pulling responses (Wilcoxon, X^2=12, df=1, P=0.0005; Fig. 1). On small and medium fragments, there were no significant differences between proportions of pulling and cutting responses (Wilcoxon; small: X^2=1.48, df=1, P=0.22; medium: X^2=0.025, df=1, P=0.87; Fig. 1). Four of eight small leaves, three of eight medium leaves, and no large leaves were completely removed from the trail during the 10 min trial.

Worker ants performed 98% of all trail-clearing behavior observed (cutting and pulling). Also, there was no change in recruitment of ants from the colony over time after the introduction of small, medium, and large leaf fragments (Table 1; Least Squares/2-Way Anova: small fragments: P=0.80; medium fragments: P=0.95; large fragments: P=0.59).

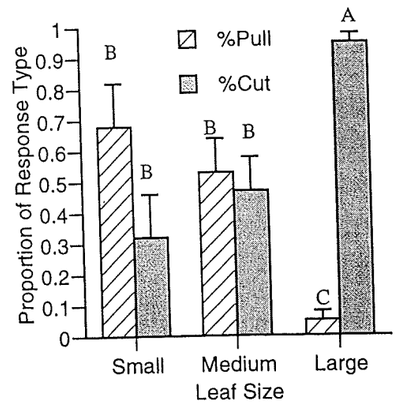

Fig. 1. Response (pull or cut) to introduced leaves of different sizes on *Atta colombica* trails at Corcovado National Park, Costa Rica. Letters indicate values which differ significantly.

Table 1 - Number of leaf-cutter ants/min (mean ± SE; n=4) crossing a designated point before and at intervals after introduction of obstructing leaf fragment to ant trails at Corcovado National Park, Costa Rica.

	Before	2 min	4 min	6 min	8 min	10 min
Small	35.3 ± 7.95	37.3 ± 8.32	33.7 ± 5.78	37.5 ± 10.9	39.2 ± 9.69	36.5 ± 6.65
Med	30.1 ± 8.92	31.2 ± 6.37	31.5 ± 8.7	27 ± 10.37	27.5 ± 7.96	27.3 ± 7.63
Large	44.9 ± 12.5	29.5 ± 5.12	35.2 ± 3.5	34 ± 8.88	28.8 ± 8.59	26.5 ± 7.15

Discussion

As leaf fragment size increased, *A. colombica* tended to cut rather than pull the obstructing leaf off the trail. This indicates that ants attempt to maximize leaf removal efficiency by trying to pull the leaf off the trail and then, if unsuccessful, cutting the leaf into smaller pieces which could then be removed. Pulling appears to be faster clearing trails because some small and medium fragments were completely pulled off the trails during the trials, while no leaves were completely removed by cutting.

Contrary to our second hypothesis and the observations of Bizzarro *et al.* (1992), soldiers did not contribute to the removal of leaf obstacles, suggesting that they do not always perform this function. Workers are more abundant both travelling to and from the colony, and are therefore more likely to encounter and possibly clear trail obstructions, despite their small size.

Our results indicate that *A. colombica* did not recruit more individuals to the site of an obstruction. Obstructions caused considerable back-ups of ants so there may have been sufficient individuals to remove leaf fragments. Alternatively, our trial length might not have been long enough to observe recruitment. Furthurmore our testing was done 24 hrs after a period of heavy rain, which had washed out many trails and kept ants from foraging. These circumstances might have led ants to ignore obstacles in favor of getting more leaves to the nest or because there were more serious repairs needed in the trail at other locations. Our results show, however, that *A. colombica* did distinguish between different sized leaf obstacles and employ different trail clearing strategies depending on the size of the leaf fragments.

Literature Cited

Bizzarro, J. J., J. V. Ko, and J. A. Rettmann. 1992. The roles of soldiers on leaf cutter ant foraging trails. Pp. 68-70 in *Dartmouth Tropical Biology*, eds. Dudycha and Shabel. P. 68.

Martin, M. M. 1969. The biochemical basis of the fungus-attine ant symbiosis. *Science*. 169: 16-20. as cited by Cook, S. P., C. R. Preuss, and M. B. Royer. 1993. The effect of trail barriers on foraging in the leaf -cutting ant *Atta cephalotes*. Pp. 56-59 in *Dartmouth Tropical Biology*, ed. Bansak, T.S., and M. Seandel.

Response of *Atta colombica* to leaf fragments from foreign colonies

R. M. Brayce, D. R. Hogan, and M. S. Kim

Abstract: To test whether leaf-cutter ants recognize the leaves they are carrying, we measured time to acceptance for intra- and inter-colony leaf fragment introductions for *Atta colombica* colonies harvesting the same tree species. We found some evidence of prolonged time to acceptance for inter-colony fragment introductions as compared to intra-colony fragments. There was also a trend for prolonged time to acceptance for intra-colony fragments with delayed introduction times. These results lend support to the hypothesis of a colony-specific pheromone on leaf fragments.

Key Words: leaf-cutter ants, pheromone

Introduction

Leaf-cutter ants (*Atta* spp.) are prominent in Costa Rican lowland forests (Stephens 1983). They provide food for their colonies by cultivating fungal gardens on collected leaf fragments. It has been reported that leaf-cutters are specific in the vegetation they select, approaching new resources cautiously (Stephens 1983). Additionally, ants transporting leaf fragments of one tree species have been shown to ignore fragments from a different tree species being transported by ants on another trail within the same colony (Glennon et al. 1995). To separate factors causing leaf fragment rejection (leaf chemical markings or preference for different target tree species), we examined the response of *Atta colombica* to introduced leaf fragments from other colonies that were harvesting the same tree species. We predicted that *A. colombica* would more readily accept fragments from their own colony compared to fragments from a foreign colony, even when both colonies were foraging on the same plant species.

Methods

We selected four *A. colombica* trails from different colonies, each carrying leaf fragments from the same tree species, determined by careful examination of leaf morphology. Leaf fragments were classified as "own" when reintroduced to the originating colony, and "foreign" when introduced from another colony. For introduction of "own" leaves, we took 18 fragments from *A. colombica* moving down the tree, and waited 2 min before reintroducing the leaf fragments at 1 m intervals along the same trail. We used forceps to introduce leaf fragments in three sets of six. We waited to introduce later sets of six until all of the fragments in the previous group of six were accepted, or until 5 min had passed. We recorded the time it took for an ant to fully hoist, and begin to walk with, each leaf fragment (acceptance of the fragment). If the time exceeded 5 min, we deemed the fragment unaccepted.

For "foreign" introductions, we took 18 leaf fragments from the first *A. colombica* colony and introduced them in groups of six to the second colony. Acceptance was quantified following the procedure outlined above. These reciprocal introductions were conducted for colonies 1 and 2 (first pair), and then for colonies 3 and 4 (second pair).

Results

There was a trend for *A. colombica* to accept their own leaf fragments more rapidly than foreign ones (Fig. 1; paired t-test, df=3, P<0.07). Only 1 of 70 reintroduced fragments remained unaccepted after 5 min, and 14 of 72 introduced foreign fragments remained unaccepted after 5 min, although a single trail had 12 of these unaccepted fragments. No leaf fragments were ever removed from a trail. For intra-colony trials, ants tended to accept fragments introduced in later sets of six more slowly (Fig. 2, X^2 = 4.37, df = 2, P<0.11). There was no trend with time, however, for the sequential introduction of foreign fragment sets (X^2 = 2.85, df = 2, P = 0.24).

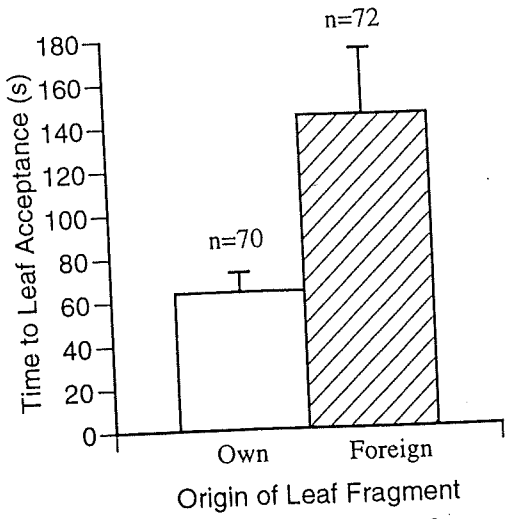

Fig. 1. Time to *A. colombica* leaf acceptance (mean ± 1 SE) for intra- and inter-colony leaf fragments from the same tree species at Corcovado National Park, Costa Rica.

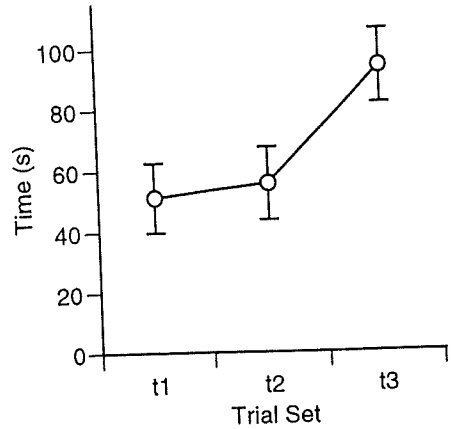

Fig. 2. Time to leaf fragment acceptance (mean ± 1 SE) by *A. colombica* for three sequential sets of intra-colony introductions at Corcovado National Park, Costa Rica.

DISCUSSION

In this experiment, since we controlled for plant species, the *A. colombica* preference for leaf fragments from their own colony is most reasonably attributed to ants marking fragments with a colony-specific recognition signal, probably a chemical pheromone. The trend of increasing time to acceptance of intra-colony fragments with later trial runs suggests that a pheromone could have dissapated after a longer waiting period. This pheromone may not serve as an offensive inter-colony signal, since we observed no ant efforts to remove foreign leaf fragments from the trail.

If the pheromone is only an intra-colony signal, it could serve in the recognition of leaf fragments. Whether this is a specific leaf-marking pheromone or one that is used to mark colony trails and that residual chemicals are left on carried fragments remains to be determined. Either way, it appears that members of a colony recognize their own leaf fragments as compared to those from another colony, even when both are harvesting the same tree species. A future study could reintroduce washed and non-washed leaf fragments to a single trail to look for more evidence of a pheromone marking of leaf fragments.

LITERATURE CITED

Stevens, G. C. 1983. *Atta cephalotes*. PP. 688-691 *in* D. H. Janzen editor. Costa Rican Natural History. Chicago: The University of Chicago Press.

Glennon, M. J., C. D. Carson, V. R. Levesque, M. A. Ginsburg, and C. D. Wray. 1995. Selection of target versus non-target leaves by leaf-cutter ants (*Atta cephalotes*). Pp. 74-75 *in* C. D. Wray and N. D. Pouliot, editors. Dartmouth Studies in Tropical Ecology. Hanover, New Hampshire, USA.