She's going the distance: Responses of individual leaf-cutter ants to removal of individual leaf loads

Nira L. Salant, Cory A. Donovan, Miguel M. Licona, Benjamin W. Guidi, and Kimberly A. Iwamoto

Abstract: Eusocial insects cooperate in caring for the young of the colony and in provisioning the colony. We examined whether individual leaf-cutter ants (*Atta cephalotes*) forced to drop leaf fragments on the way to the nest respond in such a way that the net gain in energy of the colony (energy efficiency) is maximized. We developed a model to rank the net energy intake resulting from alternative actions the ants might take after an ant loses her leaf. We found that the most frequent responses to losing a leaf were those that did maximize the energy efficiency of the colony. Sub-optimal actions occurred at lower frequencies, and the ranking of those frequencies matched the ranking of their energy efficiencies. Thus, our findings suggest that individual leaf-cutter ants most frequently (but not always) respond to a perturbance in a way that maximizes the net benefit to the colony. Such highly evolved behaviors undoubtedly contribute to the evolutionary success of eusocial insects.

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

Introduction

The success of social groups relies on individuals working together to benefit the community. Leaf-cutter ants (*Atta cephalotes*) are eusocial insects that harvest leaf fragments and cultivate a specialized fungus on which the colony feeds (Stevens 1983). Energy gained by the colony increases with the number of leaf fragments obtained by foraging ants and decreases with the energy expended in foraging efforts.

We hypothesized that leaf-cutter ants behave in a way that maximizes energy efficiency for the colony. Occasionally, an ant returning to the nest may lose her leaf due to interference by other ants or trail obstacles. Her possible responses to this loss vary in their energetic consequences for the colony. The reaction of other ants to this disturbance will also affect the overall energetic consequences. Thus, we predicted that when an individual loses her leaf, she and her sisters would respond in a way that maximizes the net energy gained by the colony.

Methods

We examined the behavior of foraging leaf cutter ants found crossing foot trails around the Sirena Biological Station, Corcovado National Park, Costa Rica. Within one trail, we haphazardly selected ants returning to the nest with leaf fragments. We then separated the leaf from each ant and placed the ant and leaf next to each other in the center of the trail (point S). For five minutes following separation, we observed the response of the ant and the recovery of the leaf. We measured the distance from point S to the nest and to the harvested tree.

The responses (n = 49 ants) were sorted into five categories (Table 1). Using the distance traveled by each ant in each response type to estimate energy expenditure, we developed equations to describe the relative energetic efficiency of each response type (Fig. 1). The equations depend on the following assumptions: equal leaf fragment size, equal ant size, and equal overall energy expenditure for each ant when loaded or unloaded. In fact, all of these factors vary. We relied on large sample sizes so that the mean values of each would approach the mean values for all ants on the trail. We also assumed that an ant going towards the tree returns with a leaf, an ant returning to the nest goes all the way to the nest, and an ant traveling in either direction reaches its expected destination. Based on the equations, we estimated the energy expenditure of the various responses, and used these estimates to rank responses by their energetic efficiency.

Results

We observed five distinct response patterns following the separation of an ant and its leaf (Table 1). The frequencies of the observed responses were inversely related to their energy efficiency, and the rank order of the observed response frequencies paralleled the expected rank order of the response frequencies (Fig. 2). The most efficient responses were most frequently observed, and the less efficient responses were less frequently observed. However, even though the energy efficiencies of strategies A and B are the greatest, we observed alternative behaviors 43% of the time.

Discussion

If our model of energy use in leaf transport were all-encompassing, the results we collected would indicate that the leaf-cutter ants were gathering energy for the colony with submaximal efficiency. When ants lost their leaves, their most frequent response maximized the energy efficiency of the colony, but 43% of the time the response was one that did not maximize the colony's net energy gain.

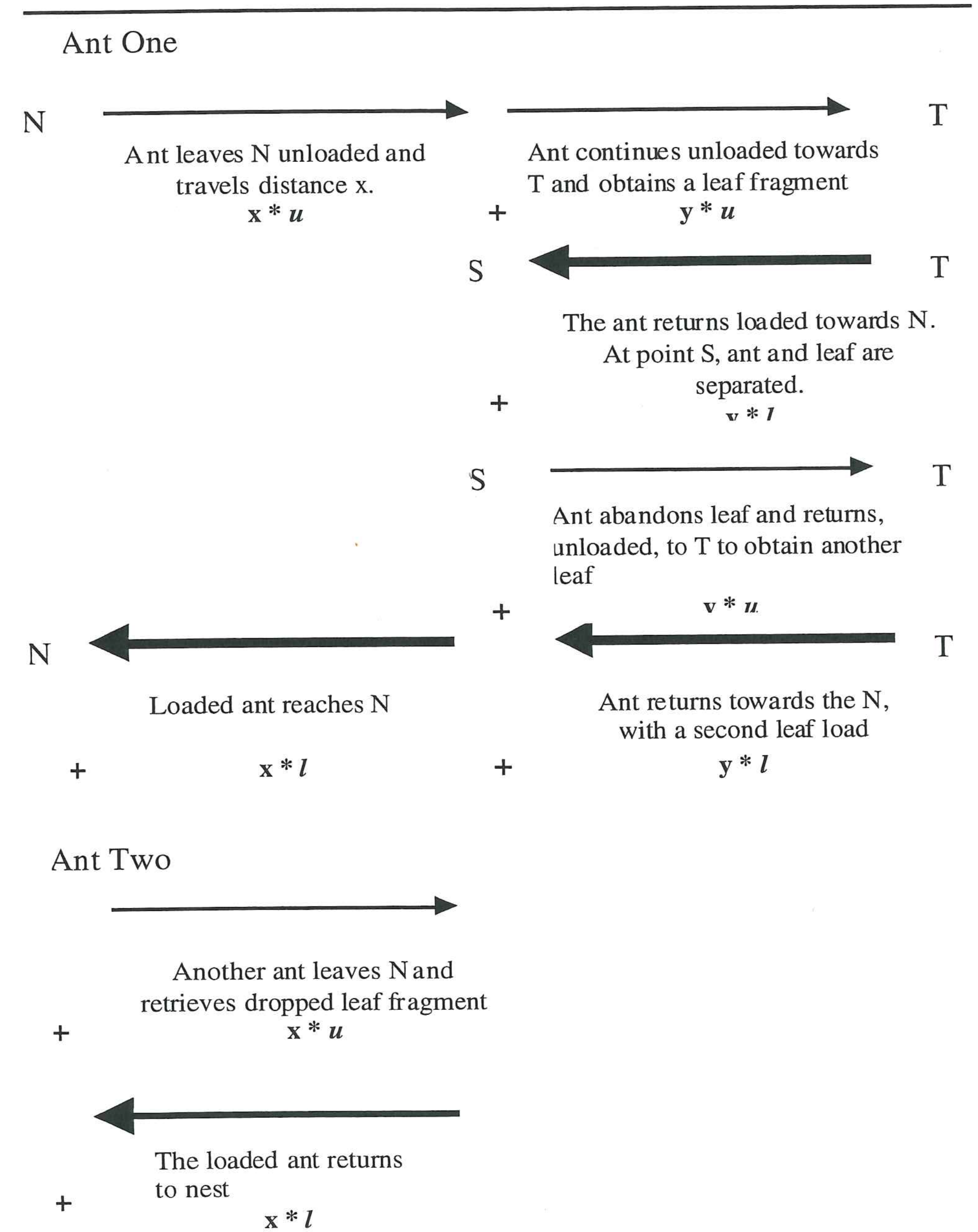
We also found that there was a tendency for individuals to exhibit response A more than response B, although we could not test this statistically. Both responses provided the colony with an equivalent gain in net energy. Individuals may have been "trying" to maximize the net energy gain by the colony through their own actions (an individual who loses her leaf uses less energy retrieving that same leaf than if she returns to the tree to procure another, for the same one-leaf energy gain). This individual cannot "know" whether another ant coming from the nest will pick up the lost leaf (as in response B), yet from the colony's perspective, responses A and B have equal net energy gains.

Individual ants may be semi-autonomous parts of the colonial super-organism and may not always behave in a perfectly efficient manner from the colony's perspective. Therefore, inefficient responses may occur, but at lower frequencies than efficient responses. Our findings indicate that leaf-cutter ants most frequently respond to these perturbations in their foraging in a manner that maximizes the colony's net energy gain. The success of social organisms hinges on the ability of individuals to act in ways that benefit the colony as a whole. Future investigations could test and identify additional factors that influence the behaviors assumed wasteful in our simple model.

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

FIG. 1. Development of the energy cost equation for response B (see Table 1), in which the ant abandons the leaf and returns to the tree, while another ant from the nest retrieves the leaf. Thin lines represent ants moving without a load while thick lines represent ants moving with a load. T represents the source tree, S represents the point where ant and leaf are separated and N represents the nest. *u* is the rate of energy expenditure when an ant is unloaded. *l* is the rate of energy expenditure when an ant is carrying a load. x is the distance between N and S, and y is the distance between T and S.



Energy cost of response B (ant 1 plus ant 2, returning a total of two leaves to the nest)

$= u * (x + y) + u * y + l * y + l * (x + y) + u * x + l * x$

Simplified and expressed in a per-leaf basis, energy cost of response B $= u * (x + y) + l * (x + y)$

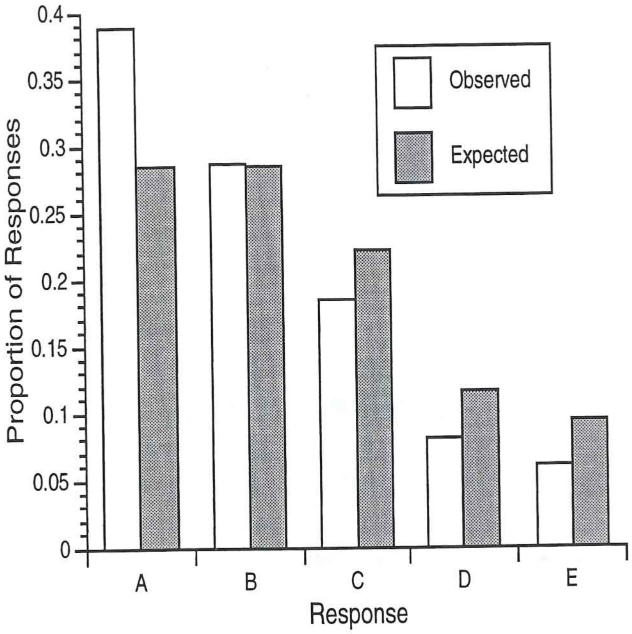


FIG. 2. Comparison of observed and expected proportions of each response category after *Atta cephalotes* ants were separated from their leaves in Corcovado National Park, Costa Rica. See text for definitions of response categories.

Literature Cited

Stevens, G. C. 1983. *Atta cephalotes*. *in* D. H. Janzen ed. Costa Rican Natural History. University of Chicago Press: Chicago, IL. Pp. 688 – 690.