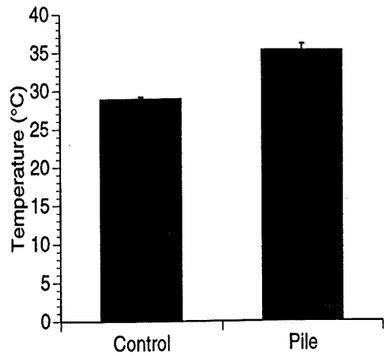

Fig. 1. Mean ground temperature at sites containing leaf piles and at sites located at 2m. intervals along the same ant trails (control). (n=85, control and n=17, piles)

Discussion

Accumulations of leaf fragments occurred only in sunny, warm areas along ant trails. This occurrence and distribution of leaf piles could be accounted for either as a physiological response of the ants to thermal stress or as an opportunistic behavior the ants use to facilitate decomposition.

Heat or light stress could induce a physiological response in the ants that causes them to drop the leaves. If the temperature or light levels exceed some threshold, ants may drop leaves to ease their load and pick them up later when conditions improve. This seems unlikely, however, since there were many patches of sunlight along the highways that did not have leaf piles (see Table 1). Additionally, there were many tiny patches of sunlight amid the shade that would seem too small to induce a physiological response, and yet contained leaf piles.

Leaf dropping could also be an opportunistic behavior of the ants to facilitate leaf decomposition. This behavior would benefit the leaf-cutters in two ways: either to allow evaporation to lighten the load of the leaves for future carriers, or to facilitate the decomposition of the leaf fragments. Further studies on both dry leaf weight and on the fungal processes would lend more insight into this phenomenon.

Several active trails we encountered were shaded and lacked leaf-piles. This suggests that leaf piling behavior is environmentally induced and any benefits from it, such as leaf decomposition, are not essential for normal colony functions. Furthermore, we observed that every time the shade encroached upon a leaf pile, the ants moved the fragments either to another sunny area along the trail or on to the nest. Further experiments using artificial shading on leaf piles would be useful to quantify these observations.

The majority of the ants that dropped their leaves on a pile immediately turned around and returned in the direction they came instead of continuing on to the nest. This suggested to us two hypotheses. The "way station" hypothesis entails a further division of labor, where there are certain ants that specialize in cutting and depositing, and others who specialize in picking up the fragments and transporting them to the nest. For this idea, the leaf piles might serve as a way station between the two divisions. A second hypothesis is that the workers maintain the leaf piles in the sun for a certain period, possibly for decomposition purposes, before taking them to the nest and therefore do not continue on their path to the nest after dropping off a leaf, but instead return to collect more leaves. This is the more likely hypothesis since the piles are found only in patches of sun, and if the piles served only as way stations they could just as easily be located in the shade.

PATTERNS IN AGGRESSIVE BEHAVIOR OF LEAF CUTTING ANTS

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Abstract. We observed the defensive behavior of leaf-cutting ants, *Atta cephalotes,*, against a conspecific intruder from another colony. We predicted that defensive response would differ depending on proximity to the nest of the intrusion, colony and worker caste of the ant intruder, and worker caste responding to the intrusion. We found that *A. cephalotes* workers and soldiers responded more aggressively toward intruders from foreign colonies than to intruders from their own colony, which suggests that *A. cephalotes* recognize members of their own colony as non-threatening. We found no difference in the number of attacks against an intruder near versus far from the nest, which suggests either that all parts of the trail are of equal importance to the ants, or that aggressive behavior in the ants is fixed. Further, while we found that workers defend the trail more actively than soldiers, possibly because they are less specialized than soldiers in their functions, we found that intruding soldiers were attacked more aggressively than intruding workers, possibly due to their superior size and a resultant increase in potential harm to the focal colony.

Key words: Atta cephalotes, *castes, defense, fixed behavior, soldier ants, worker ants*

Introduction

Leaf cutting ants, *A. cephalotes,* abundant in the lowlands of Costa Rica, are eusocial insects that create large underground nests, where they care for their larvae and grow their fungal food source on composted leaves. Their social system is divided into three castes: minimas, workers, and soldiers. The minima tend to the nest, while both the workers and soldiers leave the nest and travel on the foraging trails (Stevens 1983). Worker ants, 10mm in length on average, do most of the leaf collection (Stevens, 1983), while soldier ants, up to 20mm in length, seem more equipped to cut leaves and carry large leaf pieces. We thought that soldier ants might also use their size and strength to protect their colony from collisions with other *A. cephalotes* colonies.

In order to see how *A. cephalotes* colonies might respond to potential collisions of their trails with trails of other colonies, we investigated caste patterns in defensive behavior against ant intruders both near and far from the nest on a foraging trail. We hypothesized that the ants would respond more aggressively to ants introduced from a different colony than to displaced ants of their own colony. We predicted that leaf cutter ants have the ability to recognize each other and avoid attacking members of their own colony, while maintaining the ability to detect intruders of another colony and act defensively.

We also hypothesized that the ants would behave more aggressively near the nest than they would far from the nest because the nest holds their larvae and the valuable fungus which is their sole food source. Lastly, because soldiers are larger and stronger than workers, we hypothesized that the soldiers would be more aggressive toward the intruder ant than the workers and that the intruding soldiers would be attacked sooner and more aggressively than the intruding workers.

Methods

We located eight active *A. cephalotes* nests by following ant trails that crossed the Senderos Pavo and Espavales, north and northwest of the Sirena Biological Station, Corcovado National Park, Costa Rica. We observed two locations on a single trail at each colony: one site at one meter from a nest entrance and the other approximately 25 m down the trail from the first. At each site, we measured basal activity for one minute by counting the numbers of ants crossing an imaginary line from both directions.

At each location, we conducted four different introduction treatments. We introduced one worker ant from a separate trail of the test colony, one soldier from the same separate trail of the test colony, one worker from a foreign colony and one soldier from a foreign colony. One colony provided all the foreign ants used in all the trials and was not one of the eight test colonies. For each treatment, we recorded every contact made by an ant on the focal ant, classified the contact as either neutral (a mere bump or non-aggres-

sive inquisition), a strike (aggressive and quick movement against intruder), or a latch (aggressive movement toward and holding on to intruder) , and recorded the caste of the contacting ant. Each trial lasted for three minutes. Following the end of the trial, we removed the focal ant and waited three minutes for the effect of the introduction to pass.

Results

Ants reacted more aggressively to introduced ants from foreign colonies than to ants of their own colony (paired t-test, t=7.91, df=14, P=0.00; Fig. 1). Of all ant-to-ant interactions, a higher proportion were strikes or latches against foreign ants (72.0 + 5.1) than against ants of the same colony (19.2 + 4.3).

Mean basal activity was significantly higher near the nest (100.1 + 3.9 ants/minute) than far from the nest (65.8 + 10.5 ants/minute; t-test, t=3.09, df=14, P=0.01; Fig. 2). However, there was no difference in the number of aggressive acts observed between the near (6.08 + 0.78) and far sites (4.80 + 0.77; t-test; t=1.22, df=14, P=0.24; Fig. 3). There was no relationship between number of aggressive actions and basal activity (regression, r2=0.28, df=7, F=3.7, P=0.10).

Worker ants were more aggressive than soldier ants, but aggression upon worker ants was lower than that upon soldier ants. Of all their interactions, the proportion that were aggressive by workers (51.8 + 3.1) was higher than that by soldiers (34.5 + 4.6; t-test, t=3.19, df=14, P=0.01; Fig. 4). The proportion of total interactions that were aggressive upon workers (28.7 + 4.7) was lower than that upon soldiers (51.4 + 3.5; t-test, t=2.24, df=14, P=0.042; Fig. 4).

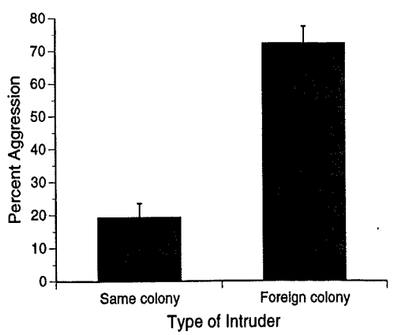


FIG. 1. Proportion of interactions that were agggressive by *A. cephalotes* in response to an introduced ant from its own colony and from a foreign colony. (n=8 trails for each type of intruder).

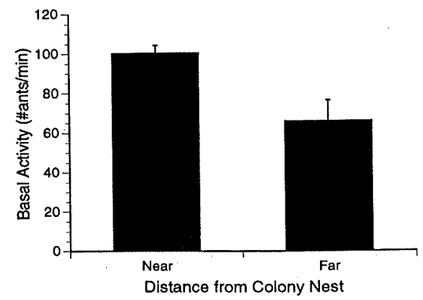
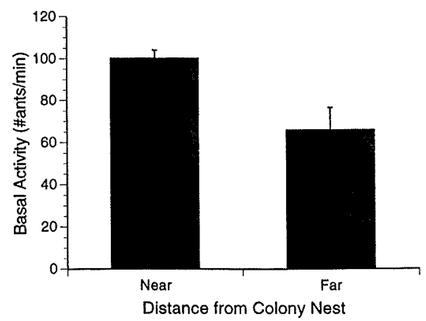


FIG. 2. Basal activity (number of ants passing a point in one minute) of *A. cephalotes* near (1 m) and far (25 m) from the colony nest. (n=8 trails for each distance from nest).



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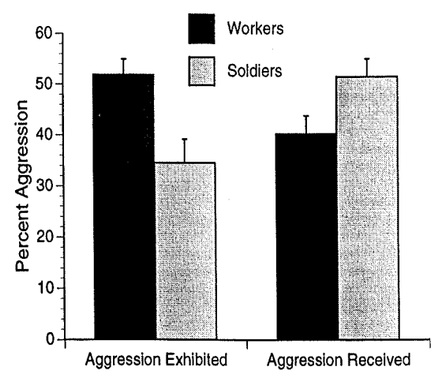

FIG. 4. Proportion of interactions that were aggressive by and on two castes of *A. cephalotes*.

There was no significant difference between time of first aggressive response by workers and soldiers, although workers tended to be the first to respond aggressively (t-test, t=1.96, df=13, P=0.071). There was no difference between the time to first aggressive response upon workers and soldiers (t-test, t=0.84, df=14, P=0.41).

Discussion

We found that *A. cephalotes* responded more aggressively toward intruding ants of a foreign colony than to ants of their own colony. This suggests that ants are able to recognize members of their own colony, which are presumably non-threatening, while they defend their colony against foreign intruders.

As expected, we found more basal activity near the nest, where the trail is not yet branched, than far from it. However, contrary to our hypothesis, the ants did not respond more aggressively to intrusions near than far from the nest. This suggests that ants may expend a constant amount of energy on defense of their trails, regardless of proximity to the nest. While an intrusion near the nest is a threat to the fungal garden and larvae, a disturbance far from the nest may present a potential threat to the food resource. Moreover, it is possible that the ants exhibit fixed defensive behavior and therefore defend their colony with equal aggression whenever they encounter an intruder they do not recognize as a member of their own colony.
We hypothesized that the aggressive response would differ between castes because colonies are highly organized and division of labor appears to be strict. Specifically, we predicted that there would be more aggressive acts toward intruders by soldiers than by workers. We found instead that workers were more aggressive than soldiers toward intruders. While we expected that the superior size and strength of soldiers would be indicative of their role as defenders of the trail, they may actually be more vital in performing other tasks that require their strength, such as cutting and removing tough, dry leaves from the trail. If this is the case, it seems that workers, which may forage, maintain trails, and defend the nest, may be more generalized in their functions than soldiers, which may be needed for more specific tasks. The caste responses that we observed might also be due to differential distributions of workers and soldiers along the foraging trails. Casual observations suggest that more workers than soldiers move along the trails. It would be revealing for future studies to examine caste distribution on foraging trails and quantify the time allocated by specific worker and soldier ants to specific tasks in order to better understand their roles in the colony.

We also predicted that ant aggression would be greater toward introduced soldiers than workers, and our data supported this prediction. We suspect that the greater size and strength of soldiers poses a larger threat to the invaded colony.

Our study quantified ant aggression toward a single intruding ant. It is possible that overall ant aggression, as well as the aggression of the individual castes, would differ if more than one ant were introduced. Further studies examining such ant responses might increase our understanding of how leaf cutting ant colonies react to stray ants from foreign colonies, accidental run-ins with foreign foraging trails, or encounters with other ant species.

Literature Cited

Stevens, G.C. 1983. *Atta cephalotes.* Pages 690-699*in* D. H. Janzen, editor. Costa Rican Natural History, University of Chicago Press: Chicago and London.