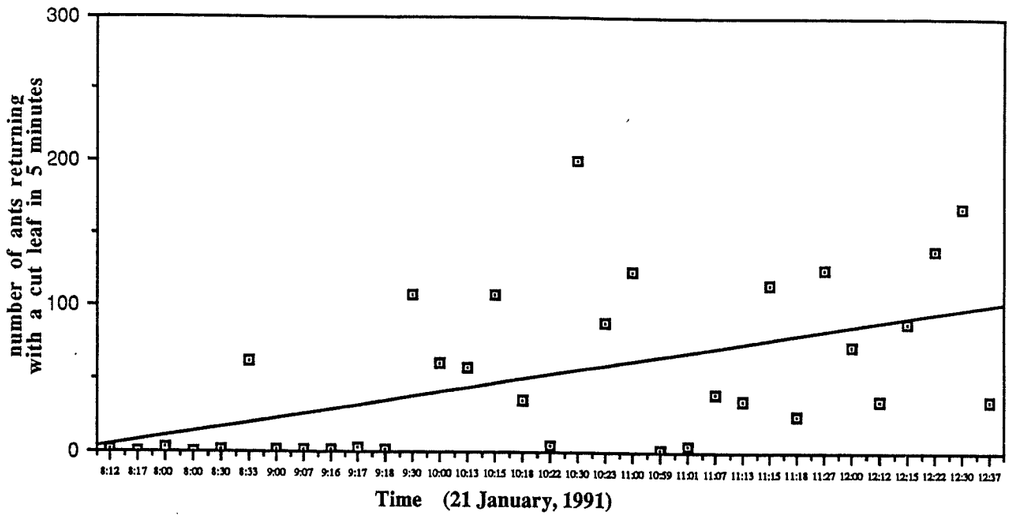
Figure 3 Effect of time of day on leaf cutter ant leaf cutting activity, as observed 0800-1230 on Janurary 21, 1991, Covcovado, Costa Rica.



Literature Cited

Howard, J.J. 1988. Leafcutting ant diet selection relative influence of leaf chemistry and physical features. Ecology 69: 250-260.

LEAFCUTTER ANT (ATTA CEPHALOTES) TREE SELECTION

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Abstract (A.B., G.K., G.G.)

We investigated the selection of trees for harvest by leaf-cutter ants (Atta cephalotes) at Corcovado National Park, Costa Rica. We found that the ants harvested balsa trees (Ochroma lagopus) in a proportion greater than their representation in the overall tree population in the area. Additionally, there were two unexploited balsas closer to the nest than the balsas being harvested. Although the ants did not use all of the balsas within their range, we found that they were harvesting about 60% of them.

Introduction (A.B., G.K.)

We observed that some leaf-cutter ants (Atta cephalotes) traveled great distances to harvest a tree although there were many trees closer to their nest. Furthermore, it appeared that many of the trees the ants were harvesting were balsas (Ochroma lagopus), while these trees represented only a small fraction of all the trees in the area.

Our first hypothesis stated that the ants prefer balsa trees to the other tree species in the area. This preference could explain why some ants traveled what seemed to be unnecessarily long distances to harvest leaves. If leaf-cutters prefer balsa trees, and are willing to travel long distances to harvest them, one might expect that the colony would resort to harvesting distant trees only after they exhausted the balsa resources closer to their nest. We thought that the ants lack the ability to conduct a systematic search of their territory and will therefore miss many of the closer balsas. Our second hypothesis stated that there are unexploited balsa trees closer to the nest than some exploited individuals. The presence of these unexploited balsa trees would suggest considerable inefficiency in the colony's foraging system.

Methods (G.G.)

The leaf-cutter ant nest we studied was located in Corcovado National Park on the southern bank of the Rio Camaronal approximately 40 meters upstream from the junction of the river and the Camaronal trail. We counted the number of balsa and non-balsa trees within the study area. From the nest we traced as many emerging ant columns and any branches of the trail as we could find to their endpoints (trees from which they were cutting leaves). We noted whether the trees targeted by the column were balsa. We

measured the travel distance from nest to occupied tree by pacing standardized our paces to 0.75 meters.

We defined the maximum travel distance of the ants by estimating the distance traveled from the nest to the furthest tree used by the ant colony. We censused the forest area encompassed in this range for other balsa trees. We calculated the distance from the nest to all unoccupied balsa trees by adding the distance from the base of an unexploited tree to the nearest ant colony to the distance from that points of the column to the nest.

In one case we found an aggregation of eleven balsas within a five square meter area. The canopies of these trees were interwoven. Although only a portion of the trees actually had leaf-cutters on them, the entire group was recorded as a single exploited unit due to the proximity of the individuals.

We conduced a Mann-Whitney U-test to compare distances between the nest and occupied balsa trees to distances from the nest to occupied non-balsa trees. We plotted all balsa and any other occupied trees on a map (See Fig. 1).

Results (G.G.)

We found that 38% (3 of 8) of leaf-cutter ant-occupied trees in the study area were balsa trees. Of all the balsa trees in the area, 60% (3 of 5) were being harvested by leaf-cutter ants. The mean distance from the nest to harvested balsa trees was significantly greater than the mean distance to harvested non-balsa trees ($p < 0.05$, $n_1 = 3$, $n_2 = 5$ MWU = 15 Crit. Value = 14).

Discussion (T.G., V.V.)

We supported both of our hypotheses in this experiment. We found that leaf-cutter ants harvest balsa trees in a proportion greater than the balsa's representation in the environment. It has been demonstrated that ants harvest more than one tree species, but concentrate on one preferred species (Rockwood and Hubbell, 1987). It appears that balsa is the preferred species for this colony (Table 1). Balsa's pioneer growth strategy may contribute to its attractiveness. Because it devotes so much of its energy to rapid growth, the balsa may produce the costly secondary compounds that deter herbivores. Additionally, the balsa's rapid growth results in high leaf turnover, making it more suitable for long-term herbivory, because it can grow new leaves quickly to replace destroyed ones. These two factors may contribute to the ants' preference for balsa leaves.

Also, in support of Rockwood and Hubbell's study, we found that ants were more selective at further distances from the nest than non-balsas. It would seem worthwhile for the ants to forage far from the nest only if they procure a more productive resource.

Preliminary observations led us to formulate our second hypothesis, that there are unexploited balsas closer to the nest than some exploited balsa individuals. An optimally foraging colony would minimize the energy it expends, in this case in the form of the distance traveled in foraging. It appears from these data, then, that the ants are not foraging optimally. Perhaps this wasted energy does not affect their fitness because they are already operating above a subsistence level, and thus this colony is not foraging optimally.

Though we found that the ants are in fact missing some of the nearer trees, we also found that they are utilizing 60% of the balsas in their area. It is possible that the ants could discover and harvest 60% of the balsas but fewer other species by chance alone, but considering the low abundance of balsas in the area, this seems improbable.

How do these ants, then, find this sparse resource?

Perhaps natural selection is a driving force in tree selection. If trails from individual trees have distinct fungal gardens, then it is possible that the ants using the most suitable resource would have the most successful gardens and therefore the highest fitness. These successful gardens would outcompete gardens fed leaves from less productive trees. Over time, only gardens from trails using the most productive resources will be left. This theory seems improbably, though, because we observed that many trails merge before they enter the nest. It is possible that the trails diverge again once inside the nest, but it seems unlikely. This could be tested on a lab colony where it is possible to observe the fungal gardens directly. By marking ants and leaves for each trail, one could record whether the ants always use one trail and whether the leaves are brought to distinct fungal gardens.

A more probable explanation is that scout ants sample trees to find leaf sources suitable for their gardens. When they find a tree that meets their requirements, they recruit workers to harvest the tree. This idea could be tested by offering different species of leaves to a lab colony. To support this theory, the ants would find a suitable leaf by trial and error and begin to harvest it regularly.

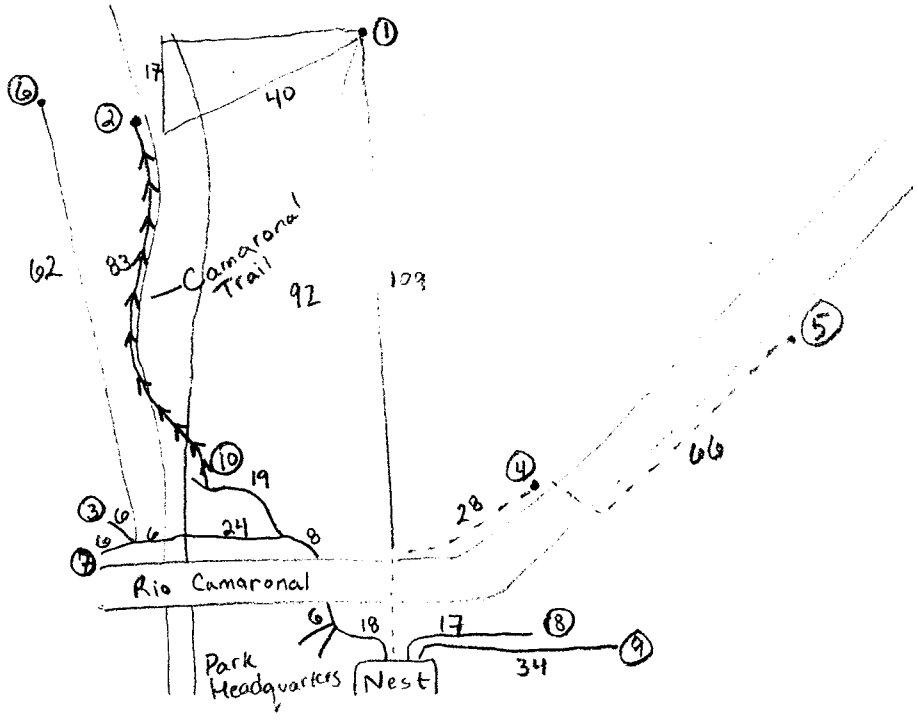
Another probable explanation involves chemical cues from the tree. It may be that the ants are differentially attracted by airborne chemical cues emitted by suitable trees. This initial attraction could be followed by additional recruitment from the nest. This could be tested using the same set up as the previous test. To support this explanation, however, the ants would have to visit only the suitable leaf species.

Though our colony does not seem to be foraging optimally, it still appears to be very effective. The ants were far more successful at locating the balsa trees than we expected, suggesting that the mechanisms employed for leaf harvesting are more sophisticated than we originally thought.

Table 1: Distances of harvested and non-harvested trees from nest.

Tree	Balsa/Non-balsa	Dist. from Nest	Occupied?
1	B	72	No
2	B	81	Yes
3	B	40	Yes
4	B	13	No
5	B	66	Yes
6	NB	54	Yes
7	NB	32	Yes
8	NB	11	Yes
9	NB	22	Yes
10	NB	38	Yes

Figure 1: Map of sampled area.



Literature Cited

Rockwood, L.L. and Hubbell, S.P.; 1987. Host-plant selection, diet diversity, and optimal foraging in a tropical leaf-cutting ant; Oecologia.