Desert ants (Melophorus bagoti) navigating with robustness to distortions of the natural panorama

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Abstract

Many insects are known to use the terrestrial visual panorama for navigation. Research suggests that large-scale panoramic properties are often used for orientation rather than individual objects, usually called landmarks. We degraded the natural panorama encountered by Australian red honey ants, *Melophorus bagoti*, to test how robust their orientation based on the terrestrial panorama is. Foraging ants were lured to a feeder at a constant location. Trained ants were allowed to run home individually with food, but were captured just before they entered their nest. The tested ant was brought back to the location of the feeder, now covered, and allowed to run home again under different distortions of the natural panorama. In one experiment, a large tract of the view on one side of the feeder was obstructed by a tall plastic sheet. In a second experiment, the visual heights of terrestrial objects were altered by raising or lowering the ant by 80 cm. Under both kinds of distortions, the ants continued to be well oriented in the homeward direction. Navigation based on the natural terrestrial panorama proved robust to large distortions.

Introduction

Path integration and view-based navigation utilising the visual panorama are major means of navigation in animals (Cheng and Spetch, 1998; Wehner and Srinivasan, 2003; Etienne and Jeffery, 2004; Wiener et al., 2011). In path integration, the navigator keeps track of the straight-line distance and direction from the starting point (typically home), and then uses this constantly updated vector to navigate back. In navigation based on the visual panorama, terrestrial objects are used to chart the way to a goal. The terrestrial objects have often been thought of as individually identified elements, usually called landmarks, a term that appears, for example, in the title of Cheng and Spetch's (1998) review. But more recently, especially in insect navigation, representations encompassing large tracts or the entirety of the terrestrial panorama are thought to play a role in view-based navigation (Towne, 2008; Towne and Moscrip, 2008; Wystrach et al., 2011a, b, 2012; for some not so recent evidence, see von Frisch and Lindauer, 1954). In controlled laboratory conditions as well, global characteristics of large tracts of the scene have been shown to play an important role in navigation (Lent et al., 2013). Various models have also been based on the whole terrestrial panorama without separating out or individuating any landmarks (Zeil et al., 2003; Baddeley et al., 2012; Mo� ller, 2012; Wystrach et al., 2012, 2013a; Lent et 2013), showing that it is not necessary to identify objects for navigation.

Evidence suggests that simplified summary information about the terrestrial panorama can suffice for orientation in insects, although much remains to be determined concerning what range of information is encoded and how it is used in navigation. The skyline has been implicated as one kind of panoramic information used by insects. The skyline is some record of the heights of the tops of terrestrial objects in the surround. Honeybees, *Apis mellifera*, learn directions of travel associated with panoramic views (Dyer, 1987; Towne, 2008; Towne and Moscrip, 2008). In these studies, honeybees could head out to a feeder using terrestrial cues after they had been displaced to a different place with similar terrestrial cues oriented in a different compass direction. Furthermore, the bees had learned the celestial cues associated with the scene, because they often reported in their dances the original direction to the feeder (before their displacement) according to celestial cues. One finding from Towne and Moscrip (2008) suggested that honeybees use the skyline of the panorama. The authors displaced a hive of honeybees to an unfamiliar location and expected the group to be disoriented. Surprisingly, the bees showed a preferred direction. Towne and Moscrip noted a similarity in the skyline at the two locations: the original location of the hive and the test location (see their Fig. 6), and suggested that this might be the basis of orientation in the bees. If that was the case, the views at the two locations, although sharing similar skylines, differed a lot, as different objects made up the two skylines.

Graham and Cheng (2009a) re-constructed the skyline experimentally for our study species, the Central Australian red honey ant *Melophorus bagoti*. Based on a panoramic photo taken at the feeder that the ants were trained to visit, an artificial panorama all in black was constructed by matching elevations every 15° of azimuth. Ants displaced to the middle of the artificial panorama showed initial headings oriented according to the experimental panorama, even when the arena was rotated so that its orientation indicated a different compass direction home from the actual feeder-nest direction. In short, the ants followed the dictates of the rotated panorama.

The red honey ant lives in a habitat filled with distinguishing terrestrial visual features in the form of tussocks, bushes, and trees (Muser et al., 2005; Cheng et al., 2009; Schultheiss and Nooten, 2013; Cheng et al., 2014). It is well known to establish and stick to stereotypical routes through its visually cluttered habitat (Kohler and Wehner, 2005; Wehner et al., 2006; Sommer et al., 2008; Wystrach et al., 2011c). A combination of empirical results and modelling based just on skyline information suggests that a panoramic visual compass might provide the crux of a mechanism for navigating on a familiar route (Wystrach et al., 2012). This mechanism is based on a comparison of remembered and perceived panoramic skylines at any point on the route, as one rotates one against the other. The compass direction at which the two views match the best is the direction to travel in. Videotaped observations of this species show that the ants actually turn on the spot in a saccadic fashion, as if comparing views when facing different directions (Wystrach et al., 2014a). Similar turning behaviours are found in another Australian species living in visually

cluttered conditions, the bull ant *Myrmecia croslandi* (Zeil et al., 2014). The entire process may work as a direction-determining mechanism based on view comparisons, a class of models that Möller (2012) called ''recognition-triggered'' (p. 118). The panoramic visual compass may be augmented by predicting views to be found in any direction of travel (Möller, 2012). That is, the agent computes what the panoramic view would be like if it was to move in the direction that it is facing. The augmented set of views, including the predicted views, is used for comparing with a remembered target view. Global summary characteristics of the skyline might also suffice for matching. One such characteristic is the proportion of the skyline to the left vs. to the right (fractional position of mass), so far found to be important for wood ants navigating in laboratory conditions (Lent et al., 2013). The panoramic visual compass may not be based on a set of discrete views, found at various points along the route. Baddeley et al. (2012) proposed a single holistic representation of all features encountered along the route, based on the notion of familiarity. Views perceived when aligned in the correct direction of travel look familiar under this model. The model can even account for some findings taken as support for the use of multiple views (Wystrach et al., 2013a).

To further theoretical developments, it is important to delimit how much the visual panorama may be degraded before orientation breaks down. To that end, we have degraded the panorama of homing *M. bagoti* ants in two ways that can be readily effected in field experiments in their natural habitat. In both experiments, ants were trained to visit a feeder provisioned with food. Trained ants were then allowed to run home and captured just before they entered their nest. These are called zero-vector ants because they have run off their vector calculated according to path integration. They are forced to rely on view-based navigation. The ants were then released again at the feeder, now covered by a board, under various conditions. In one experiment, about half the natural panorama at the feeder was obliterated by the presence of tall white plastic sheets erected on one side of the feeder. At two of the feeder locations, one side had far more changes in skyline height than the other, which was mostly flat. We wondered if covering the intuitively more informative half of view would have a larger effect. In a second experiment, absolute skyline heights were much altered by raising or lowering the test location without displacing it horizontally from the feeder location. And because objects at different distances change retinal elevations differently when the viewer is raised or lowered, the contour or 'shape' of the skyline was also distorted. Would the ants still be oriented in the feeder-nest direction under these distorted conditions?

Methods

Study animals

Experiments were carried out on the red honey ant, *Melophorus bagoti*, a highly thermophilic ant (Christian and Morton, 1992) that forages solitarily on dead insects and plant materials (Muser et al., 2005; Schultheiss and Nooten, 2013). Ants from one nest were tested in Experiment 1, while a different nest was

tested in Experiment 2. Ants that arrived at a feeder were painted with a dot of enamel paint signifying the day that they started training.

Field site

The field site was located ~10 km south of Alice Springs, Australia, on the grounds of the Centre for Appropriate Technology, in a semi-arid desert habitat characterised by red soil. The main vegetation includes grass tussocks, largely of the invasive buffel grass (*Cenchrus ciliaris*), bushes, and trees of Acacia and Eucalyptus species (Muser et al., 2005; Schultheiss and Nooten, 2013).

Set up

For each condition, a 'route' to a feeder was set up. Flexible wooden boards (10 cm wide) were sunk in the ground with the smooth side facing inwards, surrounding a track including the nest and the feeder. This encouraged more foragers to visit the feeder, a square-shaped plastic tub ~15 x 15 cm in width and ~9 cm deep. The feeder was sunk in the ground with its top edge at ground level, and provisioned with cookie crumbs (Arnott[TM] brand) and pieces of mealworm. In one condition described more fully in Experiment 2, the feeder was sunk in the middle of a 'table'. Its inside walls were also coated with fluon, making it well-nigh impossible for the ants inside to climb out. During training, wooden sticks were added to the feeder as bridges to allow ants to climb out. These sticks were removed at testing time to trap trained ants for testing.

A large white plastic sheet (242 x 72 cm) was used to obstruct part of the view in Experiment 1. We measured the spectral characteristics of the sheet 3 times, each measurement relative to a standard white reflecting all wavelengths, including those in the ultraviolet (UV) range. The sheet reflected more in the green range than in the UV range. In the range 475–525 nm, reflectance averaged 105 % relative to standard white, while in the range 325–375 nm, it averaged 66 %. The sheet thus resembles other terrestrial objects in reflecting more in the green range than in the UV range.

Procedures for Experiment 1

In Experiment 1, we effected manipulations on key tests to block almost half of the natural panoramic view of returning ants. In three different conditions, we set up the feeder 7.5 m to the north, south, or east of the nest. Around this nest, the west side had the most cluttered view (Fig. 1). Ants were trained for at least one full day with unobstructed view of the entire panorama before being tested. A trained ant was given one and only one test.

We conducted experimentation during the latter part of the morning, after the ants became active (~10:00–12:00) and in the afternoon (from ~14:30 onwards). The ants were hardly active during the midday period, making it not worthwhile conducting experiments.

On a test, the ant was allowed to run home with food, and was caught just before it entered the nest. Ants were only tested if they held on to a piece of food, to ensure motivation for homing. We effected three types of tests on these zerovector ants. On a control test, the panorama was not manipulated and left as it had always been throughout training. On a left-cover test, the left side of the panorama in the feeder-nest direction was blocked. The large white plastic sheet stood parallel to the line joining the feeder to the nest, centred at the feeder and 0.7 m distant on the left side. This meant that the sheet spanned about 148° azimuth, close to estimated 150° span of view of an eye in this ant (Schwarz et al., 2011). On a right-cover test, the same white sheet stood parallel to the line joining the feeder to the nest, but on the right side, 0.7 m distant. Numbers of ants tested are given in the data figures.

In the South-route conditions, we tested in addition full-vector ants in the left-cover and right-cover tests. These ants were simply picked up from the feeder while they held a piece of food, and tested immediately. Full-vector ants still have their vector home calculated using path integration, in addition to panoramic visual information.

On all tests, a goniometer (60 cm radius) was placed centred over the feeder. The goniometer was divided into 24 sectors of 15° each, with the boundary between sectors 24 and 1 pointing to the nest. The sector at which the tested ant crossed at 60 cm distance constituted the data (we also noted where the ant crossed at 30 cm, but the data were largely similar and are thus not reported here).

A

360° view at the nest

B

Open side   cluttered side

Fig. 1 Panorama around the nest used in Experiment 1. **a** Panoramic photo taken at the nest. The photo was taken using a panoramic lens and then 'unwarped' to a cylindrical view using PhotoWarp™ software (EyeSee Inc.,

Pittsburgh, USA), in which the right and left edges coincide. The poles sticking out are aluminium rods for attaching the view-blocking sheets to, left in place for all ants. **b** The panoramic photo from (a) rendered to give an impression of what the study animals might see. The photo has been blurred to 4° resolution, the approximate resolution of the ants' eyes (Schwarz et al., 2011), and 60° of view to the back has been eliminated, again on the basis of Schwarz et al.'s (2011) findings

Procedures for Experiment 2

In Experiment 2, we distorted the skyline height of the panorama on key tests by raising it or lowering it as a whole, as compared to the panorama encountered during training. The feeder was approximately 5 m west of the nest entrance on a curved path. We also surrounded the feeder and nest area with pliable wooden boards, but the surrounding enclosure bent to the right from nest to feeder to skirt around vegetation and also follow the observed paths of foragers who headed off in that direction. We chose this nest and this feeder location because it contained nearby landmarks (trees, a building) of heights that would change elevations greatly when the ants were raised or lowered on a test. A fence ran between the nest and the feeder, and on the fence, we draped and pegged a sizeable sheet of black cloth to add yet another nearby medium-height landmark (Fig. 2).

Fig. 2 Photo of the set up used in Experiment 2, with the wooden table in place. The ramp to the table and the feeder is not shown

We set up two different training conditions, called ground and table. In the ground training condition, the feeder was sunk into the ground as in Experiment 1. In the table training condition (Fig. 2), we lured ants to a feeder set on a 'table', constructed of a wooden board (about 1 m square) set on a bamboo container (80 cm high). The board had a hole cut in the middle to which the feeder was attached. To induce the ants to climb up to the table, the nest was surrounded with boards whose only opening was to a 'ramp' up to the table. The ramp consisted of 3 m of narrow plastic channels (10 cm wide and 10 cm high), supported in the middle by a plank of wood. Two metal stakes helped to support the ramp. Some sand from the ground was sprinkled on the ramp to give the ants better traction. From the feeder, the ramp with the entrance to and exit from the table pointed in the feeder-nest direction.

In Experiment 2, the design consisted of four conditions in a 2 9 2 factorial. Ants were trained to the feeder located either on the ground or on the table. For each training condition, ants were tested either on the ground or on the table, again as zero-vector ants. Each is an independent group with different ants (ground condition: N = 31 tested on the ground, N = 39 tested on the table; table condition: N = 30 tested on the table, N = 30 tested on the ground). Due to space constraints, we used a smaller goniometer (30 cm radius) on tests, with the goniometer again divided into 24 15° sectors. In this experiment, sector 1 faced the nest direction. Sector crossings were noted at 15 and 30 cm. They proved to be similar, so that we will report only data at 15 cm.

Data analysis

Circular statistics (Batschelet, 1981) were used to analyse the data. For each test type, the V test was used to test whether the distribution was significantly oriented in the nest direction. The Var test, of our own invention, was used to compare differences in scatter between a distribution and its appropriate control comparison case. In the Var test, headings were transformed to absolute deviations from the mean heading direction, and a non-parametric Wilcoxon test comparing the two groups was performed. The Watson–Williams test was used to compare the mean heading direction of a distribution against its appropriate control comparison case. In Experiment 1, we set alpha at 0.01 because many comparisons were made. In Experiment 2, we set alpha at 0.05. We also compared panoramic photos of the set ups in the two experiments, described fully in the Results.

Results

Experiment 1

The zero-vector ants in all conditions were oriented in the general direction of the nest (Figs. 3, 4; Table 1). But with one half of the panorama covered, most veered towards the open uncovered part of the view. With some variability, they appeared more scattered in headings than the control groups. At the North and South feeder, whether the more cluttered or the more open half was covered did not seem to matter: ants were well oriented in both cases. Formal statistics gathered in Table 1 confirm some of these impressions. All groups were significantly oriented towards the goal direction (Vs > 11, $ps \leq 0.001$). But the Watson–Williams test showed that in all but one case, each experimental group with half the panorama covered differed in mean direction from its control group at the 0.001 level. The one exception (Fig. 3c) does not look that different from the other experimental groups. While the scatter in headings appears larger in groups with half the panorama covered, the Var test delivered significant results only in groups with the feeder to the North (Table 1). Inspection of Fig. 3 shows that at the North feeder, the control group was exceptionally well oriented (Fig. 3a), and it might be the 'outlier' in lacking variance.

Turning to full-vector ants with half the panorama covered, effected only with the feeder to the South, both groups were also significantly oriented in the nest direction (Fig. 4; Table 1). Both groups, however, differed significantly from the zero-vector control group in mean direction, although not in scatter (Table 1). Interestingly, Fig. 4 suggests that the full-vector groups deviated less from the zero-vector controls than did the zero-vector groups with half the panorama covered. Watson–Williams tests against their respective zero-vector half-covered counterparts confirmed this impression (left-cover: p = 0.008; right-cover: p < 0.001).

Finally, we measured image difference functions, as explained in Fig. 5, indicating one measure of the level of misfit with the home direction in training conditions, as a function of the direction in which a navigator is facing in a test condition. The mismatch level was based on pixel-bypixel mismatch, a proxy measure that should not be taken to be the way that ants are matching. Figure 5 shows that the best match (lowest level of mismatch) is always in the home direction, but the scales shown on the y axes tell an important story. The mismatch rises steeply in control conditions (top row) as the navigator turns. With half the view covered, however (bottom 2 rows), the rise is often smaller.

In sum, all groups were oriented in the feeder-nest direction, even with close to half the panorama covered. Covering half the panorama, however, led the ants to veer away from the covering sheets towards the open landscape, more so in zero-vector ants than in full-vector ants. These deviations are not explained by the image-discrepancy functions caused by the added sheet (Fig. 5), as the best match continued to be in the feeder-nest direction.

Experiment 2
We first compared the panoramic views at the feeder on the ground and on the table (Fig. 6). This comparison showed that the two views were most similar when they were aligned in compass direction. That is, in whichever direction a navigator faced on the ground, the view was most similar when facing the same direction on the table, and vice versa. In each case, the minimum sat at the bottom of a valley of lower mismatch, indicating that reliable directional information was available despite the alteration of the perceived scenery.

As for the ants' behaviour, all groups were, as in Experiment 1, generally oriented in the feeder-nest direction (Fig. 7). Ants tested on the table headed initially slightly to the left of the feeder-nest direction on average, whereas ants tested on the ground headed initially to the right of the feeder-nest direction on average. Although we did not record training runs, the observed route home for the ants on the ground generally veered from right to left, following the gentle bend in the enclosure (see Fig. 2). For the groups

trained to climb onto the table, the mean direction differed more according to test situation (Fig. 7f), compared with the groups trained on the ground (Fig. 7e).
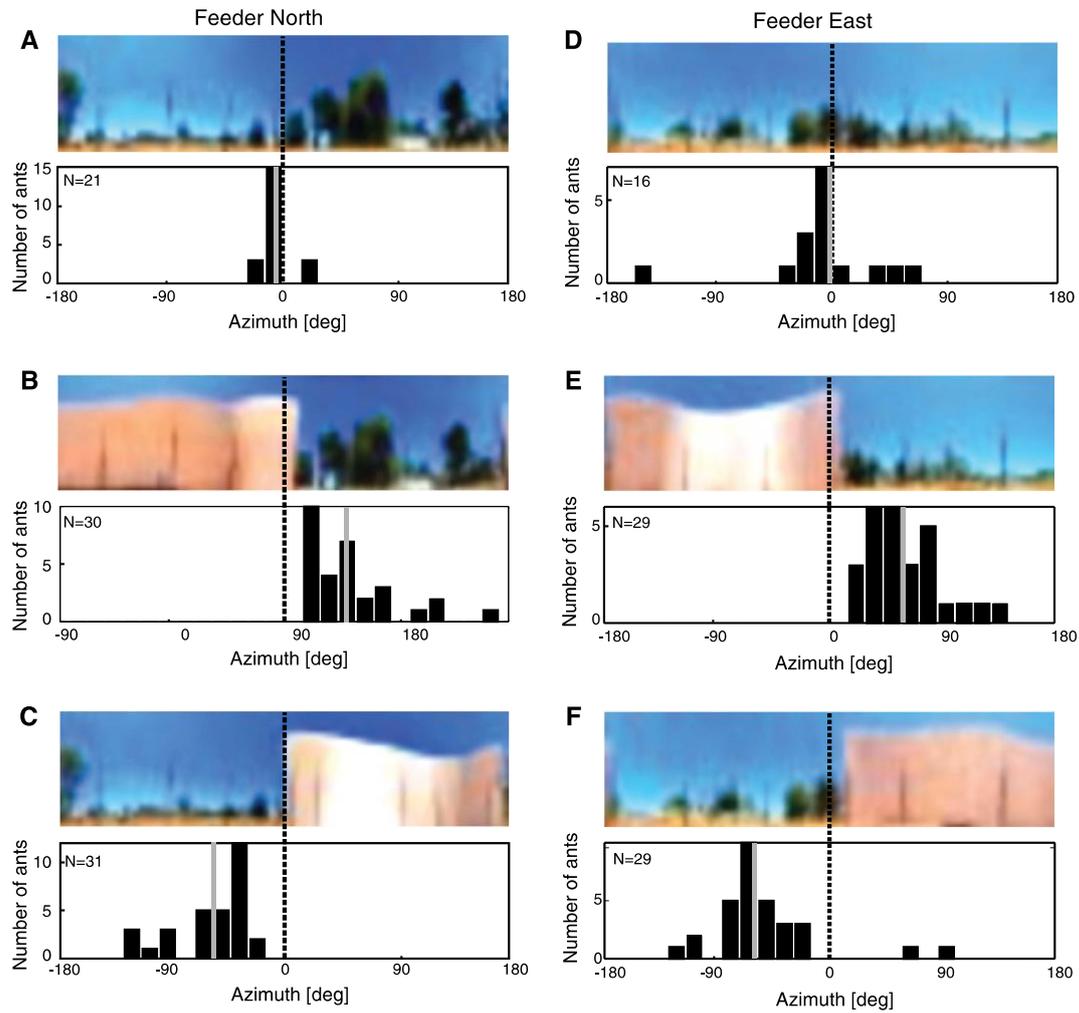

Fig. 3 Panoramic views in ant's-eye resolution (4") at the feeder and distributions of homing heading directions at 60 cm from the feeder set up to the north (**a–c**) and east (**d–f**) of the nest in Experiment 1. **a** and **d** Control condition with unobstructed view. **b** and **e** Left-cover condition with the left side of the panoramic view covered by a white sheet. **c** and **f** Right-cover condition with the right side of the panoramic view covered by a white sheet. The graphs are cylindrical, such that the right and left edges represent the same direction in space, the nest-feeder direction. The *grey vertical line* indicates the mean direction calculated with circular statistics. The dotted line at 0° indicates the feeder-nest direction. *N* indicates the number of ants tested in each condition

Formal circular statistical tests confirm these impressions. V tests showed that all groups were significantly oriented towards the feeder-nest direction (*V*s > 22, *p*s < 0.001). Scatter did not differ significantly between control and experimental groups, neither in those trained on the ground (Var test, Z = 0.11, *p* = 0.911) nor in those trained to visit the table (Z = 0.14, p = 0.890). For ants trained on the ground, the control and experimental groups did not differ in mean direction by the Watson–Williams test (*F* = 1.88, *p* = 0.175). For ants trained on the table, the two groups did differ significantly in mean direction (*F* = 10.35, *p* = 0.002).
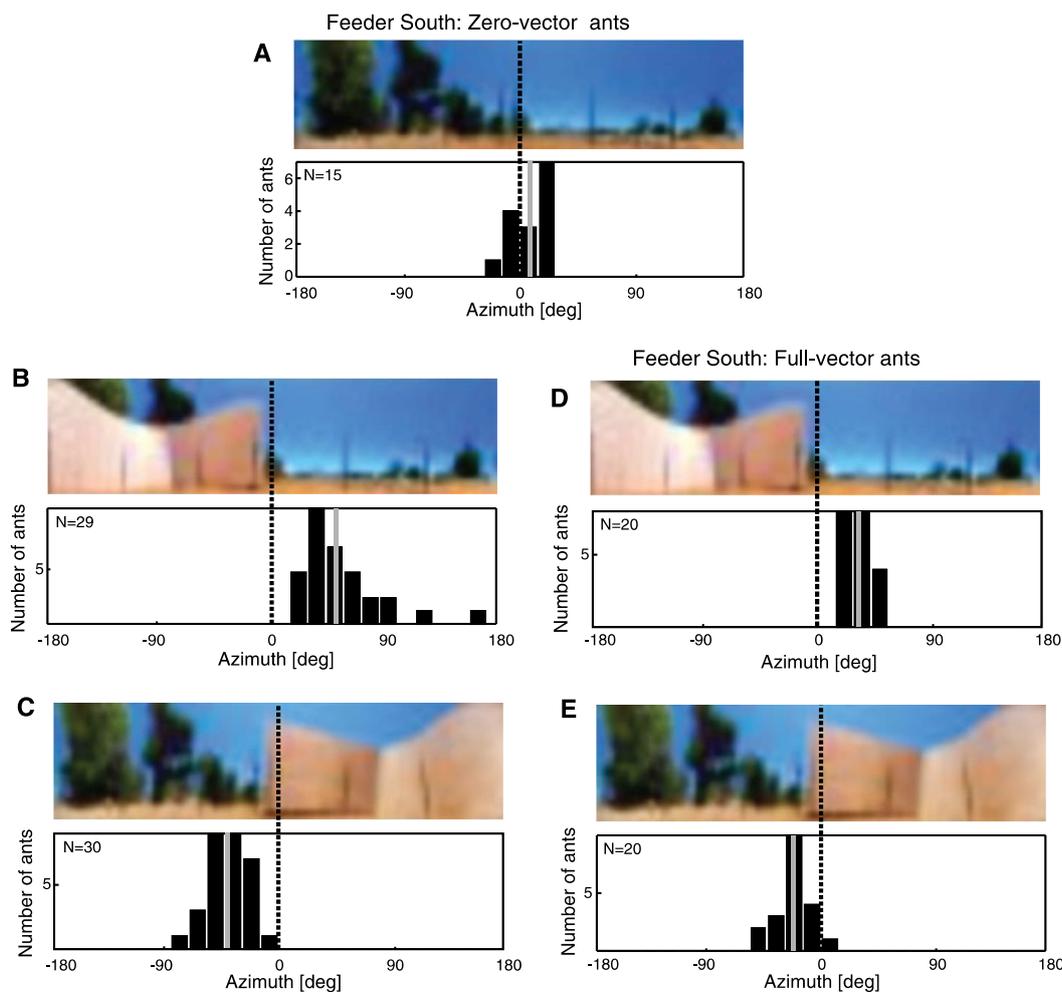
Fig. 4 Panoramic views in ant's-eye resolution (4°) at the feeder and distributions of homing heading directions at 60 cm from the feeder set up to the south for zero-vector ants (**a–c**) and full-vector ants (**d, e**) in Experiment 1. **a** Control condition with unobstructed view. **b** and **d** Left-cover condition with the left side of the panoramic view covered by a white sheet. **c** and **e** Right-cover condition with the right side of the panoramic view covered by a white sheet. The graphs are cylindrical, such that the right and left edges represent the same direction in space, the nest-feeder direction. The *grey vertical line* indicates the mean direction calculated with circular statistics. The *dotted line* indicates the feeder-nest direction. *N* indicates the number of ants tested in each condition

Discussion

In two experiments, we manipulated the skyline contour of homing ants that have already run off their vector according to path integration (zero-vector ants), and were captured and re-released at the feeder. In Experiment 1, we obliterated almost a half of the panorama with a tall sheet. In Experiment 2, we raised or lowered the ant, thus changing the average elevation of the panorama. The ants' performance showed robustness: in both experiments, they were well oriented in the feeder-nest direction, significant at the 0.001 level or beyond. In some cases, however, the mean direction of experimental groups differed significantly from that of their relevant control groups. In Experiment 1, all but one experimental group showed a significant deflection away from the tall white sheet, while the last group showed a deflection that failed to reach significance. In the groups trained on the table in Experiment 2, the group tested on the

ground differed in their mean heading from the group tested on the table. We focus the discussion on the two main themes of robustness, and deflections from the feeder-nest direction.

Table 1 Circular statistics for Experiment 1, with the Var test and Watson–Williams test having the zero-vector control group in that feeder direction as comparison group

Feeder direction	Condition	V	p	R mean vector	Var test p	Watson-Williams p
North	Zero-vector control	20.4	<0.001	0.98		
North	Zero-vector left-cover	15.3	< 0.001	0.82	0.003	< 0.001
North	Zero-vector right-cover	13.8	< 0.001	0.86	< 0.001	0.222
East	Zero-vector control	12.4	< 0.001	0.78		
East	Zero-vector left-cover	11.1	0.001	0.87	0.676	< 0.001
East	Zero-vector right-cover	11.6	0.001	0.8	0.920	< 0.001
South	Zero-vector control	14.4	< 0.001	0.97		
South	Zero-vector left-cover	21.4	< 0.001	0.86	0.110	< 0.001
South	Zero-vector right-cover	14.5	< 0.001	0.96	0.721	< 0.001
South	Full-vector left-cover	16.2	< 0.001	0.98	0.370	< 0.001
South	Full-vector right-cover	17.8	< 0.001	0.97	0.138	< 0.001

In the *V* test, a significant *V* indicates significant orientation of the group in the feeder-nest direction
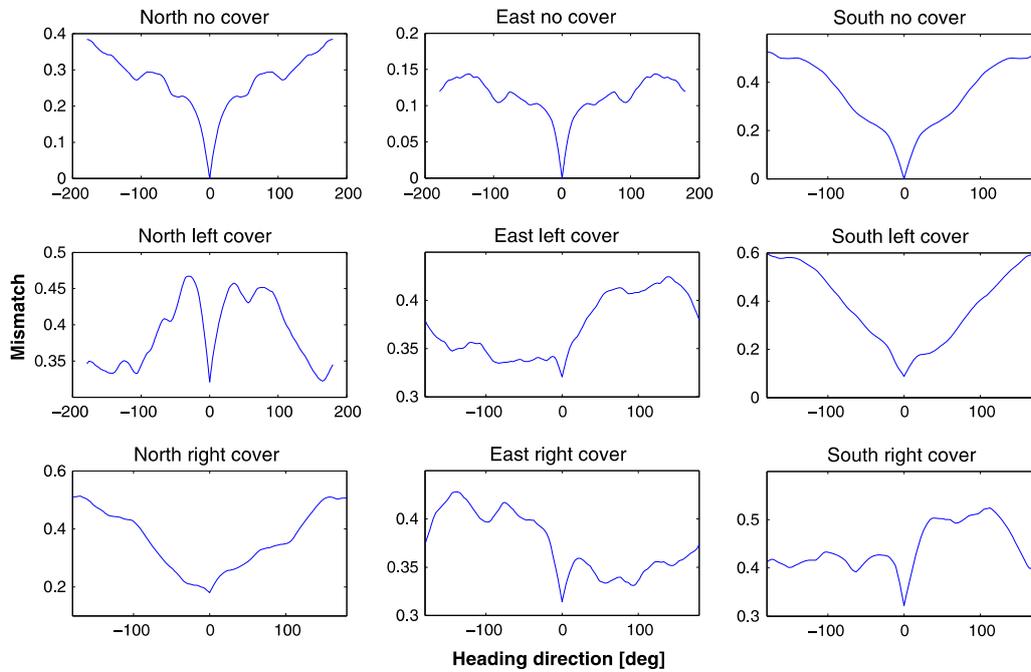

Fig. 5 Rotational image difference functions for conditions in Experiment 1. Panoramic photos taken at the release point of each of the set ups were first unwarped into cylindrical form (with Photo-Warp™). Each photo was cropped just below the horizon, and rendered into black and white, with the sky white and all ground objects black. The resolution was reduced to 4°, approximating the resolution of *M. bagoti* eyes (Schwarz et al., 2011). The 90 pixels of azimuth were 'stretched' to 360 pixels, without increasing the resolution. The functions show the mismatch level in proportion of mismatching pixels as the second image is rotated against the first image. The image from the control conditions (*top row*) served as the comparison case for all rotational image difference functions in each column. Note different y-axis scales for different graphs

As the experimental ants continued to head significantly in the homeward direction, our manipulations failed to disrupt navigation in any major way. A range of reasons might contribute to robustness, perhaps different ones for the two experiments. When skyline elevations were raised or lowered as a whole (in Experiment 2), our analysis of the panoramic views (Fig. 6) showed a clear valley of lower mismatch when

the viewer is oriented in the feeder-nest direction. But the overall mismatch level had increased, and the shape of the contour of the skyline had also changed in places. Perhaps the mismatch level will have to increase by even more to disrupt orientation, or else the valley will have to be flattened. It is also possible, however, that absolute elevations are not encoded or not used.

One possibility is that the ants use only the pattern of elevations, that is, the ups and downs. This form of encoding would largely neutralise mean changes in elevation, including those arising from changes in pitch when the ant walks over sloped ground or small objects. The shape of the contour also changed in places (compare Fig. 7c with d), but these changes were found only in limited segments of the panorama, whereas changes in elevation of the skyline spanned a larger range. We can think of two ways to encode this pattern of ups and downs. One way is to filter out the average elevation in the panorama, basically coding elevations as something akin to normalised scores above or below the average. A second way is to encode the slopes of edges in the skyline contour. Assuming that the skyline contour is encoded as green-UV contrast edges, as Möller (2002) theorised, then the orientations of the strongest green-UV contrasting edges as a function of compass direction can be a code for the skyline. Such edge orientations will be robust to global changes in mean elevation. While edge detection is well known in many kinds of visual systems (e.g., Hubel and Wiesel, 1959), including those of insects (Lehrer et al., 1990; Zhou et al., 2012; Seelig and Jayaraman, 2013), no evidence is at hand concerning whether the orientation of green-UV edges is encoded. For that matter, we do not have evidence yet whether green-UV contrast actually defines the skyline for insects.

Another explanation came to us after the experiments were done. Lent et al. (2013) found evidence that wood ants used what they called fractional position of mass in some circumstances in the lab. Translated to our outdoor situation, this would be a global parameter measuring the proportion of the terrestrial surround to the left of the target direction. Thus, if the left side of the home direction was uniformly 15° in elevation and the right side was uniformly 5° in elevation, the fractional position of mass would be 0.75 to the left side. This measure should be similar on the table and on the ground. We estimated the fractional position of mass in each training condition by measuring the heights of skylines used to calculate the rIDFs in Fig. 6 at regular intervals. The estimates were indeed similar: 0.57 to the left on the ground and 0.54 to the left on the table. If the desert ants used this parameter, they would continue to head roughly in the home direction.
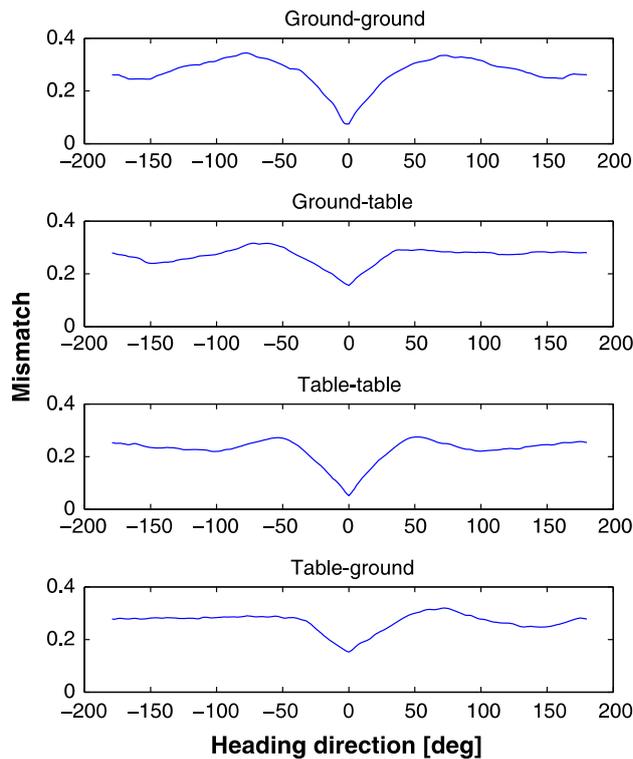
Fig. 6 Rotational image difference functions for the four conditions in Experiment 2. Panoramic photos taken on the table or on the ground where the feeder was located were first unwarped into cylindrical form (with PhotoWarp™). Each photo was cropped just below the horizon, and rendered into black and white, with the sky white and all ground objects black. The resolution was reduced to 4°, approximating the resolution of *M. bagoti* eyes (Schwarz et al., 2011). The 90 pixels of azimuth were 'stretched' to 360 pixels, without increasing the resolution. The functions show the mismatch level in proportion of mismatching pixels as the second image is rotated against the first image

Turning to Experiment 1, in which close to half the skyline was obliterated by a high wall, the distortion differed from that effected in Experiment 2. In this case, one large chunk of the current panorama, where the sheet was, found no match at all, but the rest matched perfectly. It is possible that the ants somehow filtered out the mismatching sheet, and the view-matching process focused on the part of the panorama that matched. Indeed, under other training conditions, Lent et al. (2013) found evidence for such segmentation in wood ants. Functionally, the ant might encounter new objects along a familiar route, such as fast growing grass or trees being felled by storms. Mechanistically, for our ants, since such objects affect the scene drastically only when the ant passes close to them, a filter based on information from motion parallax would be enough. A very near object could thus be treated as an obstacle to be avoided rather than part of the memorised scenery. In a habitat with lots of tussocks, obstacles are often encountered in travel. As with Experiment 2, however, it is also possible that the level of distortion is simply not large enough to trouble the ants, and they continued to orient using the available cues.
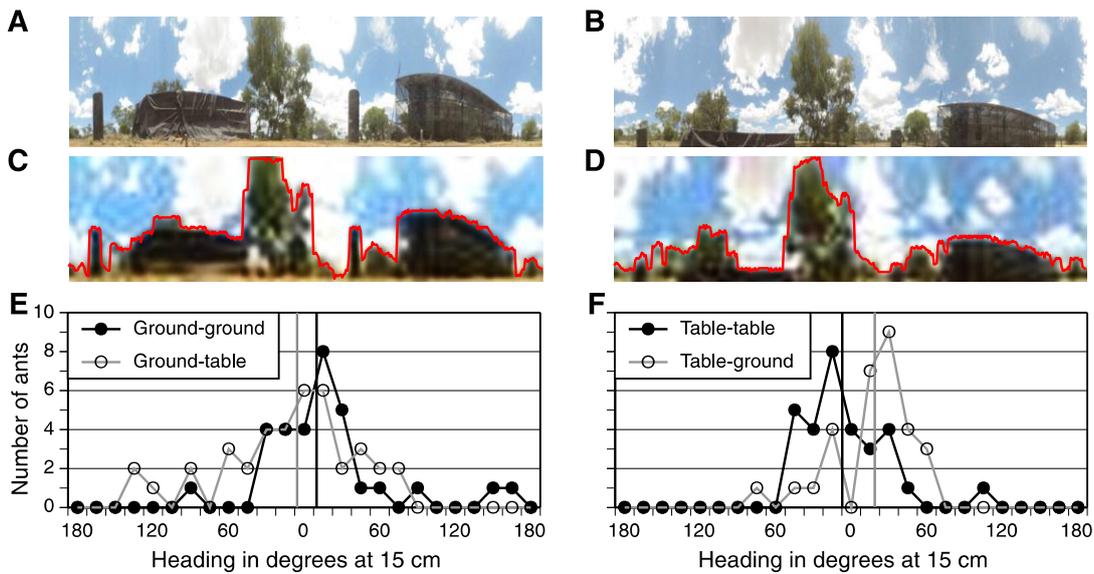
Fig. 7 Panoramic views at the feeder and the distribution of heading directions at 15 cm from the feeder in Experiment 2. **a, b** Panoramic photos taken at the feeder located on the ground (**a**) or on the table (**b**). The photos have been unwarped and cropped just below the horizon. **c, d** The panoramic photos at ground level (**c**) and on the table (**d**) blurred to 4° resolution. The red curves show the approximate skyline contour, drawn by hand. **e, f** Distributions for ants trained to find a feeder on the ground and tested on the ground or on a table (**e**), or trained to find a feeder on a table and tested on the table or on the ground (**f**). The photos and graphs are cylindrical, such that the rightmost and leftmost data points represent the same direction in space, the nest-feeder direction. 0° represents the feeder-nest direction. The vertical lines represent the mean heading direction calculated by circular statistics

Our manipulations were aimed at changing the terrestrial panorama, but they left other cues unaffected. Thus, all celestial compass cues were available, including the polarisation compass, the sun, and spectral cues (Wehner, 1994, 1997; Wehner and Müller, 2006; Wystrach et al., 2014b). Evidence from zero-vector ants of this species shows that the use of potential celestial cues differs according to circumstances. Legge et al. (2010) found evidence for the use of celestial compass cues in zero-vector ants in the impoverished conditions of an artificial arena. When zero-vector *M. bagoti* ants trained with natural panoramas were deprived of all terrestrial cues, on the other hand, they were disoriented in homing (Graham and Cheng, 2009b; Schultheiss et al. in prep.). Although potential celestial sources of direction would have been available to these ants, they appeared not to make use of them.

The reason for the disorientation, however, may not be a failure to learn the celestial cues associated with the feederhome direction, but reflects a strategy not to use those cues, a learning vs. performance distinction. Solid evidence from another hymenopteran, the honeybee, shows that the sun's direction (and by implication other celestial cues too) can be associated with a direction in the panoramic landscape (Dyer, 1987; Towne, 2008; Towne and Moscrip, 2008). In *M. bagoti* too, Wystrach et al. (2012) suggested that the panoramic cues were linked to sky-compass cues, based on modelling route behaviour. And Wystrach et al. (2013b) found that when zero-vector ants homing from a habitual feeder were displaced to an unfamiliar spot and released, they headed systematically in the nest-feeder direction, or backtracked.

The unfamiliar release point had no usable terrestrial cues, verified empirically, so that the backtracking ants must have been using celestial cues to head in the nest-feeder direction. Functionally, it was thought that backtracking serves to steer the displaced ant back to familiar terrain, the unfamiliar terrain being most likely the area beyond the nest in the feeder-nest direction.

It makes functional sense to use both terrestrial and celestial sources of directions for homing, as two sources are better than one when it comes to accuracy and precision (Cheng et al., 2007). As suggested by a reviewer as well, we now (between drafts of this manuscript) think that perhaps when the dictates of the celestial sources are too discrepant from the dictates of the panorama, for example when Graham and Cheng (2009a) rotated the artificial skyline, then the terrestrial cues win out. This also makes some functional sense, as two highly discrepant sources of information are unlikely to be indicating the same entity, direction to home in the example (Cheng et al., 2007; Körding et al., 2007). It may also be the case that when the panorama was blocked out, as in Graham and Cheng's (2009b) study, then it becomes too unfamiliar, so that both the panorama and its associated celestial cues are not relied on. It may make little sense to head in the feeder-home direction when signs indicate that the navigator is clearly not at the feeder any more. The very strange surround of an artificial arena might make the ants 'think' that they are also unlikely to be in the area beyond the nest, so that they do not engage in backtracking. Perhaps the ants then engage in a systematic search strategy, which would produce a random initial heading direction.

If celestial cues are used on routes under normal conditions, as a component of local vectors defining the route (Collett et al., 1998), this could help explain why the ants headed more or less in the home direction under drastic panoramic changes. As long as the scene is recognisable, the associated celestial compass cues would help them stay on course no matter how distorted the panorama looks. It would be worth testing the role of celestial cues for zero-vector ants. If they are used, blocking celestial cues should result in slightly worse performance, and rotating celestial cues by a smaller amount (than what Graham and Cheng, 2009a effected) might result in the ants averaging celestial and terrestrial dictates.

Turning to the systematic deflections from the homeward direction found in both experiments, these deviations do not detract from the fact that the ants remained significantly oriented in the homeward direction. Explanations for the deviations in the two experiments probably differ. In Experiment 2, the homing ants walking on the ground had a natural tendency to head to the right of the feeder-nest direction. This was the typical route that ants foraging in this corridor followed, as is evident from Fig. 7e. This could be a case of obstacle avoidance, as Fig. 2 shows that the left side in the feeder-nest direction (right side in the figure) featured not only a wall of black cloth that we constructed, but also some tussocks. When ants trained on the table were tested on the ground, they took on this bias, and thus differed in initial heading from their counterparts trained and tested on the table. The same trend was found in ants

trained on the ground, although the difference in mean heading between the two test situations did not reach statistical significance.

In Experiment 1 on the other hand, the ants deviated away from the white sheet in all cases. All groups of zerovector ants deviated to a similar extent with either the right or left side obstructed, and all groups deviated similarly to one another (Figs. 3, 4). All groups were also similarly well oriented. Thus, it did not matter whether the tall sheet covered a half of view with more or less skyline-contour information in the form of changes in skyline elevation. Covering the intuitively more informative part of the view was not enough to disrupt navigation.

As for the systematic deflections, several explanations come to mind. One that we would deem unlikely is that the ants found the skyline at the sheet too high compared with what they remembered. A region in which the skyline was too high might indicate that the navigator had drifted towards that region, and veering away from it might serve to correct that drift (Wystrach et al., 2012). We found solid evidence that increasing skyline height systematically on one side caused a deflection away from that side (Julle-Daniere et al., 2014). Work on other ant species has also revealed deflections from a wall that was higher than what the ants encountered in training (Pratt et al., 2001; Graham and Collett, 2002). This explanation for our findings, however, sits uncomfortably with the fact that different conditions showed similar deflections. By the skyline-height-comparison account, if the tall sheet covered a lower part of the panorama, it should cause a larger deflection because the elevation mismatch is larger. This was not the case (Fig. 3b vs. c, 4b vs. c). The expected 'dose response' was found in the study by Julle-Daniere et al. (2014), in which larger skylineheight mismatches led to larger deviations.

A more likely explanation is the avoidance of high elevations, perhaps limited to structures nearby, a kind of obstacle-avoidance strategy. We have already mentioned that obstacles are often encountered in this habitat, mostly in the form of tussocks and some bushes. These ants typically do not run through tussocks, but weave around them (see paths shown in Kohler and Wehner, 2005; Cheng, 2012; in North African desert ants, see Wehner et al., 1996). The major exception is that they sometimes climb on to plants to escape the heat of the ground (Christian and Morton, 1992; pers. obs.). The large sheet nearby might have been seen as an obstacle to be skirted around, causing a small deviation away from it. This account explains why the deviation was similar in all cases (Figs. 3, 4), whether the sheet covered a higher or lower part of the panorama.

Whatever the explanation for the systematic deviations, the full-vector ants deviated less than the zero-vector ants (Fig. 4). The explanation for this difference is straightforward, as the full-vector ants had, in addition to cues from view matching, a vector derived from path integration whose direction would point in

the nest direction. We suggest that the full-vector ants averaged the dictates of three different signals: (1) a dictate from path integration pointing to the nest, (2) a dictate from using the panoramic view, and possibly associated celestial cues as well, also pointing to the nest, and (3) a dictate from obstacle avoidance, or perhaps some other factor, pointing in an unknown direction away from the high wall. The zero-vector ants only had one dictate (2) pointing to the nest, so that (3) had a larger effect. Our interpretation of the simultaneous use of views and celestial compass cues corroborates findings in other situations and species. Thus, when Reid and colleagues (Reid et al., 2011) manipulated the direction of cues from polarised light with a filter, their bull ants (*Myrmecia pyriformis*) struck an intermediate direction between the dictates of the terrestrial panorama and those of the polarised light. Collett (2012) displaced outgoing desert ants in North Africa (*Cataglyphis fortis*), and observed that they too compromised between the dictates of path integration and terrestrial cues. We also have observed similar compromises in the current study species (Legge et al. submitted). Several recent models of ant navigation have featured multiple navigational systems or 'modules' converging on one summator/central processor that determines a final output (Cruse and Wehner, 2011; Collett, 2012; Wystrach et al., 2013b).

Conclusions

We degraded the terrestrial visual panorama of homing zero-vector *M. bagoti* ants by either raising or lowering the elevations of the terrestrial panorama (by raising or lowering the ant on a test) or else by obliterating close to half the panorama with a tall white sheet erected on one side of the feeder. Under both manipulations, the ants were still well oriented in the homeward direction. Systematic deviations were found in some cases, and these had a number of plausible explanations.

Conflict of interest

The authors declare no conflict of interest.

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