrangement of flowers. As we have previously found (Ohashi et al. 2007), bees learned to repeat foraging circuits or traplines in the independent array—where choosing nearest neighbors could be achieved without making sharp turns, whereas they failed to achieve similar levels of route repeatability even after they gained experience in the negative array—where choosing nearest neighbors conflicted with choosing straightest movements (Figure 2a). In addition, bees in the negative array sped up after they gained experience, traveling faster than those in the independent array by further sacrificing repeatability of foraging routes (Figure 2b). This seems consistent with our initial prediction that bees travel more rapidly between flowers to supplement for the lack of accuracy in traplining. To put it in other words, accurate traplining is incompatible with the speediest travel. This trade-off has already been demonstrated by examining speed and accuracy in traplining with their effects on competitive performance in a larger independent array (Ohashi et al. 2008). However, our new results show that solo bees actively chose to travel faster at the cost of traplining accuracy when it was more feasible, providing another indirect support for the existence of the trade-off. Chittka et al. (2003) described other consequences of speed–accuracy trade-offs in bumble-bee foraging: bees could choose between flowers with different values wisely or rapidly, but not both at once. As discussed later by Burns (2005), in that example the benefits of higher speed outweighed the costs of more accurate discrimination. Such trade-offs between decision speed and accuracy have also been suggested in many ecologically relevant tasks (reviewed by Chittka et al. 2009). Although the underlying mechanism of the trade-off is unknown, it is possible that accurate route following requires some additional information such as the memory of sequential order of visual stimuli associated with particular movements (Collett et al. 1993; Zhang et al. 1996; Chameron et al. 1998), whereas fast movement only requires at most memory of flower locations or distributions. Such an explanation is consistent with our finding that the "negative" distribution of flowers hampered accurate traplining without limiting speed, together with our previous report that naive bees sped up but failed to increase route repeatability in the presence of experienced competitors (Ohashi and Thomson 2009). The requirement for such high levels of cognitive, perceptual, or motor skills for accurate traplining may therefore generate a speed–accuracy trade-off by increasing the time costs for memory retrieval and comparison.

Even though there was a trade-off between speed and accuracy in traplining, and even though both behavioral aspects could have positive effects on foraging performance (Ohashi et al. 2008), bees gave priority to traplining accuracy over fast movement unless it was hampered by the distribution of flowers (Figure 2). Because it is quite unlikely that fast movements were less beneficial (or more costly) in the independent than in the negative array, our results suggest that bumble bees are predisposed to accurate traplining when feasible, possibly because it often produces a greater net benefit than fast movements in field conditions. For example, accurate trapliners may acquire detailed knowledge of individual patches during their periodical returns, thereby reaping extra benefits, such as an increased selectivity for nectar-rich flowers within patches (Williams and Thomson 1998), quicker responses to newly arrived competitors (Gill 1988; Garrison and Gass 1999), or a more efficient avoidance

a) Route repeatability



b) Travel speed between flowers

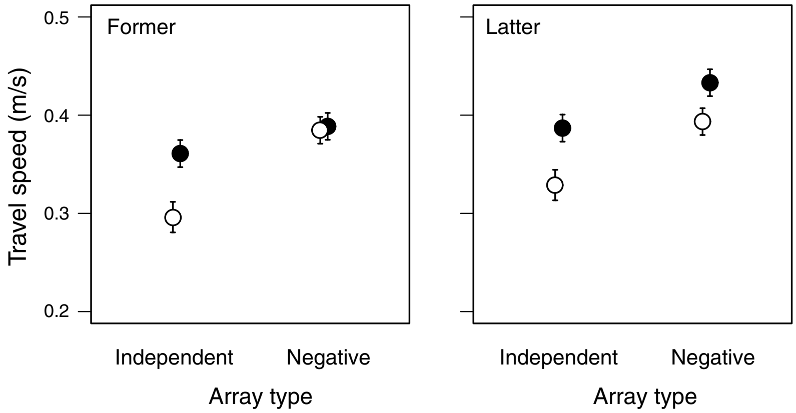


Figure 2
Route repeatability (i.e., traplining accuracy) and travel speed between flowers in different learning conditions as to array type and landmark availability. Circles (open = treatment, closed = control) and error bars represent the estimated values of least-squares mean and SE for (a) the former and (b) the latter half, respectively.

of aggressive competitors or predators (Thomson 1989; Dukas and Morse 2003). Alternatively, faster flights may increase the frequency of wing collisions with vegetation and cause permanent wing damage (Foster and Cartar 2011). It has been suggested that wing wear results in a higher mortality rate in bumble bees, possibly through a decreased ability to escape from predators (Cartar 1992; Hedenström et al. 2001).

Landmark effects

As opposed to our initial predictions, addition of landmarks on the periphery did not improve the bees' route repeatability in either spatial arrangement of flowers even after they gained experience; rather, these landmarks significantly reduced the bees' travel speed in both types of array (Figure 2b). The lack of improvement in trapline accuracy seems inconsistent with the proposal that route-following insects store retinotopic views or "snapshots" of the surrounding landmarks and use them to get to a goal or intermediate points on the way (Cartwright and Collett 1983; Collett et al. 2003). The most probable explanation for this discrepancy is that our bees could produce stable traplines in the absence of additional landmarks. This may be because the flowers themselves served as proximal cues or "beacons" at the spatial scale of our experiments, and these beacons encouraged bees to learn a sequence of motor patterns. Alternatively, perhaps the limited number of landmarks in the control conditions provided enough information for bees to trapline.

Why, then, did the bees decrease their travel speed when we added more landmarks? It is probable that the bees used the additional information for traplining, which required more time for retrieving stored snapshots and comparing them with the current view. Similarly, a human navigator in a giant metropolis might be slowed down by a plethora of landmarks, pausing for confirmation at every corner, when one or a few symbolic landmarks might suffice for adequate goal-finding at a faster speed. It is possible that animals hold such apparently "redundant" information, partly because it assures some advantages in other situations. For example, landmark use may serve as a back-up system for bumble bees to minimize the risk of losing their routes in the field, where they would experience occasional displacements by the wind (Comba 1999) or interference competition from other organisms (Thomson 1989). The time cost will be larger when landmarks have similar visual features for the navigator. This may apply to our case, where the landmarks differed from one another in the combinations, but not in the repertoire, of color and shape (Figure 1). In future studies it would be interesting to see whether there is such an "information load" or an "optimal number" of visual landmarks for animals to solve a certain spatial task, as well as whether greater distinctiveness among landmarks could improve performance.

Yet another possibility is that bees were actually distracted by the additional landmarks throughout the trials. In other words, bees in the treatment experiments failed to ignore the redundant information provided by the landmarks and suffered a heavier time cost of "paying attention" in return for no economic benefits. Generally, animals are able to dismiss redundant information in spatial or associative learning (reviewed by Shettleworth 1998). If the stimuli were perceptually strong, however, such "overshadowing" or "blocking" may not function properly. For example, Manning (1956) observed that bumble bees foraging in a dense stand of *Cynoglossum* plants spent more time in reacting to peripheral plants even if they seemed to have established their own traplines. Although we did not observe noticeable "exploration flights" during our experiments, it is conceivable that the bees' travel speed between flowers was depressed by their continuing curiosity regarding peripheral landmarks.

In contrast to the reduction in travel speed, the bees in the negative array made a quicker shift in their priority from traplining to fast traveling when the additional landmarks were available (Figure 2). This result suggests that the additional landmarks may have helped the bees grasp some essential features of the array geometry, even while providing redundant (or distractive) information for route following. Because each landmark would indicate the distance to the array periphery or individual flowers, it is not improbable that the additional landmarks encouraged the bees to make quicker decisions in choosing between alternative tactics for a certain configuration of flowers. When sufficient options are available in a large plant population, such landmarks may further allow bees to select a set of plants or patches with a circular or oval arrangement, in which traplining is less cognitively challenging (Ohashi et al. 2007).

Although it was not tested in this study, it should be noted that another condition of learning may also affect the point at which traplining and fast-traveling tactics balance out: conspicuousness of resource patches. In contrast to our conditions where the flowers were easily perceived from a distance, bees foraging on a plant population with low density, indistinctive displays, or visual obstacles would have to remember their exact locations to return faithfully (Manning 1956). In such conditions, accurate memories for locations and routes may provide bees with greater benefits as they gain experience, although those memories may be costly to acquire. For example, it may become more beneficial for bees to have more accurate spatial memories when plants are inconspicuous, because the detection of next plants incurs heavier time costs than the memory retrievals. Active memory use may also encourage bees to find more efficient route geometry, resulting in an additional improvement of their foraging performance, especially when plant density is low (Lihoreau et al. 2010, 2011, 2012). When these benefits of traplining cannot be equaled by faster foraging, then bees should give priority to traplining even if it entails heavy time and energy costs in early stages of their foraging career. It is thus possible that the observed differences in spatial-use patterns between the arrays would diminish as each flower became less salient (due to low density, inconspicuous displays, or complex landscape, etc.), especially when local landmarks significantly improve accuracy of place memory and route following.

Our results may also have some implications for the coevolution of plants and pollinators. The spatial-use patterns of pollinators will influence pollen dispersal among plants and, in turn, plant fitness. Our results suggest that landmarks may not function as a remedy for plant distributions that hamper pollinators from establishing their own traplines, but that they may help pollinators to select suitable configurations of plants for traplining. Therefore, plants growing in populations with rich visual landmarks may experience increased mating distance, mate diversity, and outcrossing rate (or reduced "iterogamy", i.e., self-pollination caused by immediate return visits) due to the increased proportion of trapliners (Ohashi and Thomson 2009), while they may suffer an increased geitonogamous self-pollination (Williams and Thomson 1998). Although we need to test it empirically, it is also possible that visual landmarks encourage pollinators to trapline in plant populations with low density, inconspicuous displays, or complex landscapes, thereby promoting pollen flow among plants. We hope that our study serves as a motivation to consider how changes in environmental conditions could alter plant reproduction through their effects on the use of space by pollinators.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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