

Institut für Neurobiologie, Freie Universität Berlin, Berlin

Honeybee Long-distance Orientation in a Controlled Environment

LARS CHITTKA & KARL GEIGER

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Abstract

The integration of artificial movable landmarks (tetrahedral tents of 3.46 m height) into the long-distance course control of bees was investigated in an environment that provided a minimum of natural orientation cues. Bees were trained along a row of four landmarks which were equally spaced in a setup of 300 m in length. The animals were then tested in situations where the position of the landmark line indicated a direction of the feeding site other than the (originally trained) sun-compass direction. This discrepancy was systematically varied. We show that the sun compass is dominant over the landmarks. This preference is negligible if the deviation between the two indicated directions is small, but it increases as the angle of deviation becomes larger. In contrast, if the entire sky is overcast by clouds, more bees will follow the direction indicated by the artificial landmarks than under sunny conditions. However, as the deviation between the trained direction and the landmark direction increases, more individuals will land at the training site.

Corresponding author: Lars CHITTKA, Ecology and Evolution, State University of New York, Stony Brook, NY 11794-5245, USA.

Introduction

One of the most intriguing problems in work on animal orientation is the question of how insects with minute brains manage to navigate with high precision over long distances (VON FRISCH 1967; GOULD 1986; WEHNER 1991; COLLETT 1992). When leaving the home site for a given food source that is either familiar or has been indicated by a colony member's dance, the bee is equipped with the information pertaining to the distance and direction of the goal. The sun-compass system defines the direction (WOLF 1927). If the sun is obscured by clouds, but patches of blue sky are visible, the bees' ability to interpret the plane of polarized light is used to reconstruct the position of the sun (VON FRISCH 1967;

ROSSEL & WEHNER 1982). The compass system is, however, not sufficient for a reliable long-distance orientation under all weather conditions. If the sky is entirely obscured by clouds, the sun compass cannot be employed. If the bee is displaced sideways by wind squalls, the compass system will guide the bee on a parallel course, and it will obviously miss the goal.

Thus, the bee must integrate landmarks into the course control. Several studies have addressed the question of how bees evaluate the sun compass, local landmarks such as single trees, and distant landmarks such as prominent parts of the horizon profile (VON FRISCH 1967; DYER & GOULD 1981; GOULD 1986; MENZEL et al. 1990; WEHNER et al. 1990; DYER 1991). The drawback of these investigations is that bees were displaced within natural landscapes where the navigational parameters could not be varied in a controlled fashion.

BAERENDS (1941) took a step in the right direction by building artificial trees that guided digger wasps to their nests. He found that after displacement of these landmarks, the wasps would search for their nest in the new location indicated by the artificial trees. However, success in deviating the animals was limited, because the surrounding landscape was rich in external orientation cues.

Consequently, one would have to find an environment devoid of natural landmarks (WOLF 1927), a flat desert being the ideal case. Additionally, one needs artificial landmarks conspicuous enough to be used by the bees during long-distance orientation. These landmarks have to be both stable and moveable.

Here, we report on experiments which tested the influence of different setups of tetrahedral tents as landmarks on the bees' choice of goal direction.

Material and Methods

Landscape

The experiments were carried out on an even meadow (2 km²) south of the train station of Kuhblank, 5 km east of Wittenberg, Brandenburg, Germany. The forest edge around this meadow was virtually uniform and did not exceed an elevation of 1.5° over the edge of the meadow (Fig. 1, above). The shortest distance from the test area to a forest edge measured 670 m. However, there were a number of single trees in northwest direction, that stood at ~3° over the meadow, and which may have been used by the bees as orientation cues. Thus, the flight path between hive and feeder was set up in a southeast direction, so that bees flew away from these trees on their way to the food source.

The visual acuity of honeybees is approximately 2.5° (LAUGHLIN & HORRIDGE 1971; EHEIM & WEHNER 1972). In order to assess whether this horizon profile contains any directional information for bees, we plotted it with a 2.5° resolution (Fig. 1, below). It should be clear that this is not a picture 'as the bee sees it'. The 'coarse-grained' panorama merely renders a rough approximation of what spatial detail the bee might be aware of, and this is indeed very little.

Artificial Landmarks

The landmarks were yellow tents of a tetrahedral shape (3.46 m in height; bunting by Fahnen-Sachsen, Radebeul, Dresden, Germany). Their framework consisted of three tubular aluminium bars (4 m length, diameter 6 cm). These bars were flexibly connected at the top by a rope. The three bottom corners of the tents were fixed to the ground by means of one peg each. These constructions could be easily folded up, carried away and rebuilt in another place by a single person. They also proved to be stable enough to withstand strong winds.

We define our tents as 'local landmarks'. Local landmarks change their apparent shape and

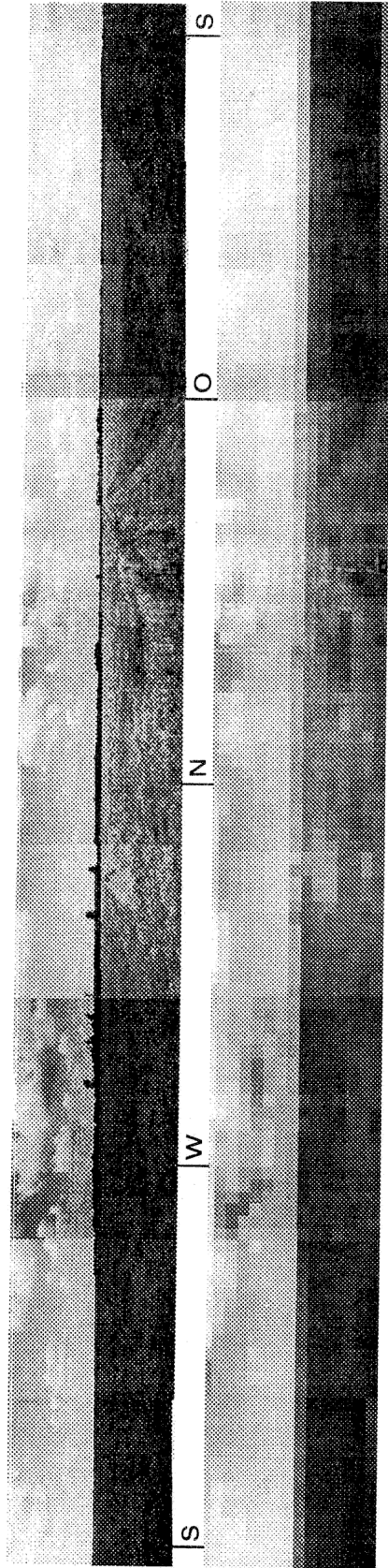


Fig. 1: Above: 360° horizon profile as seen from the hive site. The bees were trained to collect sucrose solution at a site 10° to the left from the S direction. The tallest trees in the NW direction rise approximately 3° over the edge of the meadow. Below: In order to assess roughly which details of this profile a bee might be able to resolve, we plotted the same panorama in a coarse-grained fashion, approximating a bee's visual resolution. Every square measures 2.5° × 2.5°. The horizon profile obviously contains very little information pertaining to goal direction for bees

configuration when they are passed, they are subject to motion parallax, and they can usually not be seen during the entire flight. Distant landmarks, i.e. features of the horizon profile, on the other hand, change their configuration only marginally during flight and are thus reliable marks for reconstructing the sun compass.

All angles and distances in the setup of tents were controlled by means of a theodolite in combination with an infrared laser telemeter (Distomat Di4, Theodolite T1, Wild company, Heerbrugg, Switzerland).

Training the Bees

Bees (*Apis mellifera*) were trained to collect sucrose solution at a site 262.5 m SE of the hive. Depending on weather conditions, between 20 and 30 bees were continuously flying back and forth between the hive and the feeder. We employed traditional 'von Frisch feeders' (VON FRISCH 1967). Prior to the first test, bees were given a full day of continuous foraging at the food site.

The route from the hive to the food source was marked by a row of four tents that were placed at distances of 75, 150, 225 and 300 m from the hive (Fig. 2 (below left)). The feeding site was thus located halfway between the third and the fourth landmark. The distance between the feeder and each adjacent landmark measured 37.5 m.

We intended to preclude the bees from using the row of tents as some kind of continuous landmark denoting the entire route from the hive to the feeder in the sense of a forest edge, as employed by DYER & GOULD (1981). To this end, the distances between the tents were chosen such that the spatial acuity of the bee eye (2.5°) set a limit as to how many landmarks could be seen from a given position within the flight path. The first tent (at 75 m) appeared under a visual angle of $\alpha_{75} = 2.64^\circ$ as seen from the hive. The respective angles for the other tents were: $\alpha_{150} = 1.32^\circ$; $\alpha_{225} = 0.88^\circ$; $\alpha_{300} = 0.66^\circ$. This means that the artificial landmarks merely reduced the effective light flux in single photoreceptors to different degrees. We thus assume that the bee could, from the hive or any other given landmark, detect only the respective next (or last) landmark, but did not perceive the row of tents as a continuous landmark.

Tests

All tests were prepared by removing all bees from the feeder and closing the hive entrance. Hence, during the time in which the setting of landmarks was altered, no bees could leave the hive, and all bees returning from foraging flights gathered in front of the hive entrance. Subsequently, the entire row of landmarks was displaced to either 7.5° , 15° , 22.5° or 30° from the original position, the axis being the hive site (Fig. 2 (below)). This procedure took about 15 min. The hive was then opened, and the flight behaviour of the bees was assessed in terms of dual-choice tests. The bees had to choose between two test feeders, one of which was sited in the position of the original training feeder. The other was placed in the position indicated by the displaced landmark row, i.e. halfway between the third and fourth tent.

A researcher was positioned at each feeder and counted a choice when a bee landed on one of them. Each bee was captured immediately on arrival. The bees were caught using forceps on a leg or wing and kept in a box until the end of the test. In this way, the bees were not rewarded at any site during the tests. Any reward during tests might have influenced their choice behaviour in subsequent tests. Furthermore, this procedure precluded individual bees from rendering multiple choices at the feeders in one particular experiment.

The tests were discontinued when no further bees arrived at the test feeders (usually after about 30 min). After each experiment, the original arrangement of landmarks was restored. Before the next test, bees were allowed to collect sucrose solution and fly regularly back and forth between hive and feeder for at least 45 min.

The feeders themselves were inconspicuous and unscented; they were placed on a red (honeybee: black/uncoloured) beer-bottle box in order to raise them above the high grass. This setup could only be used as a landmark from a very short distance.

Tests were repeated with identical landmark alterations until a sufficiently high number of choices had been recorded. All tests were performed both in sunshine and under 100% overcast sky, so that the influence of the sun-compass system could be tested. We rated the weather as '100% overcast' only if there were absolutely no patches of blue sky and the sun was not visible through the clouds as

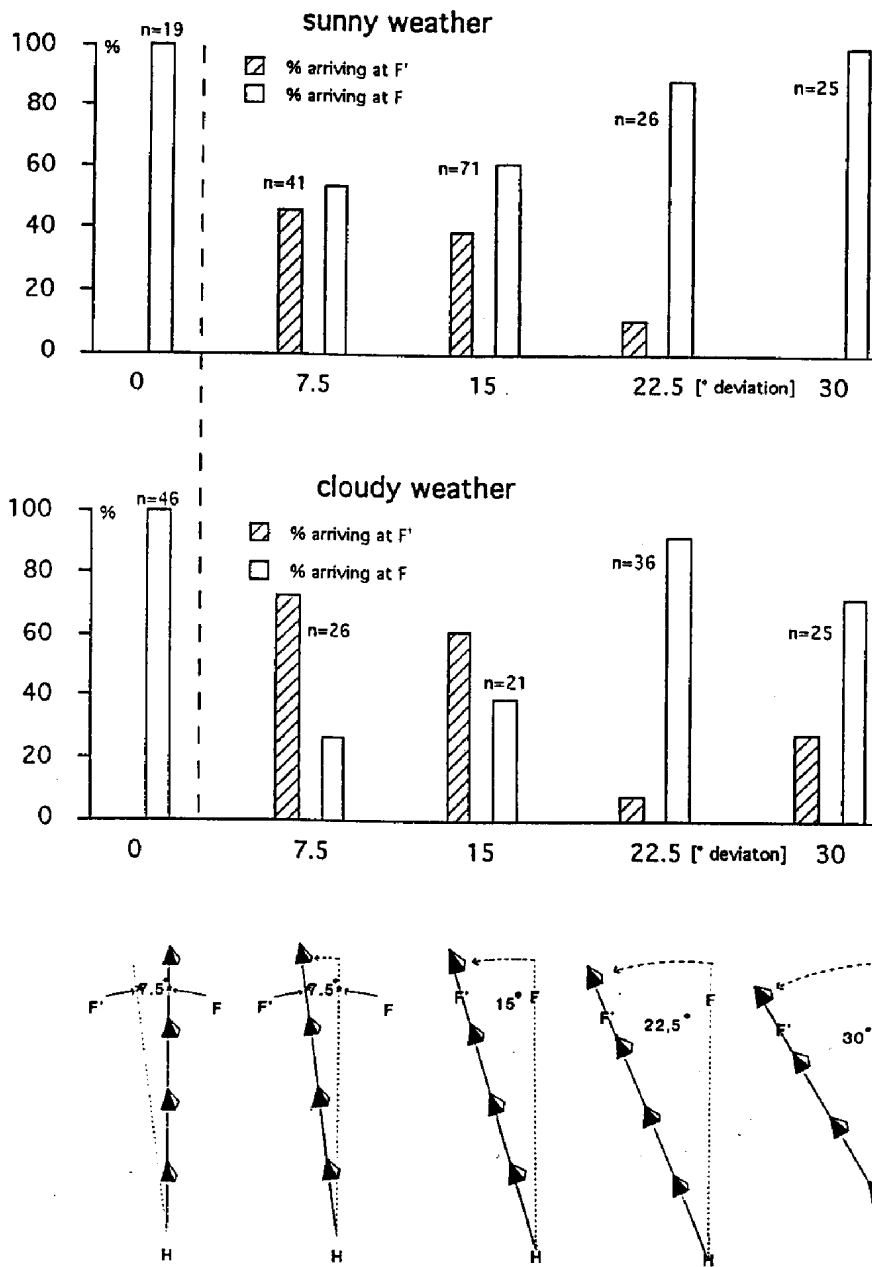


Fig. 2: Below: experimental setup of the five test situations. The entire row of landmarks was set up at either 0° (control test), 7.5°, 15°, 22.5° and 30° from the original position; H = hive. Tests were performed both under sunny conditions (above) and under 100% overcast sky (centre). Shaded columns: percentage of bees that followed the landmark direction; white columns: percentage of bees that landed at the originally trained site

a disk or some kind of local light spot. Under such conditions, no e-vector information is available to the bees (BRINES & GOULD 1982).

Results

In order to test how precisely the bees had learned the direction of the food

source, we first performed a control experiment. We simply placed one test feeder in the original position and another at the same distance from the hive, but in a direction of 7.5° to the left of the training direction. The landmark setting remained unchanged. In this situation, all bees arrived at the original feeder both in sunny and cloudy weather (Fig. 2 (below left)).

We then proceeded to displace the row of landmarks under sunny conditions (Fig. 2 (above)), starting with an angle of 7.5° to the left of the original flight path. In this situation, 46 % of the bees arrived at the position indicated by the landmarks. The choice numbers are not significantly different from random on both feeders ($p > 0.5$; two-sided χ^2 goodness-of-fit test). On the other hand, they are highly significantly different from the choice numbers of the control test described above ($p < 0.001$). This result indicates that the landmarks have a strong potential to deviate the bees from their memorized compass direction.

Subsequently, the deviation of the landmark row from the compass direction was progressively increased. At a deviation of 15° , only 39 % of the bees arrived at the test position indicated by the displaced landmarks. The choice values differ significantly from a random distribution of choices on both feeders ($p < 0.05$). This finding shows that, as the deviation increases, the sun compass becomes dominant over the landmarks.

This general tendency is continued at higher deviations. At 22.5° , only 11 % of the bees followed the artificial landmarks ($p < 0.001$), and at 30° , all bees ignored the tents and arrived exclusively at the original (training) position.

We thereupon repeated the same series of experiments under completely overcast sky (Fig. 2 (centre)). At a deviation of 7.5° , 73 % of the bees followed the landmark direction. This distribution of choices is significantly different from the control test ($p < 0.001$); it also differs significantly from a random distribution ($p < 0.01$) and from the same test under sunny conditions ($p < 0.05$). At this small deviation, most bees prefer the direction indicated by the tents. However, had the tents been the only cues for the estimation of direction used by the bees, they should all have followed the landmark row. Thus, some of the bees must have employed an additional system to reconstruct the compass direction, despite the lack of the sun compass. One might argue that a difference of 7.5° (or 34 m between the two alternative feeders) is too small to be accurately discriminated by the bees. However, the control test with unchanged landmarks (Fig. 2 (below left)) is symmetrical with respect to this deviation. It clearly shows that a difference of 7.5° is large enough for all bees to find the original feeder if there is no discrepancy between the landmarks and additional cues.

At a deviation of 15° , an even smaller percentage of bees (61 %) arrived at the test feeder marked by the tents. The landmarks were still dominant over other orientation cues, but the distribution was no longer significantly different from random ($p > 0.25$).

At 22.5° and 30° , significantly more bees arrived at the original position of the feeder (92 % and 72 %) than at the one indicated by the artificial landmarks (8 % and 28 %; $p < 0.05$).

It must be presumed, therefore, that had we increased the deviation further,

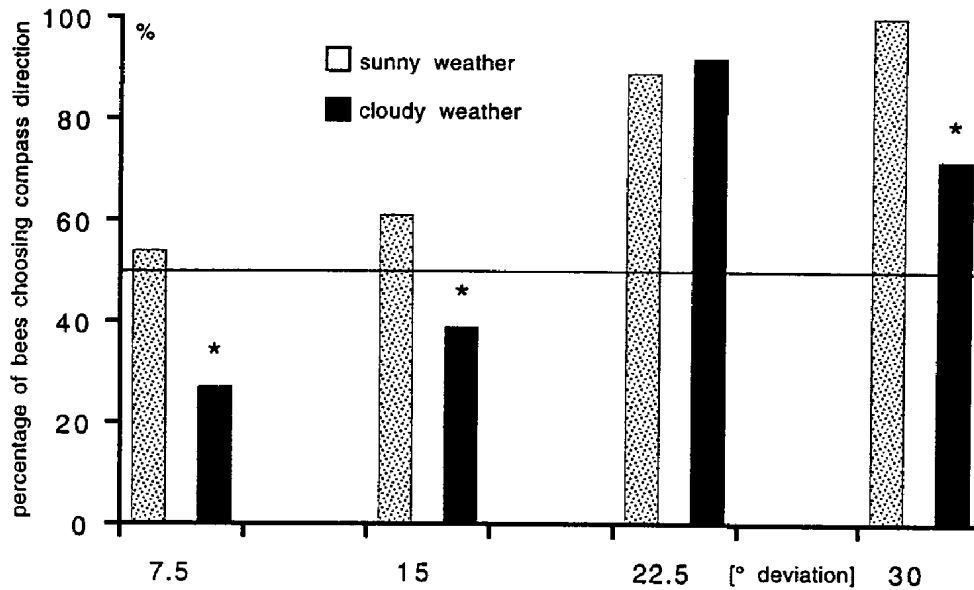


Fig. 3: Comparison of the percentages of bees that arrived at the training site under sunny conditions and under overcast sky. For all angles except 22.5° between the trained direction and the one indicated by landmarks, the number of bees arriving at the originally trained food source is significantly higher in sunshine (* $p < 0.05$)

100 % of the bees would have landed at the training site. Summarizing these results, we conclude that:

1. If the sun or patches of blue sky are visible, most bees prefer the site indicated by their compass system. The degree of dominance of the sun compass over the landmark direction is gradually dependent on the magnitude of the deviation between the two.
2. The cloud cover strongly influences the bee's orientation. At all angles except 22.5°, the dual-choice proportions under sunny conditions are significantly different from the ones recorded under an overcast sky (7.5°: $p < 0.05$; 15°: $p < 0.05$; 30°: $p < 0.01$). Thus, if the sun compass is available, a higher percentage of bees arrives at the original feeder at all angles of deviation except one (Fig. 3).
3. If, on the other hand, the compass-deprived bees exclusively oriented themselves according to the landmarks, 100 % would have followed this direction independently of the deviation. This was not, however, the case. Obviously, bees use cues other than the tents to reconstruct the training position of the feeder. The influence of these cues becomes stronger as the deviation between the two possible directions increases.

Discussion

Methods

Numerous experiments to infer the bee's use of landmarks or landscape

panoramas in relation to the sun compass have been conducted in the past (VON FRISCH 1967; DYER & GOULD 1981; GOULD 1986; MENZEL et al. 1990; WEHNER et al. 1990; DYER 1991). Whenever the flight behaviour was obviously not entirely compass-oriented, it was not possible to conclude whether, for example, this was caused by nearby or distant landmarks, or both. Thus, every possible interpretation of how landmarks were integrated into the course control was bound to remain unsatisfactory. This problem gave rise to the idea of employing artificial landmarks for such purposes.

This approach not only requires the construction of appropriate landmarks, but, in addition, one has to find a suitable landscape which provides a minimum of natural orientation characteristics. Both the landscape and the artificial landmarks must then be tested in combination. This basic test was performed here. It was successful in that the landmark setup does indeed have a potential to deviate the bees from their trained route to the goal.

The applied methods for investigating the bees' navigational performance are simple and straightforward. The employment of dual-choice tests implies that each individual choice recorded in the test forms an unambiguous piece of data. The researcher is left with much less uncertainty than in tests where vanishing bearings are recorded. Furthermore, the methods allow a very fast accumulation of behavioural data, which is not usually the case in displacement experiments.

Estimation of Goal Direction by Means of Landmarks and the Sun Compass

VON FRISCH & LINDAUER (1954) reported that single trees or small groups of trees, as opposed to a continuous forest edge, had no influence on the choice of direction by the bees when tested under a sunny sky. In these experiments, however, the discrepancy between the direction indicated by the trees and the sun compass direction measured 90° . Our findings with artificial landmarks indicate an absolute preference for the sun-compass direction at only 30° deviation of the landmark row from its training position. Only below this value does one find a measurable influence of the landmarks. Hence, the result of the VON FRISCH & LINDAUER (1954) experiment at a deviation of 90° is not surprising. A comparison of these two results vividly illustrates the necessity of varying the landmark setup in a controlled fashion rather than displacing bees from one natural landscape into another. The same is true for the following observation.

If bees that are about to leave the hive with a defined destination are displaced and released in another location, they were observed to ignore even prominent landmarks such as a conspicuous mountain and to follow exclusively the sun compass (MENZEL et al. 1990). Our local landmarks, however, were only ignored if they indicated directions very different from the trained flight path. As the discrepancy between the two possible directions becomes smaller, the influence of the landmarks increases. We infer that local landmarks are employed for the fine-tuning of the bee's estimation of direction. It is likely that bees are frequently blown off course for small distances. In such cases, the discrepancy between the direction indicated by the current landscape panorama and the compass direction should never be very large. The use of landmarks is essential in such situations

because the sun compass only defines the direction, i.e. it does not prevent the bee from being parallelly displaced by a cross-wind. However, under sunny conditions, the sun compass always outweighs the line of landmarks.

This is not the case if the sun is not visible and the polarization pattern of the skylight cannot be evaluated because of 100 % cloud cover. Under these conditions, more bees followed the landmark direction at most tested deviation angles than under direct sunlight. If, on the other hand, our landmarks had been the only orientation cues, 100 % of the bees should have chosen this direction irrespective of the degree of deviation. Since this was not the case, the bees must obviously be able to take into account other reference systems to reconstruct the position of the training feeder.

BAERENDS (1941) reported a similar observation in the digger wasp *Ammophila*. He marked the wasp's nest entrance with an artificial tree of 1 m height. If this tree was displaced 1 m, the wasp searched for the nest entrance at the site indicated by the new location of the tree. When he displaced it 2 m, the wasp was no longer 'fooled' and searched at the original nest site. It was concluded that the nest site was reconstructed from 'other, unchanged landmarks'.

In our experiments, we have minimized the influence of such 'other landmarks'. Nonetheless, we were surprised at the high rate at which bees still found the training site under conditions in which the sun compass was not available. We can only speculate how the bees managed to do this. First of all, the hive entrance pointed towards the training site. However, it is rather unlikely that the bees could maintain this directional information over several 100 m. It is also possible that the bees used local structural cues in the meadow, although such cues were not obvious, even to the human observer.

Another possible explanation is that bees simply flew towards the researcher who had to be present at the feeder to catch and count the bees (see also WOLF 1927). This possibility can be ruled out by comparing the data from the control test with unchanged landmarks and the test with the tent row displaced to 7.5°. In both cases, the deviation between the feeder indicated by the landmarks and the second feeder (which might have been 'marked' by a researcher) measures 7.5°. However, in the control test, no bees flew towards the feeder at 7.5°, whereas in the test with displaced landmarks, 27 % chose the feeder at the original position. In both of these tests, observers were present at the feeders; nonetheless, the choice proportions were significantly different. It is also possible that bees make use of a magnet-compass system. Bees have been shown to use the earth's magnetic field in several contexts (LINDAUER & MARTIN 1972; GOULD et al. 1978; COLLETT & BARON 1994), but, so far, nothing is known about a magnet-compass system during long-distance orientation.

We conclude that the method presented here supplies a powerful tool for systematically investigating the integration of long-distance course-control mechanisms by flying insects.

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