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Foraging by Bucket-Brigade in Leaf-Cutter Ants

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ABSTRACT

Atta cephalotes foragers transfer leaf fragments to "carrier" ants at junctions of new branch trails and the established trail. A more pronounced specialization into "harvesters" and "carriers" is exhibited by *A. sexdens rubropilosa* in which smaller ants harvesting in the tops of tall trees drop material to the ground where larger workers collect it.

COLUMNS OF LEAF-CUTTER ANTS (Myrmeciinae: Attini), carrying leaf and flower fragments along trails to the nest, are a common sight in the neotropics. Workers cut fragments from a variety of trees, shrubs, and crop plants, and culture a fungus on them, the specialized hyphae of which serve as their sole food source (Weber 1966, Hubbell and Rockwood 1980). As in many other eusocial insects, including bees, termites, and especially ants, a trail pheromone helps to guide the workers between nest and food source (Wilson 1971, Moser and Blum 1963).

We describe here a novel two-stage relay process in foraging leaf-cutter ants, involving a transfer of material from one ant to another. This relay process serves to increase the speed of new food-source utilization, and to increase the efficiency of exploitation of established food sources. Foraging efficiency is a significant problem for leaf-cutters which must often travel long distances, sometimes over 100 meters, to harvest leaves of tree species best able to support fungus growth (Cherrett 1968, Hubbell and Rockwood 1980).

RELAY COOPERATION DURING NEW TRAIL FORMATION

We studied the foraging of *Atta cephalotes* L. in a tropical dry forest in Santa Rosa National Park, Guanacaste Province, Costa Rica (lat. 10° 50', long. 85° 37'). Trails from the nest lead to particular trees or shrubs or to small, oval, ground-foraging areas where ants forage solitarily. The ants may later establish a trail leading to a particularly acceptable plant within the oval. The discoverer ant lays a pheromone trail connecting the new source to the main trail, and within an hour a branch is established.

Laden *A. cephalotes* normally carry their loads all the way into the nest. The first ants to visit a new

source, however, carry their loads only as far as the main trail, where they drop them, or antennate other ants and transfer their load to them. These "carriers" then carry the fragments to the nest.

To learn more about branch trail formation and about the transfer of information regarding the locations of new, high-quality food sources to other workers, we performed experiments in October and November 1975. In these experiments, bread crumbs or leaves of *Bursera simaruba*, a preferred tree species, were placed in an oval ground-foraging area 1 meter from an established trail. Figure 1 shows that in one such experiment a trail to the bread crumbs (black circle) developed as a branch off the main trail (heavy line), and figure 1A traces the tortuous paths of the first two crumb-bearing ants back to the main trail. Both touched their gasters repeatedly to the ground, a behavior which indicates pheromone deposition (Moser and Blum 1963).

Typically such individual trails gradually consolidate as more ants visit the food and lay pheromone. Figure 1B shows the paths of three ants returning to the main trail 40 minutes after discovering the bread. The trail has become narrow and points directly to the nest (not shown in the figure).

A decline in the percentage of ants dropping or transferring their loads upon reaching the main trail was always found to accompany trail consolidation. Table 1 shows how, in another experiment, this percentage declined over a 50-minute period subsequent to the discovery of bread. In this experiment, 12 percent of the drops and transfers occurred along the way between the bread and the main trail, 83 percent occurred along the first meter of the main trail, 5 percent occurred along the second meter of the main trail, and none in the last two meters to the nest.

This typical localization of dropping or transfer-

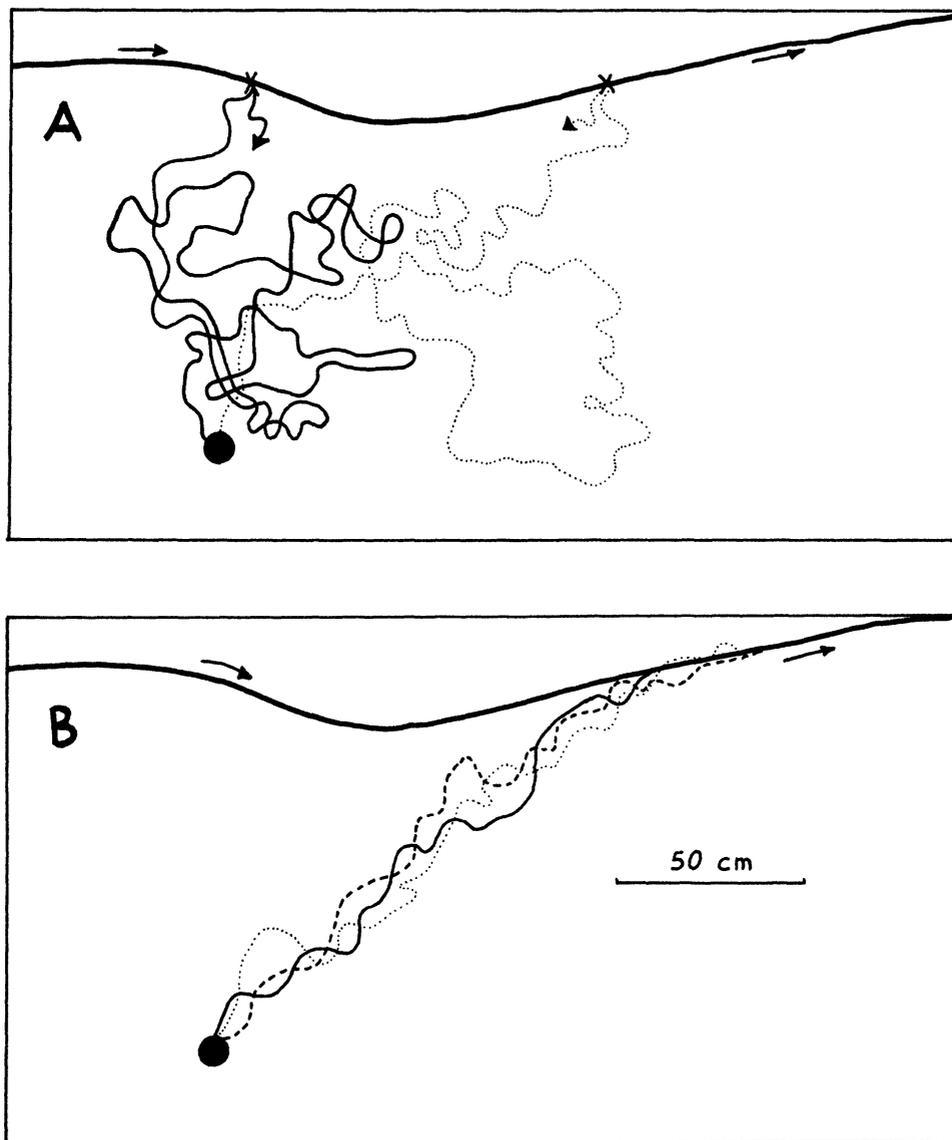


FIGURE 1. A. Paths back to the main trail (heavy line) of the first two ants to discover the new food source (black circle). The x's mark the sites where the ants dropped or transferred their loads. B. Paths of three recruits 40 minutes after discovery of the food. These ants continued straight to the nest (to the right) with their loads.

ring the bread led us to hypothesize that some abruptly encountered feature of the main trail, such as familiar landmarks, trail pheromone, or heavy ant traffic, stimulates these behaviors. As the new branch trail becomes more like the main trail, dropping and transferring is less often stimulated.

Although main trails sometimes appear as distinct grooves worn in the ground, this characteristic was not a distinguishing feature in the experimental site, so we began exploring the other possibilities.

We determined in another experiment in May

1976 that sudden encountering of trail pheromone by itself could produce dropping or transferring behavior. Two 46 x 61 cm cardboard rectangles were nailed to the ground for 30 hours, the "control cardboard" at a site where ants were not foraging, and the "trail cardboard" on an active trail, the long axis parallel to the trail. Ants marked the trail cardboard. The next evening each cardboard was laid between a pile of bread crumbs in an oval ground-foraging area and a main trail one meter away. Care was taken that the two sites where the cardboards were laid were equiv-

alent in terms of ground cover, slope, and traffic of the main trail; at neither site had the ants previously been exposed to bread. Each cardboard was oriented with its long axis parallel to the main trail, so that the pheromone trail on the trail cardboard lay perpendicular to the most direct path from crumbs to main trail.

TABLE 1. Percentage of ants dropping or transferring loads in each of five 10-minute periods after discovery of the food.

10-minute period	% Dropping or transferring load	Total number of ants
1	88.9	18
2	66.7	18
3	68.0	25
4	38.0	21
5	25.0	24

None of the discoverer ants crossing the control cardboard in the first 15 minutes dropped their loads until they reached the main trail; stray ants without loads took erratic paths across the cardboard, not appearing to detect any trail. In contrast, all discoverer ants crossing the trail cardboard in the first 15 minutes dropped their loads at the center band where ants had walked previously for 30 hours; two stray ants without loads appeared to pick up the trail on the cardboard and followed it to the edge.

That a discoverer ant travels only as far as the main trail before returning for another load means the ant can find its way back to the new source while its odor trail and memory are freshest. If discoverers did travel all the way to the nest with their first load on a trail of typical length (30 meters), the round trip would take approximately an hour, according to calculations based on Coyne and Schneider (1974) and Weber (1972). During this time learning of the new route between trail and food would not be reinforced, and the volatile component of the trail pheromone would have evaporated (Moser and Silverstein 1967), making it more difficult for the ant to find the food again. Even worse, *Atta cephalotes* in our study area forages up to 120 m from the nest, in which case the round trip would take four hours.

The dropping and transferring behavior also allows a quicker buildup of ants at the new source. Rapidity of occupation *per se*, however, is not critical for these ants. Because their food resources are not transient, and because colonies are hyperdispersed and have largely nonoverlapping foraging ranges (Rockwood 1973, Hubbell and Rockwood 1980), a defensive build-up of workers at good food sources is not needed.

LOAD DROPPING FROM TREES

A two-stage foraging method may also be used when *Atta* harvest from tree crowns. The *Atta cephalotes* in Costa Rica sometimes drop leaf fragments to the trail under the tree, where they may be picked up and carried to the nest. The habit of dropping material from trees is much more pronounced in *Atta sexdens rubropilosa* Forel inhabiting a second-growth *Eucalyptus* woodland in Paraguay (cf. Fowler and Robinson 1979). Just before the general exodus of workers, about 0.1-0.5 percent of the total foragers (the "harvesters") climb trees and begin severing leaves, leaflets, leaf clusters, and small branches. The leaf "carriers" emerge half an hour later and begin cutting up the dropped vegetation and taking it to the nest. Nearly all harvesters descend the tree empty; during 40 full days of observation over a 10-month period only two ants were seen carrying a fragment down the trunk. The leaf-carriers of this species are significantly heavier than the harvesters which climb trees (22.0 vs. 17.5 mg in July 1975, $p < 0.02$; 20.7 vs. 14.1 mg in October 1975, $p < 0.01$). Similar load dropping from trees and specialization into harvesters and carriers has been observed in *A. saltensis* (Daguerre 1945).

The pick-up efficiency of *A. sexdens rubropilosa* foragers in the second-growth *Eucalyptus* woodland was determined by comparing the number of dropped fragments left in 44 control trays to which the carrier ants had access, to the number of fragments left in 44 experimental trays filled with water, which deterred the ants. The aluminum trays were set 3 m apart in a grid under the trees where one colony was foraging. After foraging had ceased for the day, fragments from each tray were dried and weighed. The controls contained a mean of 0.21 g per tray, while the trays to which the ants were denied access contained a mean of 0.43 g per tray ($p < 0.05$). Thus the pick-up efficiency was 53 percent.

Dropping the fragments saves a trip down and up the trunk. The caloric costs of the one-forager system can be compared with those of the two-forager "harvester/carrier" system, as follows: If T is the cost of a round trip down and up a tree, C is the cutting cost per fragment, and R is the cost of a round trip to a tree, then the one-forager cost for n fragments is given by $nT + nC + nR$, and the group cost for n fragments, assuming one harvester and one carrier, is given by $T + (n + m)C + (n + 1)R$. Here m additional fragments are cut for each n found and carried back to the nest. The above assumes the cutter does not carry back a fragment.

If we assume n is large, so that $nR \approx (n + 1)R$,

then the two-forager system is less costly than the one-forager system when $n(T + C) > T + (n + m)C$ or when $\frac{C}{T} < \frac{n-1}{m} \approx \frac{n}{m}$.

Thus it is better to use two-stage foraging with harvesters and carriers when the ratio of the cost of cutting a fragment to that of climbing a tree is less than the ratio of the number of fragments cut and carried to the nest to the number of fragments cut but not found. The data for *A. sexdens rubropilosa* indicate that n/m is .22g/.21g or about 1, that is, about half of all cut fragments are found and carried back to the nest. This finding means that if cutting a frag-

ment is less costly than climbing down and up a tree, it pays the colony to forage in two stages.

Extra work is involved in the cut through the stem when leaf clusters or small branches are dropped, but with each such unit of leafy material dropped, dozens of trips down and up the tree are saved, a distance, in some tropical tree species, of 25 meters or more. This practice represents a potentially large saving to the colony in retrieval costs of harvest.

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