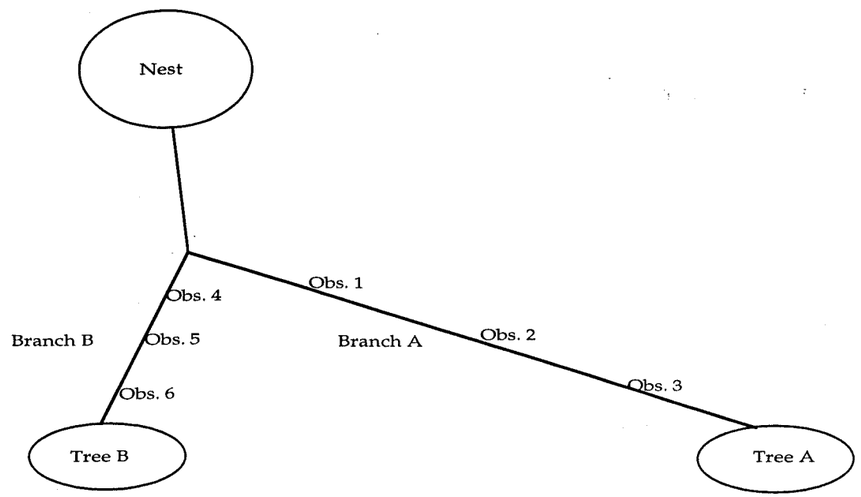

FIG. 1 Diagram showing testing site of a leaf-cutter ant colony in Corcovado National Park, Costa Rica. Obs. = observation points. Branch A was 24 m long, while branch B was 12m long. Distance from the branch junction to nest site was 80m.

Table 1: Time(mean + 1 S.E.) taken by Atta cephalotes to initiate contact with a leaf from its own trail and a more distant branch trail. N= 30, based on 10 pairs of A and B leaves placed at each of three evenly spaced locations on trails A and B.

Trail type	Time to initiate contact for A leaves ± S.E.	Time to initiate contact for B leaves ± S. E.	tpaired	df	P
Trail A	43.3 + 8.5	73.3 + 11.2	2.11	29	0.044
Trail B	30.0 + 5.5	61.3 + 10.3	2.61	29	0.014

Table 2: Time (mean + 1 S.E.)taken by Atta cephalotes to begin carrying an introduced leaf in the direction other leaves were being carried ("pick up time"). N=30, based on 10 pairs of A and B leaves placed at each of three evenly spaced locations on trails A and B.

Trail type	Pick-up time for A leaves (s) + 1 S.E.	Pick-up time for B leaves (s) + 1 S.E.	tpaired	df	P
Trail A	78.0 + 10.7	117.3 + 12.4	2.71	29	0.011
Trail B	60.0 + 8.1	188.7 + 12.7	3.81	29	0.0007

LEAF CUTTER ANT TRAIL COMPOSITION AS A FUNCTION OF RESOURCE REQUIREMENTS

JOSEPH W. GILBERTSON, BRETT T. JENSEN, ADAM J. SIEGEL, AND JAMES P. ZAK

Abstract. We studied the means by which the leaf cutting ants (*Atta Cephalotes*) increase total input of foraged material into the colony. We hypothesized that an increase in the rate of input of plant material into the colony is achieved by an increase in the number of trails extending from the colony. Next, we hypothesized that an increase in the rate of input of plant material is also achieved by increasing the total length of the trails extending from the colony. Our first hypothesis was refuted; there is no significant positive correlation between the number of trails from the colony and input rate. Our second hypothesis was supported; as the total length of a trail increased, there was a significant increase in the rate of input of plant material. In addition, as the plant material input rate increases, ants not only lengthen their trails, but they increase the extent of branching and consequently, the number of trees per trail. We suggest that the ants forage further from the colony as their demand for plant matter increases in order to sustain the surrounding resources.

Key Words: Atta cephalotes, *foraging*

INTRODUCTION

Leaf-cutting ants (*Atta cephalotes*) are highly social insects who harvest leaf fragments for their fungal gardens. The leaf fragments are digested by the fungus, and the ants consume the fungal hyphae as food. The colonies of *Atta cephalotes* contain up to five million workers (Stevens 1983). Further, it was shown that colony populations reach their maximum number within three or four years after colonization (Stevens 1983). Accompanying the large numbers of ants and their rapid colony growth rate are high energetic costs. Assuming that the amount of energy available to the ants is related to the number of leaf fragments brought in by the ants, we examined how leaf-cutting ants achieve increased input of leaf fragments.

Based on field observations, we hypothesized that ant colonies could achieve a higher input rate of leaves by having a higher number of total trails radiating from the central colony. With many trails off the central colony, the ants would be able to disperse to more foraging sites. Alternatively, the input rate could be increased by having a greater total trail length. By the latter means, the ants would be able to access a higher number of trees and therefore a greater potential foraging area.

METHODS

On the morning of 2 February, 1997 at the Sirena Biological Station in Corcovada National Park, we sampled a total of five colonies of leaf cutter ants along Senderos Pavo and Espaveles. We measured the number and total length of trails, including branches from the 'trunk trail', extending from the colony center using a 50 meter drag line. We then counted the total number of branches per trail and determined the foraging site (destination) of each trail, counting total number of trees foraged per trail.

In order to assess the resource needs of individual colonies, we measured the plant material being brought back to the colony per minute. Therefore, data reported as total input of leaf particles per minute is being used as an index of ant resource requirements. This method of approximating A. cephalotes resource demands has been utilized in previous studies (Hubble & Rockwood,1987). These rates were recorded by observing a fixed point at the entrance of the trail near the colony. Rate recordings were repeated five times and averaged and were all taken within a half hour time span to avoid variability and to eliminate the counfounding factor of daily rate changes. Items recorded as plant input included all plant, flower, and leaf materials. The data collected was then analyzed using Student's t-test.

Results

We found no positive correlation between the average total leaf particle input per leafcutter ant colony and the total number of trails emanating from the colony (r2=0.0186, df=3, P=0.8265).

However, we did find a significant positive correlation between the total length of trails (m) and the total input of leaf particles/minute/trail (r2=0.5361, df=8, P=0.0161, Fig. 1), the total number of trail branches and the total input of leaf particles/minute/trail (r2=0.8506, df=8, P=0.0001, Fig. 2), and the total number of trees foraged upon by the leafcutters and the total input of leaf particles/minute/trail (r2=0.8726, df=8, P=0.0001, Fig. 3).

We also found a significant positive correlation between the total length of trails (m) and the number of trees utilized by the leafcutters (r2=0.4503, df=8, P=0.0336) as well as a positive correlation between the number of trail branches and the number of trees foraged upon (r2=0.8877, df=8, P=0.0000).

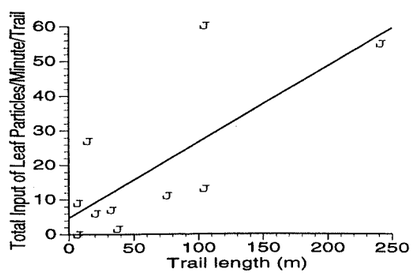

Fig.1. Relationship between the total input of leaf particles per minute and the total length of trails as measured in 5 leaf-cutter ant colonies (r^2=.5361, P=.0161).

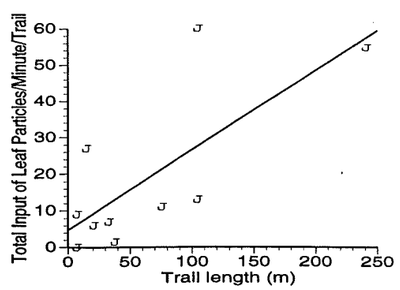

Fig.1. Relationship between the total input of leaf particles per minute and the total length of trails as measured in 5 leaf-cutter ant colonies (r^2=.5361, P=.0161).

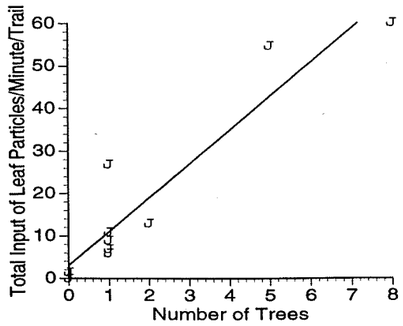

Fig. 3. Relationship between the total input of leaf particles per minute per trail and the total number of trees foraged upon by leaf-cutter ants in 5 colonies (r^2=.8726, P=.0001).

Discussion

Our results indicate that an increase in colony resource needs is accomplished by an overall increase in trail length, rather than by an increase in the number of main trails emanating from the nest. Furthermore, we show that increased trail length is accompanied by an increase in the number of trail branches, which results in access to a greater number of trees in which to forage. This pattern of trail extension and branching may result in ants foraging in preferred tree species far from the nest, even when some individuals of these same species may be closer to the colony. Rockwood and Hubbell (1987) noted that the closest desired tree species are not always those being attacked. They estimated that the ants could improve their foraging efficiency by up to 40% if they were utilizing preferred trees closest to the nest. Explaining this foraging behavior in terms of optimal foraging theory is somewhat challenging, and Hubbell and Rockwood cite Cherette (1968) in providing five possible explanations for this apparent inefficient foraging. Cherette concluded that nearby preferred trees are not exploited because leaf-cutting ants pursue "a conservational harvesting strategy."

An alternative, and to us more reasonable, explanation for why leaf-cutter ants select trees far from the colony is because these trees are in close proximity to pre-established trunk trails or trail branches. It has been found that a leaf-carrying ant can travel 4-10 times faster on an established trail compared to no trail (Rockwood and

Hubbell, 1987). The costs to the colony of attacking preferred trees far from the nest, yet near a pre-existing trail is presumably less than the cost of constructing and maintaining new trails closer to preferred trees. If *A. cephalotes* foraging behavior is an example of sustainable harvesting methods, it is a fortuitive secondary effect.

Literature Cited

Rockwood, L.L.. Host-plant selection, diet diversity, and optimal foraging in a tropical leafcutting ant. Oecologia (Berlin) 74: 55-61 1987

Cherrett, JM. The foraging behavior of *Atta cephalotes*, foraging pattern and plant species attacked in tropical rain forest. J. Anim. Ecol. 41:647-660 1968

Mannan, A.L., Taliaferro, H.E., Little, M.E. Annual Harvest Rates of Leaf Cutter Ants. Dartmouth Studies in Tropical Ecology. Hanover, N.H. 1996. pp.78-79

Stevens, G. C. 1983. *Atta Cephalotes*. In Costa Rican Natural History, ed. D. H. Janzen, 688-690. Chicago: University of Chicago Press.