

1. Kudo, R.R.: Protozoology. Springfield, Ill.: Thomas 1954
2. Harland, W.B., Armstrong, R.L., Cox, A.V., Craig, L.E., Smith, A.G., Smith D.G.: A Geological Time Scale 1989. Cambridge: Cambridge Univ. Press 1989
3. Maxwell, R.D.: Introduction to Protozoology. New York: St. Martin's Press 1961
4. Smith, G.M.: The Fresh-water Algae of the United States. New York: McGraw-Hill 1933
5. Tappan, H.: The Paleobiology of Plant Protists. San Francisco: Freeman 1980
6. Poinar, Jr., G.O., Waggoner, B.M., Bauer, U.C.: Science 259, 222 (1993)
7. Thiessen, R., Sprunk, G.C.: U.S. Dept. Interior Tech. Pap. No. 631, p. 1 (1941)
8. Glaessner, M.F.: The Dawn of Animal Life: A Biohistorical Study. Cambridge: Cambridge Univ. Press 1984
9. Schuster, F.L., in: Handbook of Protocista (L. Margulis, J.O. Corliss, M. Melkonian, D.J. Chapman, eds.). Boston: Jones and Bartlett 1989
10. Clark, C.G., Gross, G.A.M.: Mol. Biol. Evol. 5, 512 (1988)
11. Christen, R., Ratto, A., Baroin, A., Perasso, R., Grell, K.G., Adoutte, A.: EMBO J. 10, 499 (1991)
12. Allison, C.W., Hilgert, J.W.: J. Paleontol. 60, 973 (1986)
13. Pokorny, V.: Principles of Zoological Micropaleontology. New York: Macmillan 1963
14. Loeblich, A.R., Tappan, H., in: Treatise on Invertebrate Paleontology C(2), Vol. 1. (R.C. Moore, ed.). Lawrence: Geol. Soc. of America and Univ. of Kansas Press 1964
15. Waggoner, B.M.: J. Protozool. 40, 98 (1993)
16. Waggoner, B.M.: PaleoBios (in press)

## Magnetic Orientation in the Fire Ant, *Solenopsis invicta*

J.B. Anderson\*

Zoology Department, Bartram Hall, University of Florida, Gainesville, Florida 32611, USA

R.K. Vander Meer

United States Department of Agriculture, Agricultural Research Service, Medical and Veterinary Entomology Research Laboratory, Gainesville, Florida 32604, USA

Within the thousands of ant species thus far described, a wide range of adaptations have evolved for discovering and delivering food resources to the colony. This foraging process can be broken down into the search for food, in which scout workers leave the nest and explore an area for resources, orientation and initial homing to the nest after food discovery, and return of the scout to food resources too large to carry alone, usually with recruitment of additional workers. Studies of initial homing in ants have disclosed many astronavigation mechanisms [1], e.g., *Cataglyphis bicolor* workers forage individually for food, navigating effectively by polarized light, sun compass and landmarks [2]. In addition to visual cues, chemical or kinaesthetic senses have been implicated in homing for several ant species [3]. We investigated initial homing in fire ants, and report for the first time geomagnetic

orientation abilities in an ant species. This magnetic sense provides an explanation for successful ant foraging in complete darkness and may be even more important within the dark confines of the nest environment.

The fire ant, *Solenopsis invicta*, is an exemplary model for central place foraging. Mature colonies may contain over 200 000 workers and can have population densities of 90 mounds per hectare [4]. To maintain this large biomass, the fire ant has a correspondingly sophisticated foraging strategy [5]. Over the past few decades, research has focused on recruitment behavior and its associated chemistry [6]. Surprisingly little attention has been given to initial homing – how foraging fire ants find their way back to the nest after food discovery.

A typical fire ant mound has radiating foraging tunnels with exit holes through which scout workers reach the surface. Once on the surface, the scout ranges in an irregular looping pattern until food is found. If the food material is too large to carry back, the worker lays a pheromone

trail more or less directly back to where it exited the foraging tunnel, regardless of its previous random movements [7]. Information contained in the recruitment pheromone motivates workers to follow the trail to the food source. Fire ants forage night and day [4, 8]. Thus, the ability to home under a variety of conditions is essential for effective foraging.

Fire ant workers are sensitive to light position and intensity and use the location of a light source as a visual cue in initial homing [9]. However, even in the absence of light, scouts succeed in homing to their nest and recruiting workers to food (Fig. 2, normal/normal). Possible explanations are that the scouts follow a concentration gradient of volatiles emanating from the nest, or they follow a gradient of nonvolatiles deposited on the foraging arena, or foraging fire ants may be capable of orientation to the earth's magnetic field. Circumstantial evidence supporting the latter possibility comes from reports that fire ants are attracted to and accumulate around electrical equipment [10].

The ability to sense the geomagnetic field for orientation or navigation has been demonstrated in organisms ranging from bacteria [11] to wood mice [12]. Geomagnetic orientation has been investigated in only one ant species, *Formica rufa*. Disturbance of the geomagnetic field with crude Helmholtz coils had no effect on trunk route fidelity in this ant [13]. However, trunk routes are long established foraging trails, whose fidelity is dictated by landmark and/or pheromone cues [14]. Thus, initial homing processes were not challenged.

\* Current address: Environmental Science and Engineering, P.O. Box 1703, Gainesville, FL 32602, USA

We tested the magnetic-field orientation hypothesis by measuring the time to trail formation for mature queenright fire ant colonies reared in the laboratory. All experiments were done in total darkness (the room was sealed to eliminate outside light) and at night (between 20:00 and 01:00 h) with periodic observation by red headlight. For each replicate, a Petri dish nest of ants (ca. 15 000 workers + brood) along with several hundred foraging workers was transferred to a clean assay tray ( $5 \times 40 \times 50$  cm). The nest was centered 5 cm from one end. Test colony subunits were placed within a Helmholtz coil (Fig. 1) and workers were allowed to acclimate to control or treatment conditions for 1 h; then a dead American cockroach (*Periplaneta americana*) was centered 22 cm from the nest. The time required for the ants to develop a clearly discernable trail from nest to cockroach bait was recorded. If no trail developed by 60 minutes the experiment was stopped and a score of 60 was given to that replicate. Bioassay trays were cleaned with ethanol.

The Helmholtz coil (Fig. 1) was used to produce an earth-strength magnetic field that was oriented  $180^\circ$  from the normal geomagnetic field. Five connected coils (1.68 m diam.) of electrical windings spaced 46 cm apart were positioned on a north-south axis surrounding a wooden

table in the light-tight room. A variable resistor was used to adjust the current so that the horizontal component of the local geomagnetic field was effectively reversed within the coil. The normal magnetic field (coils off) and reversed field (coils energized) were measured at 12 positions on the enclosed table with a Micropower Gaussmeter, model GM1A. The absolute strengths of the normal vs. reversed fields were not significantly different (one-factor ANOVA, Scheffé's S-procedure,  $P = 0.67$ ).

Four possible situations were tested depending on the coil's on/off (reverse/normal) status during the acclimation period and its status after cockroach introduction, e.g., coil off during the acclimation period and on after cockroach introduction = normal/reversed. On each night of tests, both conditions were run (normal/normal and normal/reverse or reverse/reverse and reverse/normal) to minimize any effect of time. For half the nights the order of testing was reversed. Also, tray directions were altered such that for half the time the nest end was south, and for half the time north.

When the magnetic field was constant throughout the experiment (normal or reversed), there was no difference in the time of trail formation (Fig. 2;  $P = 0.804$ , for normal/normal vs. reverse/

reverse). But when the magnetic field direction was changed at the time food was positioned, the ants took significantly longer to form a trail (Fig. 2;  $P = 0.0001$ , except normal/reverse vs. normal/normal, where  $P = 0.0004$ ). There was no difference between the two situations where the magnetic field was reversed after addition of the food bait ( $P = 0.989$ ).

The artificial magnetic field could have affected some other aspect of ant dynamics, such as trail marking or recruitment. If this were the case, then we would expect to find a difference in the observed trail formation times between the experiments in which the artificial magnetic field was on throughout the experiment, and those in which no artificial field was introduced, but no such difference was observed (Fig. 2). These same results are evidence that vibrations from the power supply (none were detected by the observer) were not used by the ants as an orientational cue. Similarly, the possibility of a disorienting effect from electrical artifacts caused by turning on the field can be eliminated because there were no significant differences between the two experimental situations where the electrical field was turned on or off within the experiment (normal/reverse and reverse/normal, Fig. 2).

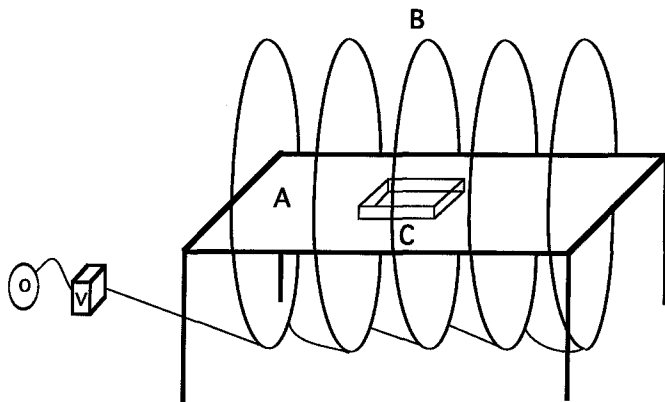


Fig. 1. Schematic diagram of the apparatus used to study the effects of the earth's magnetic field on the homing abilities of fire ant workers. A Bioassay table, B Helmholtz coil, C representative fire ant test unit, V voltage regulator, O electrical source

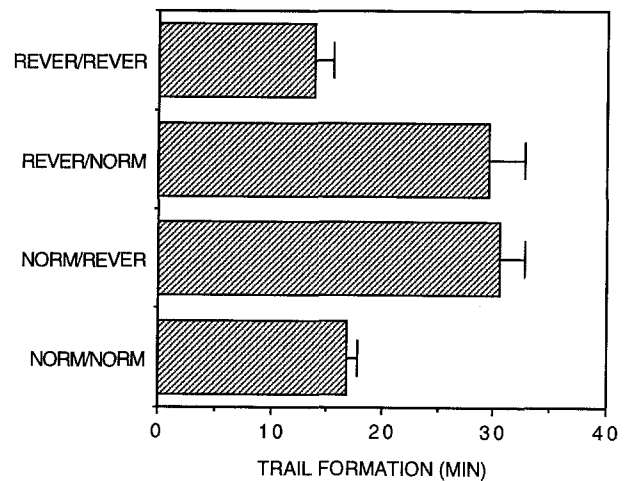


Fig. 2. Comparison of time to trail formation under four different magnetic-field conditions (mean and standard error shown). Times where the magnetic field was constant throughout the experiment (norm/norm and rever/rever) were not significantly different from each other. Times to trail formation where the magnetic field was changed after food introduction (norm/rever and rever/norm) were significantly different from times where the field was not changed. However, the two reversed-magnetic-field situations were not different from each other

These data demonstrate that the fire ant has a magnetic sense and that a change in magnetic-field direction disrupts the initial homing ability of workers. Thus, fire ants can now be included with the increasing variety of organisms having a demonstrated ability to perceive the earth's magnetic field for orientation or navigation. The sensory mechanisms by which the geomagnetic field is transduced into neural signals are still unclear, but an internal ferromagnetic material, magnetite, has been found in many of these organisms [15]. We propose that magnetite is also likely to be involved in fire ant geomagnetic sensing and plan to test for its presence.

Central place foragers such as ants must search widely, yet keep track of their location relative to their nest. Powerful selection for efficient foraging strategies in these animals has produced complex systems of navigation which use information from a variety of sources [1, 3]. It is well known that celestial information (the sun, the pattern of polarized light, the moon) and terrestrial landmarks can be important visual cues [16]. Beyond maze learning [17], and gravitational [9] and pheromonal orientation [5] already reported for fire ants, our studies add geomagnetic orientation to form a complex hierarchy of possible homing and

orientation mechanisms that contribute to the success of this species. The demonstration of geomagnetic orientation in an ant species may be broadly applicable and provide an explanation of worker orientation within subterranean nests and the ability of some ants to forage successfully without obvious cues (visual or otherwise), a puzzle which has confounded researchers for years [18].

We thank J. A. Seawright, S.D. Porter, J. Sivinski, and L. Morel for helpful comments on the manuscript.

Received May 24 and August 25, 1993

1. Wehner, R.: *Ann. Rev. Entomol.* 29, 277 (1984)
2. Wehner, R., Harkness, R.D., Schmid-Hempel, P., in: *Information Processing in Animals*, p. 1 (M. Lindauer, ed.). Stuttgart: G. Fischer 1983
3. Jaffé, K., Ramos, C., Lagalla, C., Parra, L.: *Insectes Soc.* 37, 101 (1990)
4. Porter, S.D., Tschinkel, W.R.: *Environ. Entomol.* 16, 802 (1987)
5. Wilson, E.O.: *Anim. Behav.* 10, 148 (1962)
6. Vander Meer, R.K., in: *Fire Ants and Leaf-cutting Ants: Biology and Man-*

- agement, p. 201 (C.S. Lofgren, R.K. Vander Meer, eds.). Boulder, CO: Westview 1986
7. Wilson, E.O.: *Anim. Behav.* 10, 134 (1962)
  8. Kidd, K.A., Apperson, C.S.: *J. Agric. Entomol.* 1, 212 (1984)
  9. Marak, G.E., Wolken, J. J.: *Nature* 205, 1328 (1965); Howard, D.F., Tschinkel, W.R.: *Behaviour* 56, 157 (1976); Vander Meer, R.K.: unpublished
  10. Vinson, S.B., MacKay, W.P., in: *Applied Myrmecology: A World Perspective*, p. 496 (R.K. Vander Meer, K. Jaffé, A. Cedeño, eds.). Boulder, CO: Westview 1990
  11. Blakemore, R.P.: *Science* 190, 377 (1975)
  12. Mather, J.G., Baker R.R.: *Nature* 291, 152 (1981)
  13. Rosengren, R., Fortelius, W.: *Insectes Soc.* 33, 306 (1986)
  14. Hölldobler, B.: *Behav. Ecol. Sociobiol.* 1, 3 (1976)
  15. Kirschvink, J.L., in: *Biomagnetism: An Interdisciplinary Approach*, p. 501 (S. Williamson, ed.). New York: Plenum 1983
  16. Rosengren, R.: *Acta Zool. Fenn.* 150, 1 (1977)
  17. Stratton, L.O., Coleman, W.P.: *J. Comp. Physiol. Psychol.* 83, 7 (1973)
  18. Cosens, D., Toussaint, N.: *Anim. Behav.* 33, 541 (1985)

## Inhibition of Male Calling by Heterospecific Signals Artifact of Chorusing or Abstinence During Suppression of Female Phonotaxis?

M. D. Greenfield

Department of Entomology, University of Kansas, Lawrence, Kansas 66045, USA

Various animals in which sexually advertising males signal acoustically exhibit the curious phenomenon of refraining from calling in the presence of certain heterospecific song [1]. This interaction has been reported from orthopteran insects, anurans, birds, and mammals. Typically, the response is unilateral and short-term: the inhibited species adjusts the timing of its calls such that they are broadcast during brief gaps in the inhibitor's song. In several instances the

affected species exhibits a long-term response as well in which its diel periodicity is shifted and the singing periods of the inhibitors are largely avoided [2–4]. Heterospecific inhibitory responses have been proposed to be either artifacts of intraspecific male-male chorusing interactions or abstinence from calling at a time when females would not be effectively or "correctly" influenced by it [1, 5]. My recent studies on female phonotaxis in the neotropical katydid *Neoco-*

*nocephalus spiza* (Orthoptera: Tettigoniidae) provide results consistent with the latter hypothesis but do not necessarily negate the former one. Consideration of the nature of female choice in *N. spiza* suggests that limitations in female perception ultimately drive male inhibition. Four species of *Neoconocephalus* katydids are common in the lowlands of central Panama [6], and males of each call during evening hours throughout much of the year. *N. spiza* males are inhibited from singing by the calls of any of the other three (*N. affinis*, *N. punctipes*, *N. triops*), and in areas where populations of inhibitors are high, *N. spiza* shifts from nocturnal to diurnal calling [3]. While microhabitat differences between the species exist, their songs are sufficiently loud (> 80 dB SPL at 1 m; 0 dB re 20  $\mu$ Pa) that, given the low threshold for inhibition ( $\approx$  40 dB), the calling of *N. spiza* males is commonly stifled in the