

Optimality, variability, and energy efficiency in leaf-cutter ant behavior

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Abstract: We examined the behavior of leaf-cutter ants that were forced to drop their leaves. A model proposed by Salant et al. (2003) estimated and ranked the energy cost per leaf for various combinations of responses that ants in a colony exhibit after leaf-dropping events. Salant et al. (2003) found that ants do not always exhibit the responses that would seem to benefit the colony most. However, if the rate of leaf dropping were greater than the model assumes, the behaviors would no longer have fixed energy expenditure rankings, but would vary depending on the circumstances of the leaf drop and subsequent ant responses. By measuring the change in proportion of leaf-carrying ants over a segment of trail, we confirmed that substantial leaf drop occurs under natural conditions. This implies that the observed responses do not have fixed rankings, which explains the occurrence of "suboptimal" behaviors.

Key Words: *Atta cephalotes*, energy efficiency, eusocial insects

INTRODUCTION

Ants are widely considered to be at the pinnacle of eusocial evolution. Ants in the colony cooperate in brood care, nest defense, and food gathering. Leaf cutting ants go one step further, orchestrating a work force of up to several million to gather food for the obligate mutualistic fungus they cultivate and harvest for sustenance. To maintain such a system and to be as successful as the density of leaf cutter colonies in certain locales implies, one would expect that their behavior would be highly efficient. Any systematic waste of energy by an individual, multiplied by the millions of sisters who share her genes, might result in colony failure.

Salant et al. (2003) developed an energy use model that proposes fixed rankings for the energy costs per leaf brought back to the nest. The model was based on the observed responses of ants after individuals were forced to drop their leaves. The responses are outlined in Table 1. Responses A and B had equal (and lowest) cost, while responses C, D, and E had higher energy costs. This model predicts that ants should exhibit responses A and B 50% of the time each, but should not exhibit responses C, D, or E. Salant et al. (2003) observed these sub-optimal behaviors but were unable to explain why they occurred.

Their model assumes that only one set of behaviors leads to each observed response type. However, several behavioral combinations could lead to each response, which calls into question the model's proposition of fixed ranks. Upon careful examination, it became clear that the fixed rankings in the original model are in fact based on the assumption that the behavior of interest (dropping leaves) is a vanishingly rare phenomenon.

If the rate of dropping leaves were more common than the model assumes, the behaviors would no longer have fixed energy rankings, but would vary depending on the conditions of the leaf drop and subsequent ant responses. Some ants that drop a leaf may fail to recover it, but pick up another dropped leaf and continue towards the nest. Furthermore, an unladen ant picking up a leaf may have just dropped a leaf and may either be en route to the nest or to the tree to collect another leaf. These possibilities are not considered in the original model. The energetic consequences of these behavioral combinations vary depending on what fraction of the ants' journey involves carrying a leaf, and where on the trail leaves are dropped and retrieved. This variability means that the energy rankings of the possible outcomes (A, B, C, D and E; Table 1) are not fixed. The stochastic element, introduced by the range of circumstances under-

lying any of the outcomes, causes overlap in the expected energy costs of behaviors A-E (Fig. 1). We hypothesize that under natural conditions, leaves are dropped frequently. If this is the case, there will be overlap in the rankings for energy cost per leaf resulting from the inherent variability in the transit time and distance between when a leaf is dropped and when it is picked up.

We also examined whether time of day or trail activity level influences the rate that leaves are dropped and thus the overlap in energy costs. We predicted that when trails are busier, the overlap in energy costs would be greater because the rate of dropping would increase. We predicted that the overlap would be greater in the afternoon than in the morning on the same trail because ants are under greater heat stress and may drop leaves more frequently.

METHODS

We examined the behavior of foraging leaf-cutter ants crossing foot trails near Estación Sirena, Corcovado National Park, Costa Rica on 4-6 January 2003. We followed the methods outlined in Salant et al. (2003) to observe the responses of ants to the removal of their leaf loads. We haphazardly selected ants returning to the nest with leaf fragments and separated them from their leaves. We placed the ant and leaf next to

each other in the center of the trail (point S) and observed the response of the ant and the recovery of the leaf. The responses were sorted into five categories (Table 1).

To test our assumption that ants drop leaves at relatively high rates in natural

Observed Response Ranking of Energy Cost per leaf

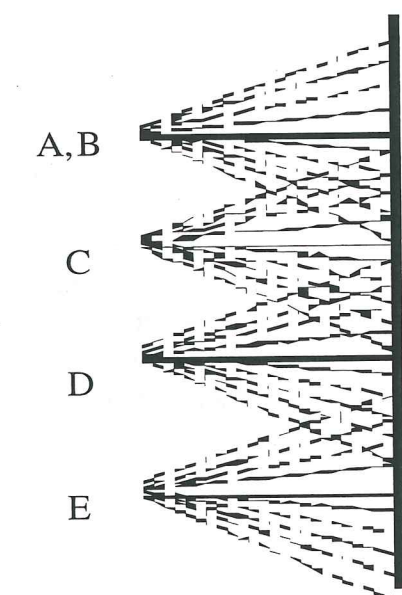


FIG. 1. Rankings for the energy costs per leaf of the five observed response types in Table 1 for leaf cutter ants (*Atta cephalotes*) in Corcovado National Park, Costa Rica. Dark lines represent the fixed rankings that arise from the original model (Salant et al. 2003). Dashed lines represent the range of possible overlap in the efficiencies of responses when the frequency of dropping leaves increases.

TABLE 1. (From Salant et al. 2003) The observed responses of leaf-cutter ants (*Atta cephalotes*) in Corcovado National Park, Costa Rica after separation from their leaves, with formulas for estimated energy cost of each response type. x = the distance from point S to the nest, and y = the distance from point S to the tree. u and l represent energy expended per meter with a load and without a load respectively.

Response	Rank Efficiency	Ant Response	Leaf Fate	Energy cost per leaf
A	1	Ant returns to nest with leaf	Original ant picks up leaf	$(x + y)u + (x + y)l$
B	1	Ant abandons leaf and returns to tree	Another ant from nest retrieves leaf	$(x + y)u + (x + y)l$
C	3	Ant abandons leaf and returns to tree	Another ant from tree retrieves leaf	$(x + 2y)u + (x + y)l$
D	4	Ant abandons leaf and returns to nest	Another ant from nest retrieves leaf	$(3x + y)u + (x + y)l$
E	5	Ant abandons leaf and returns to nest	Another ant from tree retrieves leaf	$(3x + 3y)u + (x + y)l$

conditions, we counted the number of ants returning to the nest with and without leaves at several points on three trails. Thus, we were able to compare the proportion of ants (travelling toward the nest) that were carrying leaves between points relatively early and relatively late in their return journeys from the food tree.

To determine whether the overlap in energy cost per leaf (of the behavioral outcomes in Table 1) changed with time of day, we recorded ant responses on two trails from two separate colonies in the morning and in the afternoon. We assessed trail activity level by measuring the total number of ants crossing a line perpendicular to the trail in a 2 min interval. We measured activity level five times and between each pair of measurements we observed five ant responses. When ant activity was very high, we used 30 s intervals to measure activity and estimated activity in two-minute intervals.

RESULTS

The proportion of ants carrying leaves back to the nest changed over short intervals on the trail. On the first trail, we found that over 25% of the trail, the proportion of ants carrying leaves back dropped by 20% ($t = -3.94$, $df = 8$, $P < 0.01$). On another trail the net change over 10% of the trail was a 15% loss ($t = -2.25$, $df = 8$, $P = 0.05$), but on a similar segment farther from the nest, the proportion rose by over 20% as the ants neared the nest ($t = 4.51$, $df = 8$, $P < 0.01$). Ants on a third trail lost 10% of their leaves over 20% of the trail length, but this difference was not significant ($t = 0.99$, $df = 8$, $P = 0.35$).

There was no difference in the evenness of behavioral response frequencies (A-E; Table 1) on trails tested in the morning versus the same trails tested after noon (paired- $t = 3.56$, $df = 1$, $P = 0.09$). Similarly, there was no difference in the evenness of

response frequencies on high versus low activity trails ($t = 0.02$, $df = 2$, $P = 0.99$).

DISCUSSION

Significant net loss and gain of leaves can clearly occur over short intervals along a trail, indicating that ants often drop and pick up leaves under natural conditions. These data provide the basis for modifying the model predictions to accommodate the range of possible behaviors that might give rise to the outcomes in Table 1. The range of possible (and plausible) behaviors implies a range of energy costs. Thus, the responses are not fixed in ranking, but overlap to a degree that depends on the frequency with which ants pick up and drop leaves (Fig. 1). This modification of the model is logically required whenever natural leaf drop occurs.

The modified model explains why outcomes C-E should be expected to occur with some frequency in nature. To quantify the expected frequency of these outcomes is more demanding, however, as the expected frequencies will depend on the frequency of leaf drop and the frequency distribution of the alternative component behaviors underlying outcomes A-E (Table 1; see Introduction).

Our predictions that time of day and trail activity would change the rate of leaf drop, and thus alter the frequencies (and consequently the evenness) of the five responses, were not supported. There was a marginally significant trend for increased evenness in the morning versus the afternoon, but we had predicted the opposite, i.e. more leaf drops during the heat of noon and early afternoon, causing greater evenness then.

We also found no relationship between high trail activity and evenness of response types. It seemed reasonable to expect that a greater proportion of ants on a crowded trail would drop leaves, which would alter the frequencies of responses in

Table 1. If they did drop more leaves (which unfortunately we did not test) it did not result in altered frequencies of those outcomes. With the insights gained from this study, it is clear that the frequency of leaf drop should be quantified whenever possible in experiments or observational research on this topic.

Social systems are assumed to have evolved as a mechanism of increasing efficiency through labor division and cooperation. It was therefore surprising when Salant et al. (2003) observed responses in leaf-cutter ants that seemed inefficient (with high-energy costs per leaf brought to the

nest relative to the optimal strategies). However, our findings indicate the ants' behavior may indeed be highly efficient, though it seemed inconsistent in the first analysis.

LITERATURE CITED

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