Ethology **109,** 835—846 (2003)
© 2003 Blackwell Verlag, Berlin
ISSN 0179–1613

# Orientation by magnetic field in leaf-cutter ants, *Atta colombica* (Hymenoptera: Formicidae)

Alexander N. Banks & Robert B. Srygley

*Smithsonian Tropical Research Institute, Balboa, Republic of Panama; Department of Zoology, South Parks Road, University of Oxford, Oxford, UK*

## Abstract

Leaf-cutter ants (*Atta colombica*) use trail following to travel between foraging sites and the home nest. However, this combination of pheromone and visual cues is likely to be complemented by a directional reference system such as a compass, used not only when foraging but also during colony formation, where foraging trails degrade or where ants become displaced. One candidate system is the magnetic polarity compass. We tested the orientation of leaf-cutter ants under a magnetic field of reversed-polarity, with the prediction that the ants would show 180° deflection compared with control ants in an unchanged geomagnetic field. When the sun's disc was unobstructed by clouds, orientation was the same as that of control ants, implying that magnetic cues were not used to orient. However, when the sky was overcast, ants in the experimental treatment significantly shifted their mean orientation both in comparison with controls and reversed-polarity ants under the sun. Although a total reversal in orientation was not induced, the results demonstrate that *Atta* respond to magnetic reversal in the absence of sunlight cues, and suggest a role for magnetic cues in determining direction during orientation.

Corresponding author: Alexander N. Banks, British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU, UK. E-mail: alex.banks@bto.org

## Introduction

Central place foragers such as colonial social insects have multiple tools and strategies for orientation that can be divided into two basic categories. Egocentric cues include proprioceptive information gathered en route from the nest (or a similar goal) to 'path integrate' back to the target (Collett & Collett 2000). Geocentric cues are used to derive current position, that of the nest, and similar goals relative to landmarks, odours, and other features in space (Wehner et al. 1996). Celestial cues, including the sun's azimuth (Santschi 1911) and polarized skylight (von Frisch 1949), provide bees and ants with directional references

U. S. Copyright Clearance Center Code Statement: 0179-1613/2003/10910–835/$15.00/0 www.blackwell.de/synergy

(Labhart 1986; Rossel & Wehner 1986; Labhart & Meyer 2002). Horizon and canopy landmarks can provide further geocentric cues (Rosengren 1971; Holldobler 1980; Fukushi 2001). However, the ability to return home in overcast skies and under non-polarized light suggests that at least some ants [e.g. the grass ant (*Tetramorium caespitum*); Shen et al. 1998] do not require celestial or landmark cues to path integrate, suggesting a role for a combination of proprioceptive and magnetic cues. Bumblebees (*Bombus impatiens*) are similarly capable of homing in complete darkness when odour cues are eliminated (Chittka et al. 1999).

Leaf-cutter ants (*Atta colombica*) travel between food resources and the nest by using a system of foraging trails. Pheromonal and architectural manipulations of these otherwise directionless trails provide foragers with geocentric olfactory (Wetterer et al. 1992) and visual (Vilela et al. 1987) orientation cues. A compass or other directional reference would distinguish homeward from outward journeys but celestial cues are frequently obscured beneath the tropical forest canopy where the ants often forage. In addition, the extensive underground network of trails within the nest precludes the use of celestial cues, and pheromone trails are likely to be less heavily relied upon, necessitating another orientation system (Vilela et al. 1987). Leaf-cutter ants may also require a directional reference system when faced with deterioration or destruction of foraging trails, when straying from trails, or during trail formation.

One potential option may be to exploit the Earth's magnetic field to infer direction. A few insects have been demonstrated to orient with these directional lines of force. Honeybees (*Apis mellifera*) may determine direction in this fashion (Walker & Bitterman 1989; Schmitt & Esch 1993; Collett & Baron 1994), and fire ants (*Solenopsis invicta*) also apparently respond to magnetism (Anderson & Vander Meer 1993; although see Klotz et al. 1997). Furthermore, wood ants (*Formica rufa*) and weaver ants (*Oecophylla smaragdina*) show a directional response to shifted magnetic polarity (Camlitepe & Stradling 1995; Jander & Jander 1998). The magnetic compass of birds is based on the angle of the local field compared with gravity (Wiltschko & Wiltschko 1972), but insects seem to sense polarity (Anderson & Vander Meer 1993; Schmitt & Esch 1993; Jander & Jander 1998).

We aimed to induce reorientation in foraging leaf-cutter ants when tested in reversed-polarity magnetic fields, thus indicating a reliance on magnetic cues for navigation in the absence of pheromone trails. By testing under sunny and cloudy conditions, we also attempted to assess the relative importance placed on solar and magnetic cues by *A. colombica*. Reliance on a magnetic compass would predict a shift in the orientation of experimental animals relative to controls. We also predicted that leaf-cutter ants would show a response to magnetic information only when apparently unable to use cues from the sun, in common with most organisms that have been found to have both sun and magnetic compasses (e.g. weaver ants; Jander & Jander 1998). We anticipated that control ants would continue to orient towards the direction taken at capture. We predicted similar behaviour in ants under reversed magnetic polarity and sunny

skies, but expected ants tested under reversed polarity and cloud to display a shift in comparison with both conditions.

## Methods

Experiments were carried out on Barro Colorado Island (BCI), Panama (elevation 40 m, latitude 9°09′N, longitude 79°51′W). We diverted a natural foraging trail of *A. colombica* by clearing leaf litter and scattering oat flakes along the cleared ground. Ants quickly left the original trunk trail and formed a new foraging column under our manipulation. We diverted the trail into the centre of a large electromagnet enclosed in a nylon tent, where we were able to test ants in either a normal magnetic field or a field with reversed magnetic polarity.

The electromagnet was a Merritt 4-coil (Merritt et al. 1983; Kirschvink 1992) consisting of a $2.40 \times 2.40 \times 2.43$ m wooden frame supporting 10 square standard wire gauge copper coils. The resistance of the coils was $2.4\Omega$, which was not different from the value ($2.359\Omega$) estimated from the length of the wire. The island's AC electric current (115 V) was connected to a Variac and an AC to DC transformer, allowing the voltage to be set to 6.83 V. When current flowed through the coil, the voltage and resistance yielded a 2.85 A current that produced a magnetic flux approximately twice the magnitude of the horizontal component of the Earth's magnetic field (28 121 nT, data calculated from the World Magnetic Model: http://www.geomag.usgs.gov/frames/mag_charts.htm). The total geomagnetic flux on BCI is 35 278 nT (inclination is 37° and declination −2°), and there are no known magnetic anomalies. The magnet itself was under a translucent, white nylon-reinforced plastic tent (6 m long, 3.4 m wide; height varying from 2 to 4 m, peaking at the centre north–south line; Larin Corp., Ontario, Canada), closed to all sides and above to eliminate gross landmark cues. Although the tent diffused the light that entered, a brighter spot in the direction of the sun's disc was discernible to the human eye on sunlit days.

Within the centre of the electromagnet, we placed a circular choice arena (diameter 312 mm; raised approx. 1 m from the ground by two large plastic buckets). The arena was constructed from cardboard, with the circle divided into eight 45° chambers each separated from its neighbours by cardboard walls (45 mm high, 2 mm thick). The walls did not extend to the centre of the arena, but to an inner circle (radius = 2.5 cm) scratched in sand that covered the arena floor, inside which ant orientation was not measured. This circle connected the open edges of the eight chamber walls. An ant was only measured when adjudged to have entered a chamber by crossing the line in the sand. A white cardboard rim of equal height and thickness to the arena walls denied ants a horizontal view out of the arena. A plate of glass was placed on top of the arena to prevent ants from leaving. The plate was wiped clean after each trial.

The dry sand sprinkled on the floor of the arena allowed the borderline to be drawn. It also served to prevent orientation using pheromone trails. After each trial, the layer of sand was discarded, thus removing any pheromones deposited by previous ants. In addition the arena was rotated one chamber clockwise to

eliminate any directional bias associated with the arena's construction. The time spent in each chamber was monitored using an X-cam2-XX17A (Xcamz: × 10.com, North Las Vegas, Nevada, USA) monitoring camera, suspended 10 cm over the centre of the arena. This small lens relayed pictures to a distant experimenter who recorded the data from a television monitor in a nearby building. Thus all data were collected without the recorder knowing the treatment.

To direct ants into the experimental arena, oat flakes were scattered along an artificial branch of the trunk trail that was cleared of leaf litter. Ants entered the tent across a cardboard bridge, oriented in the north–south axis, by passing through a 10 cm high gap between the substrate and the south-most dividing wall of the tent. Once inside, ants collected an oat flake from a pile and departed across the same bridge used for entry. Ants were displaced from this bridge by gripping the ant-borne oat flake with tweezers. Thus, ants were always travelling south when displaced (Fig. 1 shows spatial location of test chamber in relation to nest
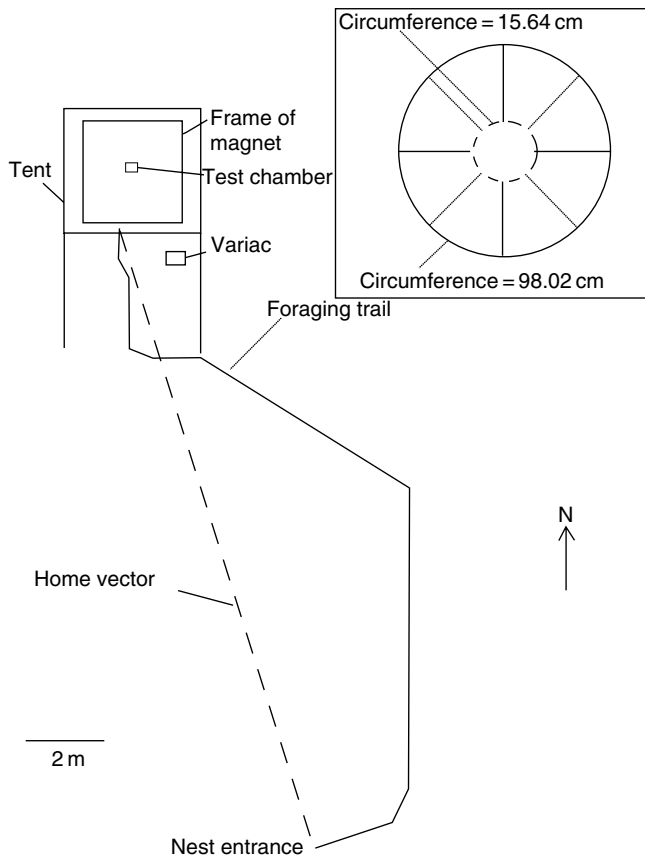


Fig. 1: Schematic overhead of experimental set-up; arena plan inset. Lines representing the foraging trail indicate the route established by foraging ants, with diversion into the tent. Dashed line indicates the home vector from the oat pile to the home nest, originating at point of capture

and schematic view of arena). Ants were transferred individually to the choice arena and released centrally by placing the ant on the arena floor facing random directions. The experimenter left the tent immediately after releasing the ant, and observations on the ant in the arena started. A remote observer recorded the time each ant spent in each chamber of the arena.

All data were collected between 10.45 and 16.00 hours local time during Nov. 2001. For data on sun altitude and azimuth at this time, see the US Navy website http://aa.usnv.navy.mil/data/docs/AltAz.html. Ants were tested for 330 s inside the arena, in either the Earth's normal magnetic field (coil off), or in a field with polarity reversed by 180° (coil on). Before each trial, the condition was selected by coin toss and the visibility of the sun's disc from outside the tent was noted. After testing, ants were released on to the exit trail and new ants were not picked off the trail until the experimenter had observed at least 50 fresh foragers reaching the oat pile.

The behaviour of individual ants was analysed by converting time spent in each chamber to a mean vector. Mean vectors have both a directional component (range 0–359°) and a distance component, which is inversely proportionate to scatter (r, range 0–1.0). Directional preferences were reflected by the proportion of time spent in each chamber. For example, an ant measured for 300 s in the north-east chamber produced a mean vector biased to the north-east (45°), with the value of r approaching 1.0. An ant measured for equivalent periods in many different chambers produced a mean vector with random direction and the value of r approaching 0.0. As ants could only choose one of eight 45° chambers, the length of the vector (r) was adjusted using a correction factor for grouped circular data (Batschelet 1981).

Individual mean vectors were grouped by experimental condition, and analysed for treatment effects using bivariate second order statistics (Batschelet 1981). The circular mean of the individual means was calculated for each treatment group, and Moore's test for directionality was employed to determine agreement within the second order mean. This test is non-parametric and has the null hypothesis of randomness; therefore a significant result indicates a directional, and not random orientation. The data did not satisfy parametric criteria, as one prerequisite is that the mean vectors should result from equivalent observations. As subjects were not recorded when in the 'neutral' centre circle of the arena, total time observed fluctuated between ants.

To test whether second order means were significantly different from predicted directions, we used the V-test. This test is parametric and therefore not strictly appropriate, as our data did not meet the parametric criteria already mentioned. However, our data do meet the assumption that grouped data are corrected for, and to our knowledge there is no non-parametric equivalent. The statistic obtained from the V-test is significant when the reference direction and the observed direction do not differ significantly (Batschelet 1981).

We predicted that control ants would orient themselves in the direction they were travelling when captured. Therefore we expected this group to be oriented at

180°, as the ants were travelling south when transferred to the arena. We also predicted that reversed-polarity ants under sun would show a similar orientation, if they could utilize solar cues. Finally, we considered reversed-polarity ants under cloudy skies to be most likely to rely on magnetic cues, and expected orientation different from controls: in the case of a full reversal, we predicted that ants would orient towards 0°.

## Results

We tested 88 control ants, 38 when the sun was visible during the trial (sun position determinable within 15°), and 50 when the sun's disc was obscured by cloud throughout the trial. There was no significant difference in orientation under either type of sky conditions (Mardia's non-parametric two sample test, adapted for bivariate data: $n_1 = 38$, $n_2 = 50$; $B = 0.018$, $p > 0.607$). Control data have therefore been pooled. It should be noted that both control and experimental ants displayed similar behaviour upon transfer to the arena. We saw no evidence of systematic searching for exits, and no ants remained motionless in the neutral part of the arena. Ants typically selected the first chamber within 5 s of release.

The control group was significantly oriented at a mean angle of 123° (Moore's test: $n = 88$, $D^* = 1.043$, $p = 0.05$; Fig. 2a). This is clearly a significant deviation from the orientation towards 180° taken when captured (V-test: $n = 88$, $r = 0.20$, $V = 1.446$, $p > 0.05$). However, the home vector from tent to nest, i.e. that distance and direction travelled if the ant returned home along a bee-line, is at an angle of 162°, 39° anti-clockwise from the observed orientation. Ants were significantly clustered around this direction (V-test: $n = 88$, $r = 0.20$, $V = 2.056$, $p < 0.05$); therefore it seems that these ants reacted to displacement by attempting to take the most direct route home.

Under sunny skies, reversed-polarity ants showed directionality towards a mean of 140° (Moore's test: $n = 31$, $D^* = 2.78$, $p < 0.001$; Fig. 2b). This significant orientation did not differ from that of controls (Mardia's non-parametric two-sample test, adapted for bivariate data: $n_1 = 88$, $n_2 = 31$; $B = 0.77$, $p > 0.607$); neither did it differ in its clustering around the home vector bearing of 162° (V-test: $n = 31$, $r = 0.36$, $V = 2.638$, $p < 0.005$). This implies that reversing the magnetic field under sunny skies did not alter the ants' orientation.

In contrast, reversed-polarity ants tested under cloud displayed a significant shift in orientation, and oriented around a mean angle of 49° (Moore's test:

---

*Fig. 2:* (a) Controls; (b) reversed magnetic polarity (RMP) sun ants; (c) RMP cloud ants. Orientation represented as circular histograms with 15° class intervals. Each unit length along a radius represents one individual's mean orientation. North is at 0° in all diagrams. Small black arrows on circle peripheries indicate direction travelling at capture (180°) and home vector (162°), or predicted reversed travelling direction (0°) and reversed home vector (342°). Arcs outside circles are 95% confidence intervals derived from parametric statistics and are illustrative only

(a)

(b)

(c)
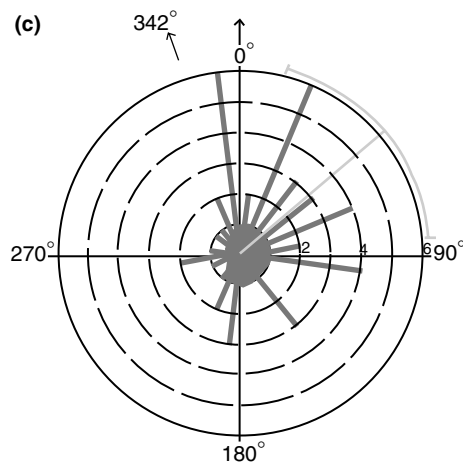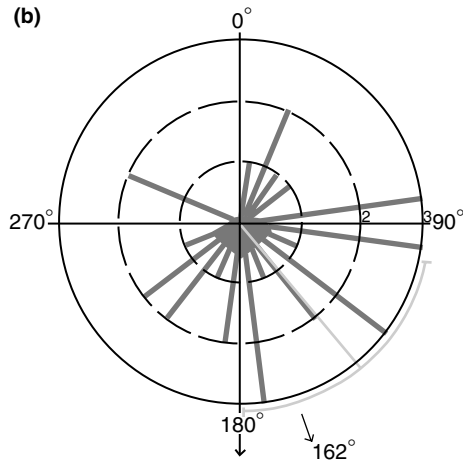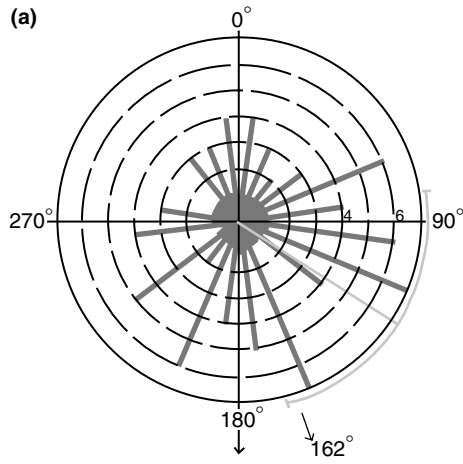
$n = 55$, $D^* = 1.087$, $p < 0.05$; Fig. 2c). This direction was significantly different from that of reversed-polarity ants under sunny skies (Mardia two-sample test: $n_1 = 31$, $n_2 = 51$; $B = 7.59$, $p < 0.03$) and controls (Mardia two-sample test: $n_1 = 88$, $n_2 = 51$; $B = 6.34$, $p < 0.05$). Therefore, shifting the magnetic field under cloudy, but not sunny, conditions affects ant orientation. Reversed-polarity ants under cloud were shifted 91° anti-clockwise to reversed-polarity ants under sun and 74° anti-clockwise of control ants, lower than the predicted 180° shift in the case that magnetic polarity alone was being used to indicate direction. However, ants tested under reversed polarity and cloud were significantly oriented towards 0° (i.e. geographic north and magnetic south), the angle predicted by a reversal of the direction travelled at capture (V-test: $n = 51$, $V = 2.030$, $p < 0.05$). Whereas the control ants and the reverse polarity ants under sun were oriented towards the home vector, this group was not significantly directed towards the reversed home vector (V-test: $n = 51$, $V = 1.202$, $p > 0.10$). Why this discrepancy should exist is unclear, but reorientation of the ants in response to reversed polarity serves as evidence that *A. colombica* attended to directional magnetic cues, when and where solar cues were unavailable.

## Discussion

Our results demonstrate that leaf-cutter ants are able to orient using magnetic cues, as reversing the Earth's magnetic field produced a shift in orientation. Thus, in common with other species of ants (*S. invicta*: Anderson & Vander Meer 1993; *F. rufa*: Camlitepe & Stradling 1995; *O. Smaragdina*: Jander & Jander 1998), leaf-cutter ants apparently rely on a magnetic polarity compass to determine direction. However, magnetic cues appeared to be utilized only when sunlight cues were unavailable during overcast skies. It appears that *A. colombica* can utilize both magnetic and sun compasses to orient in the absence of pheromone or landmark cues.

Although we measured a response to a reversal of magnetic polarity, the 180° shift expected with a complete reaction to reversed polarity was not observed as, on average, ants tested under cloud and reversed polarity did not shift to this extent. However, approximately a third of the ants were oriented to north and north-east, showing that a substantial proportion appeared to fully shift, and the group as a whole appeared significantly oriented in the predicted direction (at least if they were trying to regain the trail and head south). There are a number of possible explanations for the lack of a full reversal compared with controls. First, ants may have been able to refer to other directional indicators in addition to the magnetic field. For example, although ants were denied a view of the surroundings in the horizontal plane, it may have been possible for them to detect some cues from the view directly overhead.

The roof of the tent looked fairly uniform to us, but potential micro-cues in the canopy of the tent or in the magnetic coil may have been visible to the ants.

Secondly, it is conceivable that ants could perceive a light (or temperature) gradient even under cloud. If one side of the tent appeared brighter than the other, and the ants sensed time of day, they may have been able to infer direction. Finally, as our determination of overcast conditions relied on subjective grading of cloud cover, it is feasible that on some overcast trials, sufficient light was available to navigate using the sun. Taking a compromise orientation between conflicting magnetic and visual cues would likely have produced results consistent with our findings.

What can be elucidated from these trials is that *Atta* rely on the sun compass when it is available. We saw no significant difference between control ants and those ants tested in a reversed field under sunny skies, suggesting that magnetic information was ignored or less favoured than sun cues. The sun compass appears to be the primary biological compass, having been demonstrated in many animal classes ranging from insects [e.g. monarch butterflies (*Danaus plexippus*); Mouritsen & Frost 2002] to birds (Schmidt-Koenig 1958). Where magnetic compasses have been demonstrated, they have been typically treated as 'back-up' compasses to the sun compass [e.g. homing pigeons (*Columba livia*), Keeton 1971; weaver ants, Jander & Jander 1998], although there is likely to be an integration of the two.

Control and reversed-polarity ants under the sun appeared to be oriented towards directions consistent with the strategy of path integration. Ants such as the desert ant (*Cataglyphis fortis*) are known to employ this method to return home after foraging runs (Muller & Wehner 1988), and it is possible that *Atta* were exhibiting similar behaviour. Path integration involves reversing the outward vectors to produce a 'home vector', which supplies the bee-line to home. The bearings of 123° and 140° taken by control and reversed-polarity ants under the sun, respectively, would likely have placed liberated ants in the vicinity of their home nest.

Other studies have supported the presence of a magnetic compass in various ant species (*S. invicta*, Anderson & Vander Meer 1993; *F. rufa*, Camlitepe & Stradling 1995; *O. smaragdina*, Jander & Jander 1998). We believe that the combination of our strict design, blind testing and inducement of reorientation provides a robust test and may help to explain discrepancies between experiments that differ in their conclusions on the use of magnetic cues by ants. For example, Klotz et al. (1997) dispute the use of a magnetic compass in fire ants *Solenopsis* and disagree with the study of Anderson & Vander Meer (1993). Rosengren & Fortelius (1986) found no evidence for the use of a magnetic compass by wood ants (*F. rufa*) but the rigorous design of Camlitepe & Stradling (1995) yielded reliable evidence in its favour.

Moreover, leaf-cutter ants, which forage for predictable resources on trunk trails radiating from a central location, may have evolved to favour different modes of orientation than species in which solitary individuals search for unpredictable foods. Solitary foragers, such as the aforementioned fire ants and wood ants, in addition to the desert ant *Cataglyphis*, are more likely to require a mechanism to maintain position relative to home, and thus weigh egocentric

cues heavily (Wehner et al. 1996). Leaf-cutter ants, conversely, are likely to weigh geocentric cues that identify the trunk trail heavily. For this reason, we predicted that our leaf-cutter ants would orientate toward the trunk trail when displaced, rather than orient directly homeward. The apparent use of egocentric cues to path integrate homeward by controls and experimental ants in sunny conditions may have resulted from our experimental design, which obstructed landmarks and discarded pheromonal cues. However, it also lends credence to the importance for individual *Atta* to continually update their position relative to the nest.

Alternatives to trunk-trail foraging are especially crucial during preliminary colony formation. For example, disordered foraging patterns amongst workers are seen in Pharaoh's ant (*Monomorium pharaonis*) colonies, even when individuals number 600, but as they enlarge, colonies move through a transition to organize trunk-trails (Beekman et al. 2001). Founding queens and pioneer foragers from emergent *Atta* colonies may need to rely on compass cues to return to the nest before enough recruits are available to sustain reliable pheromone trails to resources. Hence, the ability to orient directionally homeward with a compass would be beneficial. A magnetic compass, in addition to a sun compass, provides *Atta* with directional information, and not only during overcast conditions. When foraging in the forest understorey, celestial orientation cues may be obscured, although skyline panoramas can guide navigation [wood ants (*F. japonica*), Fukushi 2001]. The complex visual environment encountered by *Atta* may necessitate spatial referencing with the magnetic field to find visual landmarks or canopy cues, as in other Hymenoptera (Collett & Baron 1994; Salo & Rosengren 2001).

In conclusion, it is evident that *Atta* show a magnetic response in orientation during overcast days. This suggests that magnetic cues can be exploited to determine direction, and form part of an integrative navigation system. Future experiments that focus on the interaction between the solar and magnetic compasses would produce interesting results, as would further investigations of potential path integration strategies.

## Acknowledgements

## Literature Cited

Anderson, J. B. & Vander Meer, R. K. 1993: Magnetic orientation in the fire ant, *Solenopsis invicta*. Naturwissenschaften. **80,** 568—570.

Batschelet, E. 1981: Circular Statistics in Biology. Academic Press, London.

Beekman, M., Sumpter, D. J. T. & Ratnieks, F. L. W. 2001: Phase transition between disordered and ordered foraging in Pharaoh's ants. Proc. Natl Acad. Sci. **98,** 9703—9706.

Camlitepe, Y. & Stradling, D. J. 1995: Wood ants orient to magnetic fields. Proc. Roy. Soc. Lond. B Biol. Sci. **261,** 37—41.

Chittka, L., Williams, N. M., Rasmussen, H. & Thomson, J. D. 1999: Navigation without vision: bumblebee orientation in complete darkness. Proc. Roy. Soc. Lond. B Biol. Sci. **266,** 45—50.

Collett, T. & Baron, J. 1994: Biological compasses and the coordinate frame of landmark memories in honeybees. Nature **368,** 137—140.

Collett, M. & Collett, T. S. 2000: How do insects use path integration for their navigation? Biol. Cybern. **83,** 245—259.

von Frisch, K. 1949: Die Polarisation des Himmelslichtes als orientierender Faktor bei den Tänzen der Bienen. Experientia **5,** 142—148.

Fukushi, T. 2001: Homing in wood ants, *Formica japonica*. J. Exp. Biol. **204,** 2063—2072.

Holldobler, B. 1980: Canopy orientation: a new kind of orientation in ants. Science **210,** 86—88.

Jander, R. & Jander, U. 1998: The light and magnetic compass of the weaver ant, *Oecophylla smaragdina* (Hymenoptera: Formicidae). Ethology **104,** 743—758.

Keeton, W. J. 1971: Magnets interfere with pigeon homing. Proc. Natl Acad. Sci. **68,** 102—106.

Kirschvink, J. L. 1992: Uniform magnetic fields and double-wrapped coil systems: improved techniques for the design of bioelectromagnetic experiments. Bioelectromagnetics **13,** 401—411.

Klotz, J. H., van Zandt, L. L., Reid, B. L. & Bennett, G. W. 1997: Evidence lacking for magnetic compass orientation in fire ants (Hymenoptera: Formicidae). J. Kansas Entomol. Soc. **70,** 64—65.

Labhart, T. 1986: The electrophysiology of photoreceptors in different eye regions of the desert ant, *Cataglyphis bicolor*. J. Comp. Phys. A Neuroethol. Sens. Neural. **158,** 1—7.

Labhart, T. & Meyer, E. P. 2002: Neural mechanisms in insect navigation: polarization compass and odometer. Curr. Opin. Neurobiol. **12,** 707—714.

Merritt, R., Purcell, C. & Stroink, G. 1983: Uniform magnetic field produced by three, four, and five square coils. Rev. Sci. Instrum. **54,** 879—882.

Mouritsen, H. & Frost, B. J. 2002: Virtual migration in tethered flying monarch butterflies reveals orientation mechanisms. Proc. Natl Acad. Sci. **99,** 10 162—10 166.

Muller, M. & Wehner, R. 1988: Path integration in desert ants, *Cataglyphis fortis*. Proc. Natl Acad. Sci. **85,** 5287—5290.

Rosengren, R. 1971: Route fidelity, visual memory and recruitment behaviour in foraging wood ants of the genus *Formica* (Hymenoptera, Formicidae). Acta Zool. Fenn. **133,** 1—106.

Rosengren, R. & Fortelius, W. 1986: Ortstreue in foraging ants of the *Formica rufa* group. Hierarchy of orienting cues and long-term memory. Insect Soc. **33,** 306—337.

Rossel, S. & Wehner, R. 1986: Polarization vision in bees. Nature **323,** 128—131.

Salo, O. & Rosengren, R. 2001: Memory of location and site recognition in the ant *Formica uralensis* (Hymenoptera: Formicidae). Ethology **107,** 737—752.

Santschi, F. 1911: Observations et remarques critiques sur le mechanisme de l'orientation chez les fourmis. Rev. Sui. Zool. **19,** 305—338.

Schmidt-Koenig, K. 1958: Experimentelle Einflussnahme auf die 24-Stunden-Periodik bei Brieftauben und deren Auswirkungen unter besonder Berücksichtigung des Heimfindevermögens. Zeit. für Tierpsychol. **15,** 301—331.

Schmitt, D. E. & Esch, H. E. 1993: Magnetic orientation of honeybees in the laboratory. Naturwissenschaften. **80,** 41—43.

Shen, J. X., Xu, Z. M. & Hankes, E. 1998: Direct homing behaviour in the ant *Tetramorium caespitum* (Formicidae, Myrmicinae). Anim. Behav. **55,** 1443—1450.

Vilela, E. F., Jaffé, K. & Howse, P. E. 1987: Orientation in leaf-cutting ants (Formicidae: Attini). Anim. Behav. **35,** 1443—1453.

Walker, M. M. & Bitterman, M. E. 1989: Honeybees can be trained to respond to very small changes in geomagnetic-field intensity. J. Exp. Biol. **145,** 489—494.

Wehner, R., Michel, B. & Antonsen, P. 1996: Visual navigation in insects: coupling of egocentric and geocentric information. J. Exp. Biol. **199,** 129—140.

Wetterer, J., Shafir, S., Morrison, L., Lips, K., Gilbert, G., Cipllini, M. & Blancy, C. 1992: On-trail and off-trail orientation in the leaf-cutting ant *Atta cephalotes* L. Hymenoptera Formicidae. J. Kansas Entomol. Soc. **70,** 64—65.

Wiltschko, W. & Wiltschko, R. 1972: Magnetic compass of European robins. Science **176,** 62—64.