

## RESEARCH ARTICLE

# A stingless bee can use visual odometry to estimate both height and distance

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### SUMMARY

**Bees move and forage within three dimensions and rely heavily on vision for navigation. The use of vision-based odometry has been studied extensively in horizontal distance measurement, but not vertical distance measurement. The honey bee *Apis mellifera* and the stingless bee *Melipona seminigra* measure distance visually using optic flow—movement of images as they pass across the retina. The honey bees gauge height using image motion in the ventral visual field. The stingless bees forage at different tropical forest canopy levels, ranging up to 40 m at our site. Thus, estimating height would be advantageous. We provide the first evidence that the stingless bee *Melipona panamica* utilizes optic flow information to gauge not only distance traveled but also height above ground, by processing information primarily from the lateral visual field. After training bees to forage at a set height in a vertical tunnel lined with black and white stripes, we observed foragers that explored a new tunnel with no feeder. In a new tunnel, bees searched at the same height they were trained to. In a narrower tunnel, bees experienced more image motion and significantly lowered their search height. In a wider tunnel, bees experienced less image motion and searched at significantly greater heights. In a tunnel without optic cues, bees were disoriented and searched at random heights. A horizontal tunnel testing these variables similarly affected foraging, but bees exhibited less precision (greater variance in search positions). Accurately gauging flight height above ground may be crucial for this species and others that compete for resources located at heights ranging from ground level to the high tropical forest canopies.**

Key words: distance, height, navigation, optic flow, stingless bees, visual odometry.

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### INTRODUCTION

Insects use the perceived movement across visual fields, or ‘visual flow’, for a number of tasks, ranging from maintaining a straight walking path to regulating flight speed (for reviews, see Srinivasan, 2001; Egelhaaf and Kern, 2002; Srinivasan and Zhang, 2004). Certain ants (*Cataglyphis fortis*) and wasps (*Polistes gallicus*) also exploit optic flow for distance measurement, although the manner in which optic flow information is processed varies among taxa [ants (Ronacher and Wehner, 1995; Ronacher et al., 2000), wasps (Ugolini, 1987)]. For insects such as social bees that live in complex, three-dimensional environments (Cartwright and Collett, 1982; Lehrer et al., 1988; Srinivasan, 2001; Egelhaaf and Kern, 2002), optical cues appear crucial for successful navigation. Such visual information allows foragers to successfully find, exploit and retrieve resources (Cartwright and Collett, 1982; Lehrer et al., 1988; Srinivasan, 2001; Egelhaaf and Kern, 2002).

Honey bee foragers rely heavily on information from their visual odometer, in some cases more than on learned landmarks (Menzel et al., 2010), which are known to be crucial for navigation and orientation (Cartwright and Collett, 1983; Cartwright and Collett, 1987; Collett, 1992). To dissect out which components of the visual field are most important for navigation, an experimental simplification of the optical environment is helpful (Egelhaaf and Kern, 2002). For example, Srinivasan and colleagues (Srinivasan et al., 1996; Srinivasan et al., 1997) devised an efficient method in which bees forage in a tunnel lined with a black and white pattern

to examine visual distance estimation in honey bees (*Apis mellifera*). By altering the optical environment that bees experienced, they predictably changed the distance that foragers would search inside the tunnel and the distance they communicated through the waggle dance (Esch et al., 2001). These experiments reveal that the honey bee odometer relies on optic flow, the perceived movement of images across the retina (for reviews, see Srinivasan and Zhang, 2004; Esch et al., 2001). More precisely, the speed of angular image motion is integrated over time to gauge distance traveled (Si et al., 2003). Images move faster and farther across the retina when objects are closer to the eye. Thus, when tunnel width decreases, image speed increases, causing foragers to search at shorter distances (Srinivasan and Zhang, 2004). The opposite occurs when tunnel width increases.

Honey bees also appear to use image motion for other flight tasks such as speed control, centering and landing (Baird et al., 2006; Srinivasan et al., 1996; Srinivasan et al., 2000; Srinivasan and Gregory, 1992). Using vertically oriented tunnels, Dacke and Srinivasan determined that honey bees can use optic flow to measure the height of a food reward, but are less precise while searching vertically (Dacke and Srinivasan, 2007). Baird and colleagues found that free-flying honey bees also modulate their height above ground in response to changes in optic flow (Baird et al., 2006). They did so within their ventral visual field, regardless of the optic flow levels in lateral fields of view. This processing rule makes sense when a bee is flying horizontally for long

distances, because the ventral field of view provides the only meaningful information for height measurement. However, foragers moving up to the flowering tree canopies of tropical forests can, in some cases, fly nearly vertical paths to approach those resources. For example, some meliponine bee species lay vertical odor trails to recruit nestmates, and recruited nestmates fly nearly vertically while following these odor marks [*Scaptotrigona postica* (Lindauer and Kerr, 1960), *Trigona spinipes* (Nieh et al., 2004)]. The meliponines or stingless bees (Hymenoptera, Apidae, Meliponini) are not closely related to honey bees, are over twice their age evolutionarily and are a much larger group (Roubik, 2006; Michener, 2007; Rasmussen and Cameron, 2007; Ramirez et al., 2010). However, the stingless bees and honey bees are the only highly social bees, and both are found in tropical forests where food is available at different heights, so they likely have similar navigational needs.

Relatively little is known about how meliponines use visual information for navigational tasks. At the nest entrance, hovering *Tetragonisca angustula* guard bees use variations in optic flow to detect and correct for unintended changes in position due to drifting, displacement by wind or other factors (Zeil and Wittmann, 1989; Kelber and Zeil, 1990; Kelber and Zeil, 1997). Hrncir and colleagues used the flight tunnel model to demonstrate that *Melipona seminigra* can use optic flow cues for distance measurement, and exhibit the same level of search accuracy as honey bees (Hrncir et al., 2003). However, it remains unclear whether stingless bees can use optic flow cues for height (vertical) orientation, or whether visual odometry is a general component of behavior in the genus *Melipona*.

There is reason to suspect that they can. Stingless bees live in a complex, competitive foraging environment, where resource patches occur throughout the upper canopy and understory (Frankie and Haber, 1983; Roubik, 1993; Roubik et al., 1995). In the tropical forests of central Panama, this canopy can reach over 40 m in height (Croat, 1978). The ability to accurately return to a specific height should therefore be advantageous. Moreover, even in tropical forests, floral resources are seasonally scarce (Roubik, 1989; Croat, 1978) and competition for resources can be intense (Johnson, 1974; Johnson and Hubbell, 1974; Johnson and Hubbell, 1987). Thus, stingless bees have experienced strong selection not only to discover resources and recruit to them but also to do so rapidly and efficiently over a shifting and complex range of heights and micro-environments. We know that *Melipona panamica* can rapidly recruit nestmates to specific distances and heights in the Panamanian forest (Nieh and Roubik, 1995). Thus, we used this species to examine the previously unexplored question of whether a stingless bee employs optic flow to gauge height and distance during foraging.

## MATERIALS AND METHODS

### Location and species

We conducted all experiments on Barro Colorado Island in the Republic of Panama, at the Smithsonian Tropical Research Institute's field station (latitude 9.165375, longitude -79.836718). We collected data from two colonies of *M. panamica* Cockerell 1912, a cavity-nesting stingless bee that lives in colonies of up to 500–800 individuals (Roubik, 1992) and has a maximum flight range of over 2 km (Roubik and Aluja, 1983). *Melipona panamica* can accurately recruit nestmates to a specific distance, direction and height without the use of a scent trail (Nieh and Roubik, 1995). Foragers should therefore be able to accurately measure these dimensions. Data collection occurred from 08:30 h to 13:00 h under cloudy conditions, from August to October in 2006 and 2007, and in August in 2008 and 2009.

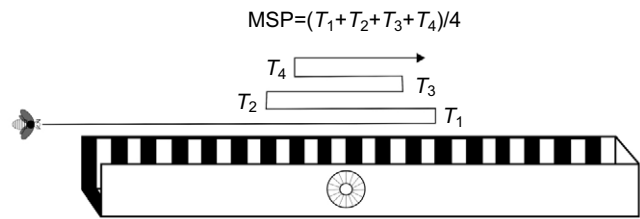


Fig. 1. *Melipona panamica* foragers were trained to a feeder located 135 cm inside a cross-striped tunnel and subsequently tested in an empty tunnel without odor marks. Bees made a series of distinct, 180 deg turns while searching in the empty tunnel. We calculated each forager's mean search position (MSP) by averaging the first four of these turns ( $T_1$ – $T_4$ ).

### Tunnels and training

We mounted a wood training tunnel on wheels (to facilitate its removal during tests) and placed the entrance 3 m from each colony at a 90 deg angle to the nest entrance. The training tunnel was 20 cm tall by 19 cm wide (interior dimensions) and was 2 m long. The inner walls of the tunnel were papered with a striped, alternating black and white pattern of 8 cm width, perpendicular to the long axis of the tunnel (Fig. 1). We covered the top of the tunnel with black mesh to provide ventilation. To deprive bees of visual landmarks, a uniform white cover was placed 75 cm above the tunnel and extended 50 cm beyond its edges. During data collection, observers remained at least 0.5 m from the tunnel and were in motion in order to avoid acting as landmarks themselves.

There are limits to how precisely an observer can quantify the position of a bee in flight. To reduce possible inaccuracies, we recorded which tunnel section each bee was in when it changed flight direction while searching. Marks were made on the outer wall of the tunnel every 10 cm, and the resulting sections ('boxes') were numbered 1–20 to facilitate data collection (see Srinivasan et al., 1996; Srinivasan et al., 1997). We marked 17–25 bees from each experimental colony with different color latex paint on the thorax and trained them to visit a feeder with unscented  $1.5 \text{ mol l}^{-1}$  sucrose solution placed 135 cm inside the 200 cm long tunnel. We offset the feeder from the center of the tunnel so that we could statistically differentiate between directed searching (the mean search position corresponds to the feeder location) and random searching (disoriented bees fly from one end of the tunnel to the other, such that their mean search position corresponds to the tunnel midpoint). The feeder consisted of an inverted glass jar placed on a grooved dish (see von Frisch, 1967). We recorded each time a bee visited the tunnel feeder and returned to its nest. A bee was considered trained when it had completed 30 trips. After training was complete, bees were allowed to forage freely at the tunnel feeder for at least 45 min before the start of each experiment. At the end of this reinforcement period, the training tunnel was closed, moved 4 m away, and covered with a plastic tarpaulin. Afterwards, the experimental period began with an identical, clean tunnel without any potential odor marks to provide positional information.

### Experimental tunnels and data collection

In the experimental period, bees were tested with one of five different tunnel configurations: (1) a tunnel 19 cm in width, identical to the training tunnel; (2) a narrower tunnel, 10 cm in width; (3) a wider tunnel, 40 cm in width; (4) a tunnel with the same dimensions as the training tunnel but lined with 4 cm wide bars (half the width of the training pattern bars to test whether bees would count the number

of bars); and (5) a tunnel with the same dimensions as the training tunnel but lined with parallel longitudinal black and white stripes (a control in which usable optic flow is all but eliminated). All tunnels were cleaned thoroughly with 70% ethanol solution between trials to completely eliminate any odor marks. Each tunnel was equipped with a door that could be slid into place to prevent bees from entering. During each experiment, the experimental tunnel was placed in the previous location of the training tunnel, but without a feeder. We allowed only one bee at a time to access the tunnel, so that they would not influence each other's foraging decisions. Each bee was used only once to avoid pseudoreplication.

Bees exhibited a very clear search behavior in the tunnels. Like honey bees trained to a similar tunnel (Srinivasan et al., 1996; Srinivasan et al., 1997), foragers flew down the center of the tunnel for some distance and then made a series of 180 deg searching turns (Fig. 1). We recorded where the first four such turns occurred, because honey bees exhibit the most precise turning behavior during these first four turns (Srinivasan et al., 1996; Srinivasan et al., 1997). After her fourth turn, each forager was captured, identified and placed in a holding container until the end of the experiment. Each bee was only tested once in each tunnel configuration. When the queue of bees outside the experimental tunnel dwindled to zero, we re-stimulated foraging by reintroducing a feeder into the training tunnel for 20 min. Experimental periods were punctuated by re-stimulation breaks, as needed, over the course of the study day.

In order to test for optic flow use during ascending and descending flight, we oriented the tunnel vertically and created a new entrance in the mesh at the bottom of the upright tunnel. The open side of the tunnel faced a white sheet to prevent any use of landmarks. We suspended the feeder from the top of the tunnel with fishing line such that it hung in the center of box 12 (125 cm from the top of the tunnel). Training and data collection followed the same methods used in the horizontal tunnel experiment. In the vertical tunnel, the feeder was gradually raised over the course of multiple bee visits until foragers reached the training position. Bees both entered and exited the tunnel through the entrance at its base. After training, foragers used a hovering flight to ascend to the feeder. Our experiments were considered complete when we had collected data from at least 25 bees per colony (50 bees per experiment).

#### Data analysis and statistics

For each bee, we calculated the mean search position (MSP), the average of the locations at which bees performed their searching turns. As foragers maintained a fairly consistent flight path through the center of the tunnel (in both horizontal and vertical tunnels), we used the same method as in other studies (Srinivasan, 2001; Hrncir et al., 2003) to calculate the approximate amount of angular image motion each bee experienced. In this calculation, for every 1 cm of forward motion, the tunnel wall image moves backwards across the retina by an angle of  $\tan \alpha = 1/\text{half tunnel width}$ . We multiply this angle by the total cm flown to estimate total angular image motion. Although this is only an approximation of what the forager actually perceives, it is a useful calculation to compare the levels of apparent image motion in each tunnel configuration and to provide comparisons with the results of other studies.

All data were analyzed using the statistical software JMP 9.0.2. All levels of significance were set as  $\alpha < 0.05$ . We used a one-sample *t*-test to compare MSPs with the original training distances. Student's *t*-tests were used to compare MSPs, as well as differences in search ranges between axially striped and cross-striped tunnels. We report MSPs as means  $\pm$  s.d. We show MSP data as relative frequency

plots to simplify comparison between different tunnel widths. Relative frequencies were calculated as the number of times all bees completed turns in a given tunnel section, divided by the highest number of turns made in any section. Thus, the tunnel section with the most turns was given the relative frequency of one, and each subsequent section received a relative frequency less than one. We performed this calculation to facilitate a visual comparison of where bees concentrated their search in each tunnel.

## RESULTS

### Optical distance estimation

In a horizontal experimental tunnel with the same width as the training tunnel (19 cm), foragers searched in the area where the feeder was previously located (feeder training location was box 13, MSP  $12.97 \pm 2.09$  boxes,  $N=53$ ,  $t_{52}=0.12$ ,  $P=0.91$ ; Fig. 2A). When bees foraged in a tunnel approximately half the width of the training tunnel (10 cm), they searched significantly closer to the tunnel entrance (MSP  $8.87 \pm 3.80$  boxes,  $N=110$ ,  $t_{1,108}=48.11$ ,  $P<0.0001$ ; Fig. 2A). Likewise, bees foraging in a tunnel approximately twice the width of the training tunnel (40 cm) searched closer to the end of the tunnel (MSP  $17.50 \pm 1.44$  boxes,  $N=109$ ,  $t_{1,107}=175.25$ ,  $P<0.0001$ ; Fig. 2A).

We conducted three horizontal control experiments (Fig. 3A). (1) We tested to see whether bees were counting stripes by doubling the tunnel pattern frequency (line width reduced to 4 cm). However, this did not affect forager MSP. Foragers did not search at a significantly different distance compared with the original pattern frequency (MSP  $11.33 \pm 2.26$  boxes,  $N=108$ ,  $t_{1,105}=1.01$ ,  $P=0.318$ ; *versus* original feeder location  $t_{53}=-1.76$ ,  $P=0.08$ ). (2) To test the effect of optic flow, we compared search behavior in axially striped and cross-striped tunnels. Bees foraging in a tunnel lined with axially oriented stripes (which does not provide the visual cues necessary for optic flow) searched significantly closer to the tunnel midpoint than those foraging in a tunnel with cross-stripes (MSP  $10.37 \pm 2.72$  boxes,  $N=83$ ,  $t_{1,81}=23.766$ ,  $P<0.0001$ ; *versus* original feeder location  $t_{29}=-5.31$ ,  $P<0.0001$ ). Thus, bees required optic flow cues to correctly orient. (3) This was also reflected in their search range. When foraging in an axially striped tunnel providing minimal usable optic flow cues, bees exhibited a larger search range (we measured the difference between the maximum and minimum search distance within the first four turns) than bees in a cross-striped tunnel, which provides a high level of optic flow (mean of search range on axial stripes  $17.07 \pm 2.20$  boxes,  $N=30$ ; mean of search range on cross-stripes  $9.44 \pm 4.21$  boxes,  $N=53$ ,  $t_{85}=11.10$ ,  $P<0.0001$ ).

### Optical height estimation

After the tunnel was reoriented vertically, forager search behavior followed the same patterns exhibited in the horizontal experiments. Bees foraging in an experimental tunnel with the same width as the training tunnel searched in the area where the feeder was originally located (feeder location box 12; MSP  $11.70 \pm 1.77$  boxes,  $N=53$ ,  $t_{50}=-1.09$ ,  $P=0.28$ ; Fig. 2B). When the width of the tunnel was halved, bees searched lower down, closer to the tunnel entrance (MSP  $7.86 \pm 2.80$  boxes,  $N=103$ ,  $t_{1,101}=70.31$ ,  $P<0.0001$ ; Fig. 2B). When the tunnel width was doubled, bees foraged higher up in the tunnel (MSP  $16.29 \pm 0.74$  boxes,  $N=109$ ,  $t_{1,107}=317.99$ ,  $P<0.0001$ ; Fig. 2B).

The three vertical control experiments (Fig. 3B) demonstrated that bees were not counting stripes and required optic flow cues. (1) When the tunnel pattern frequency was doubled to test for counting, bees did not search in a significantly different area from that while foraging on the original pattern (MSP  $12.01 \pm 1.11$  boxes,  $N=107$ ,

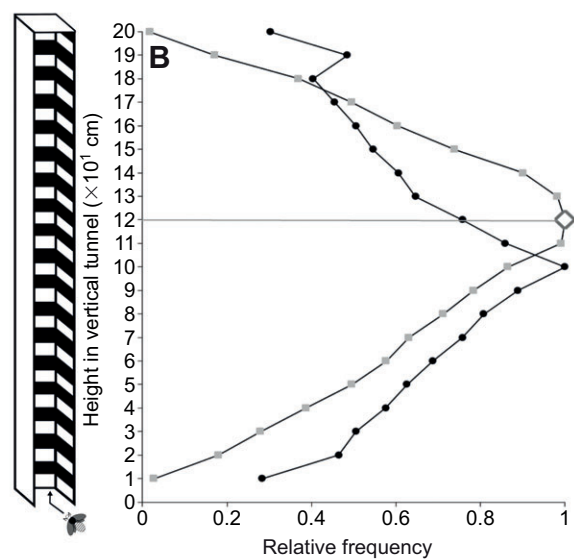
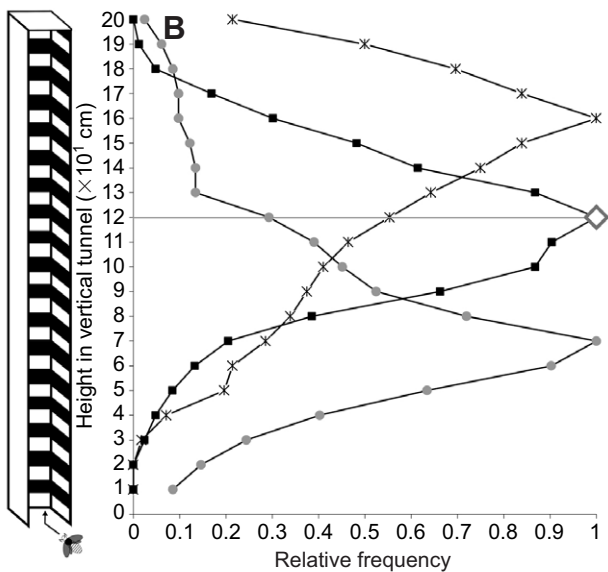
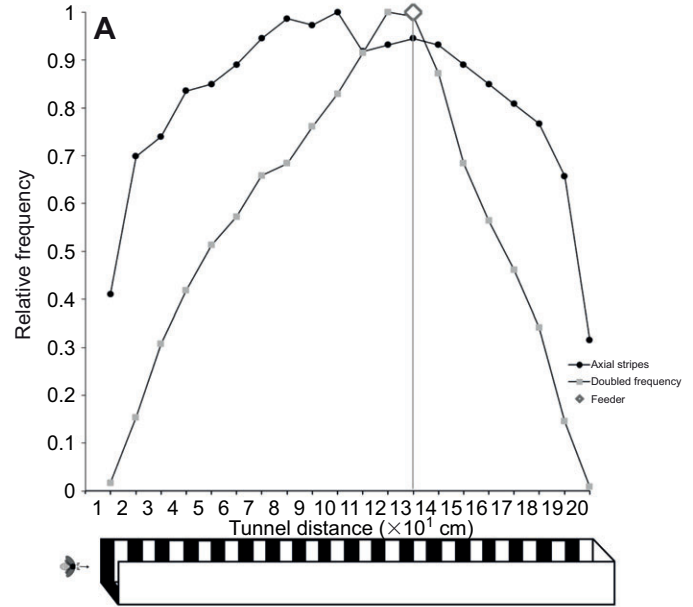
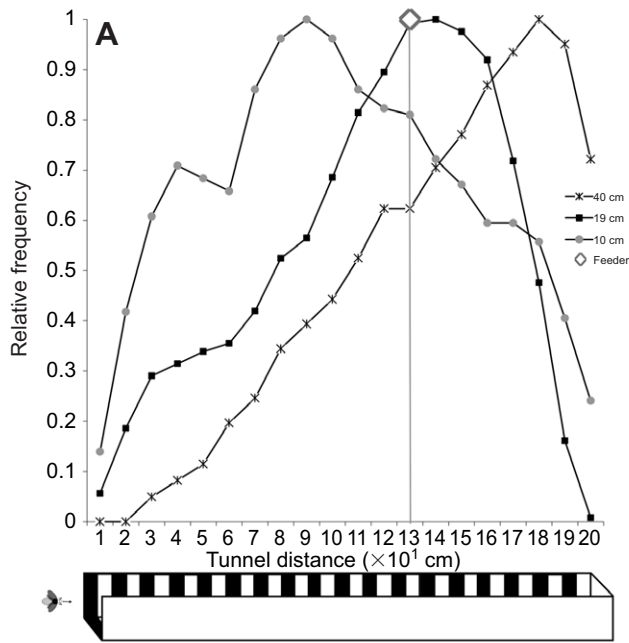


Fig. 2. Forager search behavior in the tunnels was similar in the (A) horizontal and (B) vertical experiments. In an empty tunnel (19 cm width) devoid of scent cues but identical to the training tunnel, foragers searched in the area where the feeder was previously, indicating they can navigate in the tunnels. In a narrower (10 cm width) tunnel (where image motion is increased), bees searched significantly closer to the entrance, while in a wider (40 cm width) tunnel (where image motion is decreased) bees searched significantly farther down the tunnel.

Fig. 3. Forager search behavior in the control pattern experiments was similar in the (A) horizontal and (B) vertical experiments. In the first control experiment, bees foraging in a tunnel with double the pattern frequency of the training tunnel continued to search in the area where the feeder was previously located, indicating that foragers are not counting stripes to gauge distance traveled.

$t_{1,105}=1.19, P=0.28$ ; versus original feeder location  $t_{53}=0.092, P=0.93$ ). (2) When the pattern was changed to axially oriented stripes (providing no visual cues for optic flow), bees began searching closer to the tunnel midpoint (MSP  $10.43 \pm 1.56$  boxes,  $N=83, t_{1,81}=10.98, P=0.0014$ ; versus original feeder location  $t_{29}=-5.55, P<0.0001$ ). (3) Lastly, foragers in the axially striped tunnel also covered a larger search range than those in the cross-striped tunnel (mean of search range on axial stripes  $17.03 \pm 1.96$  boxes,  $N=30$ ; mean of search range on cross-stripes  $5.64 \pm 3.01$  boxes,  $N=53, t_{79,3}=20.86, P<0.0001$ ).

**DISCUSSION**

During both horizontal and vertical flight, *M. panamica* foraged by using optic flow cues to gauge the distance traveled. This is the first study to demonstrate that a bee moving in a vertical plane can use optical flow cues present primarily in the lateral visual field. When searching in a tunnel without a reward but identical to one in which they were previously trained, bees consistently searched where the reward was located, indicating that they can correctly identify the distance to the food source. Bees that flew in a tunnel half the width



of the training tunnel searched at half the original distance to the reward. Thus, the increased amount of angular image motion perceived per unit distance traveled increased the foragers' perceived travel distance. Bees that flew in a tunnel twice the width of the training tunnel likewise experienced a decrease in angular image motion and therefore searched at a significantly greater distance (Srinivasan et al., 1996; Srinivasan et al., 1997).

Bees did not significantly alter search behavior in a tunnel with double the optical pattern frequency, indicating that this visual odometer is dependent on image motion as opposed to image density or structure: thus, like *A. mellifera* (Srinivasan et al., 1996; Srinivasan et al., 1997) and *M. seminigra* (Hrnčir et al., 2003), *M. panamica* foragers do not count stripes. It is unlikely that other cues were responsible for the changes in search behavior observed in the range of tunnel dimensions. The tunnel cover effectively eliminated the use of landmarks. Axial stripes provide no usable optic flow cues (Srinivasan et al., 1996; Srinivasan et al., 1997), and bees were disoriented and traveled over a significantly greater area in axially striped tunnels than in tunnels with optical cues displayed in a perpendicular orientation to the flight axis.

The MSP of foragers in the axially striped tunnel was much closer to the tunnel midpoint (MSP 104 cm) than the training feeder location (135 cm), or to where bees searched in the experimental tunnel that was identical to the training tunnel (MSP 129 cm). This shift in MSP is what one would expect if the bees are disoriented and flying from the tunnel entrance to the terminus and back again, instead of performing a directed search. In this case, their search is bounded by the ends of the tunnel and thus the MSP should be the tunnel's center. This is why we chose to offset the training feeder location from the center of the tunnel. It is possible that subtle visual irregularities in the axial pattern may have provided a limited amount of optic flow; however, it was insufficient for the foragers to use successfully.

During training in the horizontal tunnel of 19 cm width, bees experienced approximately 6.01 deg of angular image motion for every 1 cm of forward flight. This means they experienced an approximate total of 811.22 deg of image motion during their flight to the feeder in the center of box 13 (at 135 cm). When tested in the narrower horizontal experimental tunnel, bees experienced 11.3 deg of image motion per cm of forward flight, and would only need to fly 71.79 cm to achieve the same amount of image motion as during their training. In the wider horizontal tunnel, foragers experienced only 2.86 deg of image motion per 1 cm of flight, and thus would need to fly 283.6 cm to match the amount of image motion they originally learned. Our tunnel length of 2 m was too short to allow for a comparison between this estimate and the actual distances flown by bees in the 40 cm tunnel, although we did find a significant difference between where bees searched in the horizontal 10 cm tunnel and the estimate given by our image motion calculation ( $\text{MSP}_{10\text{cm}} = 8.87 \pm 3.80\text{ cm}$ ,  $t_{56} = 3.36$ ,  $P = 0.0014$ ). As stated previously, these image motion calculations are only estimates, and the difference in search location is one of magnitude only. The image motion calculation also predicts a shorter search distance, as seen in our data (Fig. 2A).

This is the first study to directly address how a stingless bee measures purely vertical displacement. Stingless bees live in an environment where food sources are scattered throughout the forest canopy, so a finely tuned vertical odometer may be important for navigation to resources. Bees lack the optical structures necessary for depth perception (Esch and Burns, 1995), but both honey bees (Esch and Burns, 1995) and *M. panamica* (Nieh and Roubik, 1995) are capable of accurately gauging the heights of food resources. We

suggest that foragers are able to exploit the rich optic flow cues from the surrounding forest to simultaneously track their total displacement from the nest and their degree of ascent into the canopy. Stingless bees can fly largely in a vertical plane when laying or following vertical odor trails up into the canopy (Lindauer and Kerr, 1960; Nieh et al., 2004). Honey bees are also capable of near-vertical flight while foraging (Roubik et al., 1999). We have also observed untrained *M. panamica* foragers following a vertical flight path to reach mass flowering trees located between 30 and 40 m up in the canopy (M.A.E., personal observation).

Although vastly simplified, the tunnel environment does simulate the basic visual environment a bee would experience when flying up into the canopy: the ground and other images below the bee recede in the ventral view, while images in the lateral views remain constant or increase in size as the bee leaves the understory and enters the canopy. The optically dense forest where stingless bees forage provides the perfect environment for foragers to use optic flow from the lateral field of view for height measurement. Hrnčir and colleagues found that *M. seminigra* uses visual information from both the ventral and lateral fields of view (Hrnčir et al., 2003), possibly because of the importance of flight height in an area where resources may be vertically stratified (Lehrer et al., 1988; Roubik, 1989; Esch and Burns, 1996). We did not directly examine the relative importance of the lateral *versus* ventral fields of view. Likewise, we did not eliminate visual cues from the dorsal and ventral fields, and thus cannot say that these bees use information solely from the lateral field for height measurement. It is possible that *M. panamica* may exploit all angles of the visual environment in a similar way. However, during vertical flight in a tunnel, the vast majority of image motion occurs in the lateral field of view, suggesting that *M. panamica* is able to exploit visual information when it is concentrated in this visual region. Interestingly, *M. panamica* foragers also demonstrated more precision when searching in a vertical tunnel than in a horizontal tunnel. This may be due to the increased energetics of vertical flight compared with horizontal flight (Dudley, 2000), in which case a more precise vertical search area would limit unnecessary energy loss.

In both honey bees and desert ants (*C. fortis*), it appears that odometric information is not accumulated when there is no concurrent view of the sky to provide celestial cues (Dacke and Srinivasan, 2008; Sommer and Wehner, 2005; Ronacher et al., 2006). Unlike more open environments such as deserts or temperate forests, the dense canopy of the tropic forest obscures most views of the sky, and what sunlight does penetrate is filtered through dense foliage (Croat, 1978; Leigh, 1999). Under these impoverished visual conditions, it would be necessary for any understory-dwelling bee such as *M. panamica* to develop compensatory skills to account for the lack of celestial information. Our results indicate that despite the lack of celestial cues and a relatively low light environment in the dense forest understory, *M. panamica* is able to reliably use optic flow to measure distance traveled. This contrasts with results from honey bees, which suggest that in the absence of sky cues foragers cease to collect information on distance traveled (Dacke and Srinivasan, 2008).

Despite the absence of celestial cues and other components of a bee's natural visual environment, the experimental simplifications of a forager's optical surroundings provided by optic flow tunnels provide important insight into how insects use specific types of visual information (Egelhaaf and Kern, 2002). Successful, 'natural' versions of these experiments have been performed with honey bees (Tautz et al., 2004). Thus, *M. panamica* is capable of visual odometry and, like honey bees, likely uses it to gauge distance and height

traveled while foraging. In a tropical forest where competition is intense and resources are both spatially and temporally scattered, a refined system for gauging both distance and height may be crucial for stingless bees to rapidly and efficiently exploit assets in their environment.

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