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On- and Off-Trail Orientation in the Leaf-Cutting Ant, *Atta cephalotes* (L.) (Hymenoptera: Formicidae)

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ABSTRACT: In this study, we examined orientation by *Atta cephalotes* in the field. We tested whether the presence of trail pheromones is necessary for nest-bound orientation. Laden *Atta cephalotes* foragers taken from their foraging trail and placed on a branch marked with their trail pheromones showed no evidence of using polarity of their trail pheromones as a cue for determining the correct direction back to their nest. These ants preferentially moved towards their nest both on normal and on 180° rotated trails. Laden foragers taken from their foraging trail and placed on branches lacking trail pheromones, however, did not move preferentially towards their nest, despite other cues that indicated the correct direction. Instead, these ants appeared to move in an arbitrary direction, perhaps in an attempt to relocate their lost trail.

Leaf-cutting ants (*Acromyrmex* spp. and *Atta* spp.) utilize systems of branching foraging trails marked with their chemical pheromones when traveling between their nests and distant vegetation sources (Moser and Blum, 1963; Weber, 1972). The ants keep their main foraging trails clear of debris. These trails often extend more than 100 meters and are plainly visible on the forest floor. Commonly, leaf-cutter trails run along fallen tree trunks or branches, presumably because such routes are simpler to establish and maintain (Wetterer, pers. obs.).

Laboratory studies of nest-bound orientation by laden leaf-cutting ants (Howse, 1986; Vilela et al., 1987; Guajara et al., 1989; Jaffé et al., 1990) indicated that the ants use a variety of directional cues, including visual, gravitational, and tactile information, for orientation along their trails. In addition, *Acromyrmex octospinosus* (Reich) and *Ac. subterraneus molestans* (Santschi) appeared to use cues from the polarity of the chemical pheromones on the trail for determining which direction along the trail leads towards their nest (Vilela et al., 1987; Guajara et al., 1989). *Atta cephalotes* (L.) and *A. laevigata* (Fr. Smith) foragers, however, showed no evidence of using pheromone polarity cues for orientation (Vilela et al., 1987).

In this study we examined orientation by *A. cephalotes* in the field. We tested whether the presence of the trail pheromones is necessary for nest-bound orientation under field conditions. Such off-trail orientation may be necessary under natural conditions when ants leave their trail while foraging or fall from the tree where they are cutting leaves.

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METHODS: We studied daytime orientation at a colony of *A. cephalotes* on the grounds of Estacion Biologica La Selva of the Organización para Estudios Tropicales, Heredia Province, Costa Rica, in June 1989. The study colony's main foraging trail went through a pile of dead branches (2–3 cm in diameter) located 5–10 m from the ants' nest entrance. Within this pile, the trail passed along parts of several different branches. In our experiment, we examined orientation by ants, both on sections of branches that had been used as part of the ants' foraging trail (trail pheromones present) and on sections that had not been part of the trail (trail pheromones absent). We cut 37.5 cm sections from the branches and suspended them on supports 5 cm off the ground, parallel to and approximately 5 cm to either side of the foraging trail at a location 10 meters farther from the nest than where the branches were taken. Branch sections with trail pheromones present were marked with an arrow to indicate the direction to the ants' nest in their original position. These marks also served to indicate on which side the trail pheromones lay. Sections without trail pheromones were marked with an arrow in an arbitrary direction.

Nest-bound ants laden with leaf fragments were lifted from their foraging trail and released facing perpendicular to the trail at the center of a branch section. When the laden ant crossed a line marked at 16 cm from the center of the branch section, the direction of movement relative to their nest (towards vs. away) was recorded and the ant was returned to her trail. Each ant was tested only once. For each of the two branch types (trail pheromones present or absent), we performed four sets of thirty trials (two sets on each side of the trail), reversing the direction of the branch section (180° horizontal rotation) after every five trials. Only laden ants were tested because these ants should be motivated to return with their load to the nest.

We analyzed the data using Chi-square statistics.

RESULTS: When initially released on the branch sections, laden ants typically circled one or more times in place before selecting a direction of movement. This circling behavior occurred regardless of whether trail pheromones were present or absent. In the presence of the trail pheromones, significantly more laden ants elected to move towards the nest than away from the nest (92 towards versus 28 away; $\chi^2 = 34.1$; d.f. = 1, $P < 0.0001$). The proportion of ants moving correctly towards the nest was independent of polarity of the trail pheromones (46 of 60 in original polarity versus 46 of 60 in reversed polarity; $\chi^2 = 0.0$; d.f. = 1, $P > 0.5$). On branch sections without trail pheromones, laden ants did not selectively move towards their nest. The directional movement of these ants did not differ from random (59 towards versus 61 away; $\chi^2 = 0.0$; d.f. = 1, $P > 0.5$).

DISCUSSION: As in Vilela et al.'s (1987) study, laden *A. cephalotes* foragers showed no evidence of using the polarity of their trail pheromones for orientation. When foragers suddenly found themselves off their foraging trail, but on a branch marked with their trail pheromones, they must have used cues other than trail pheromone polarity (probably visual cues; Vilela et al., 1987) for determining the correct direction to their nest. Foragers put on a branch without trail pheromones, however, did not move preferentially towards their nest, despite having these same cues that indicated the correct direction. Instead, these ants appeared to move in an arbitrary direction along the branch, perhaps in an attempt to relocate their lost trail. This behavior may be an adaptive response. The ants often cut leaves at sources over 50 m from their nest and direct off-trail orientation back to the nest over debris-covered ground could be very time consuming. A lost ant's first priority may be to relocate the foraging trail before heading towards home. If a displaced ant cannot directly detect the trail itself, available cues may not be enough to indicate on which side of the trail the ant has been displaced. The methods displaced ants use to find their way back to their foraging trail are currently unknown.

Because other leaf-cutters such as *Ac. octospinosus* use polarity cues in their trails, this suggests that, due to differences in ecology, use of these cues in *A. cephalotes* is either unneeded for orientation or precluded by other factors. *Ac. octospinosus* and *A. cephalotes* show many important differences in ecology (see Wetterer, 1992). *Ac. octospinosus* have relatively small colonies of under one hundred thousand workers and a relatively monomorphic forager caste. In contrast, *A. cephalotes* have colonies of several million workers and a wide size range of foragers with larger foragers attacking trees with thicker and tougher leaves. One possibility is that polarity cues are generally not required, or not possible, on the well-cleared and heavily travelled foraging trails of *A. cephalotes*. Polarity cues may be precluded by other functions of the trail, such as directing different size workers to different leaf sources (see Vilela et al., 1987). The ecological correlates of orientation in leaf-cutting ants deserve further investigation.

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Book Review

The "African" Honey Bee—M. Spivak, D. J. C. Fletcher, and M. D. Breed (eds.). Westview Press; Boulder, CO; 1991. 435 pp. ISBN: 0-8133-7209-7.

Perhaps at no time in the history of science has an insect received so much publicity as has the African honey bee with its introduction and spread in the Neotropics. The "killer bee," as dubbed by the press, has been the subject of scare articles, movie films, and television productions for over 30 years. Due to legitimate public health and economic concerns, coupled with the anticipated range extension of the bees into the United States, considerable research has been conducted on this insect and its biology.

This book is an attempt, as stated by the editors, "to bring together the large body of information that has become available concerning the Africanized bee and its spread and impact through the known New World." The format consists of 20 chapters partitioned into five major theme areas as follows: (1) Systematics and Identification; (2) The Spread of Africanized Bees and the Africanization Process; (3) Population Biology, Ecology, and Diseases; (4) Defensive Behavior; and (5) Beekeeping in South America. Authors were given much latitude in expressing their views, and at least some of them had access to other included manuscripts. Diverse opinions surface early, starting from such basics as what to