obtain otherwise.

Literature Cited

Beadell, J. S., C. Hansel, and J. W. Hourdequin. 1996. Effects of forage preference on trail quality and transport efficiency in *Atta cephalotes*. Pages *in* A. L. Mannan and D. S. Canny, editors. Dartmouth Studies in Tropical Ecology, Darmouth College, Hanover, NH. USA.

ANTS ON THE MOVE: COLONY-SPECIFIC PHEROMONE TRAILS OF *ATTA CEPHALOTES*

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Abstract.. Atta cephalotes ants use chemical pheromones to communicate with other individuals of the same colony. We hypothesized that ants within colonies communicate through colony-specific pheromones. We tested this by laying pheromone trails of same and different colonies across active leaf-cutter trails. Soldiers responded strongly to the pheromones of foreign colonies with an apparent alarm response (increased turning angles and frequencies). In contrast, leaf carriers traveled faster when following their own colonies' pheromone trail, but did not distinguish foreign pheromones. Colony-specific pheromones and caste-specific responses contribute to colony function and presumably increase the inclusive fitness of individual ants.

Key Words: Atta cephalotes, *pheromone trails, colony-specific pheromones. inclusive fitness*

Introduction

Ants communicate with each other through the use of chemical pheromones. The leaf-cutter ant, *Atta cephalotes*, lays down a directional path that all colony individuals follow when moving in large numbers. We hypothesized that these pheromones are colony-specific and that *A. cephalotes* from one colony will exhibit different behavior when presented with another colony's pheromone trail than when presented with its own. We predicted that ants would be more slow to cross, and have more aborted crossings on a pheromone trail from a different colony than on a trail from their own colony. We hypothesized different responses from soldier and leaf-carrier ant because different castes have specialized roles in the colony structure. The large-headed soldiers specialize in defense to ensure the safety of the small-headed leaf-carriers (Holldobler and Wilson 1990, p. 309).

Methods

Our experiment was conducted on 31 January, 1996 along Senderos Guanacaste, Sirena, and Naranjo in Corcovado National Park, Costa Rica. We tested five trails of ants (= site) for their response when introduced to each of three experimental manipulations. For each trial, a sheet of 9 x 21 cm paper was placed crosswise across the trail: the control sheets had no previous pheromones, the "same" treatment had the same colony's pheromones, and the "different" treatment had a different colony's pheromones. (We assumed that different trails, separated by > 400 m, represented different colonies of *Atta* ants). Each paper was laid so that the ants moved in the same direction with each treatment. Two papers initially used as controls were left five additional minutes on the trail and subsequently used for the "same" and "different" treatments. We waited three minutes between the control and the "same" treatments to simulate the time it would require to find a new pheromone path further down the trail. For each trial, we measured the time it took the first soldier and first leaf-carrier to cross the paper (hereafter referred to as crossing time). We also counted the number of soldiers that had aborted crossings in the first and third minutes as well as the number of leaf-carriers that aborted crossing before the first one successfully crossed the paper. Additionally, we counted the number of the ants crossing during the first and third minutes of observation. We tested ant responses with a three-way ANOVA model that included pheromone treatment, site, and minute of observation.

Results

Soldier ants had significantly longer crossing times and greater numbers of aborted crossings in the "different" compared to the "same" or control treatment (Figures 1 and 2). These effects were greater in the first minute of observation than in the third minute of observation. Soldier ants increased turning angles and turning frequencies, producing circles and zigzags, and causing them to require up to 5 times longer to cross 9 cm. Soldiers did not distinguish, or barely distinguished, between "same" and the control treatments.

Leaf carriers travel times were not affected by "diff-

Table 1. F-statistics for effects of site, pheromone treatment, and minute on crossing time and percent aborted crossings

		Time to First Successful Crossing		Percent Aborted Crossings	
Source	df	Soldier	Leaf-Carrier	Soldier	Leaf-Carrier
Site	4	5.64*	1.74	1.25	0.35
Treatment	2	155.00***	0.32	32.00**	8.84**
Minute	1	65.09***	10.15*	20.00***	--
S x M	4	1.68	1.50	2.42	--
T x M	2	51.78***	1.51	8.30*	--
S x T	8	8.92**	1.95	2.27	--

p < .05, **p < .01, ***p < .001

[a] percent aborted crossings were not measured for leaf-carriers during the third minute; error df = 8

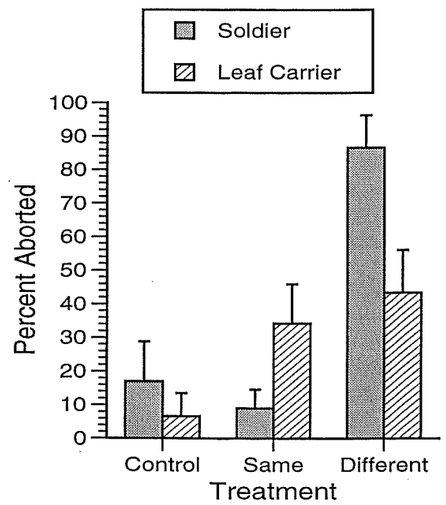

Figure 2: Percent of aborted crossings for soldier and leaf carriers in three pheromone treatments.

ferent" pheromones (Figure 1). In the first minute leaf carriers crossed the "same" pheromone path twice as fast as either the control or "different" paths, although the difference between the two was not significant (Table 1).

Discussion

Ants' travel behavior changed among pheromone treatments, supporting the hypothesis that ants distinguish between different colony pheromone trails. Results also showed differences in caste behavior: soldiers respond to "different" pheromones with alarm, while leaf carriers responded to the pheromones of their own colony with increased leaf move-

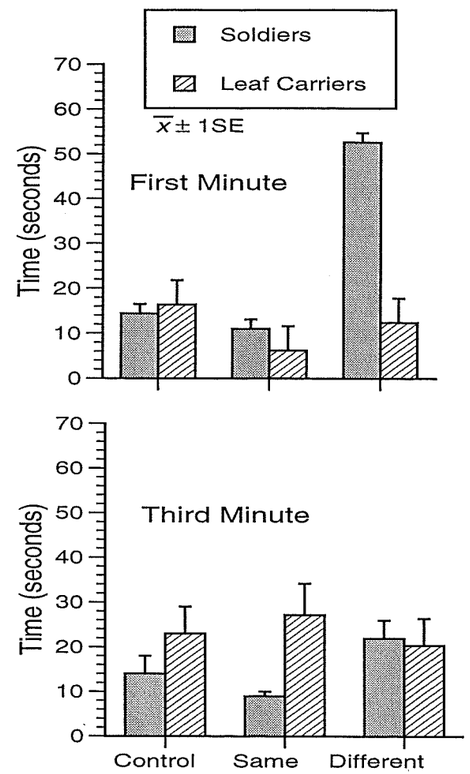

Figure 1: Time to first crossing of Atta cephalotes soldiers and leaf carriers during the first and third minutes of exposure to three pheromone treatments (a control, a trail laid down by the "same" colony, and a trail laid down by a "different" colony).

ment. Alarm behavior in ants is defined as faster movement and increased turning frequencies (Janzen, 1983). When exposed to foreign pheromones, sodiers

increased their turning frequency and explored around the periphery of the 9 x 21 cm surface. This led to increased aborted crossings and longer crossing times. In contrast, the leaf carriers seemed to actively follow their own colony's pheromones, while ignoring the presence of "different" pheromones.

Crossing times and accelerated numbers of aborted crossings increased after three minutes. This suggests that the ants rapidly re-established their own pheromone path. It may be advantageous for the ants to lay down their own pheromone pathway as swiftly as possible in order to allow the efficient transport of harvested leaves from the forest to the nest.

Colony sisters share 75% of their genes. Colony-specific pheromones presumably increase the survival and reproduction of the colony, thereby increasing the inclusive fitness of soldiers, leaf carriers, and other castes. Colony-specific pheromones allow leaf carriers to travel much faster on recognizable paths and to maximize the flow of harvested leaves into the nest. Colony-specific pheromones also increase fitness by allowing soldiers to recognize intruders, perhaps minimizing competition from other colonies.

Literature Cited

Holldobler, B. and E. O. Wilson. 1990. Page 309 *in* The Ants. Harvard University Press, Cambridge, MA, USA.

Janzen, D. H. 1983. *Pseudomyrmex ferruginea* (Hormiga del Cornizuelo, Acacia-Ant). Pages 762-764 *in* D. H. Janzen editor. Costa Rican Natural History. University of Chicago Press, Chicago, USA.