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An investigation of variables that affect foraging velocity in the leaf-cutting ant, *Atta cephalotes* (Formicidae)

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Abstract

Efficient foraging methods are essential to colony survival in the leaf-cutting ant *Atta cephalotes.* One parameter of efficiency is the speed at which laden foragers return to the nest. This study examines the effects of ant size, load size, trail activity, and the number of collisions an ant incurs with other ants or objects on velocity for four *A. cephalotes* colonies in Costa Rica. Multiple linear regression analysis yielded a model which suggests that velocity decreases as loading index and the number of collisions increase. Results of a theoretical analysis using the regression model indicate that the ants select loads smaller than those which maximize the rate of leaf transport to the colony. Possible explanations for sub-optimal load selection are discussed. Additionally, no ants were observed to travel at velocities in the range 1.3-1.5 cm/s. This result differs from those of previous studies and warrants future research.

Introduction

Leaf-cutting ants in the genera *Atta* and *Acromyrmex* display complex eusocial behavior, especially with respect to foraging practices. Perhaps the best-studied leaf-cutting ant is *Atta cephalotes*. *Atta cephalotes* is an ideal organism for investigating foraging behavior. Large colonies can have up to several million workers (Weber 1972 in lit.) which are distributed among four distinct castes. The largest ants comprise the soldier caste, which defends the colony as well as clears and maintains foraging trails. Ants of intermediate size are responsible for excavating the nest and obtaining resources. They venture from the colony, harvest leaf fragments, and return the fragments to the nest. Within the colony, the smallest workers (minima) use the leaf fragments to cultivate a specific type of fungus, which is the sole food source for the ants (Wilson, 1980). Since A. *cephalotes* workers are highly polymorphic and the material that they choose to harvest is diverse (Wetterer 1994), a wide range of ant size and load size effects can be studied. Additionally, the ants forage together on established trails so the effects of trail dynamics can be examined.

The survival of leaf-cutting ant colonies depends upon efficient foraging methods, therefore it is important to understand how efficiency is achieved (Roces and Hölldobler 1994; Burd 2001). One crucial parameter in determining foraging efficiency is the speed at which laden ants return to the colony with leaf fragments (Burd 2000). The effects of ant size and load size on the laden velocity of leaf-cutting ants have been well documented. An inverse relationship between loading index, which expresses fragment size in relation to ant size, and velocity has been reported (Rudolph and Loudon 1986; Shutler and Mullie 1991; Burd 1996; Röschard and Roces 2002). As loading index increases, velocity decreases. Rudolph and Loudon have suggested that there is an optimal range of loading indices that produce maximal leaf transport rates. However, there may be factors other than ant size and load size that play a role in determining velocity. For example, the number of obstacles an ant encounters while transporting a fragment back to the colony has been reported to influence velocity (Burd 2001). Other variables including trail activity and the positioning of the ant on the trail may also directly influence the speed at which laden ants travel, but to my knowledge, these have not been explored in the literature.

The goal of this study was to identify specific variables that affect the laden velocity of individual ants, which in turn has an effect on overall foraging efficiency. Loading index was examined to determine which load sizes maximize the rate of leaf transport. Additionally, the number of obstacles an ant encounters while returning to the colony was examined to assess the importance of efficient traffic flow.

Methods

To determine the effects of loading index and collision frequency on laden ant velocity, I studied the foraging movements of workers from four *A. cephalotes* colonies in Monteverde, Costa Rica from July 13 to August 4, 2002. Three of the colonies were located at La Finca Ecológica, while the fourth was located on a nearby farm. All sites were at approximately 1100 m elevation. The colonies were engaged in daytime foraging, so the data were collected during daylight hours. Three days were spent at each nest. Fifteen laden ants were observed each day, for a total of 45 observations per colony.

On a piece of clear glass measuring 1.5 m x 0.10 m, a one meter section was marked as the observation section. Metal legs were attached to elevate the glass. At each site, the glass was positioned over a level section of the foraging trail approximately 4.5 m from an entrance to the colony. On top of the glass, the path of one ant was traced with a marker as the individual passed under the one meter section. Simultaneously, the time was taken with a stopwatch, and the number of collisions was counted. A collision was defined as a stop or a change in direction due to the presence of another ant or an obstacle. After the ant traversed the one meter section of trail, the individual and its load were collected. The total distance the ant traveled in traversing the 1m section of trail observed was measured by laying a piece of string over the marker tracing and then measuring the string with a tape measure. Additionally, an estimation of trail activity was taken after each individual was collected. This was produced by approximating the number of ants going towards the nest during a one minute period. It was difficult to count each ant individually, therefore a 2 cm section was observed as a sample. The number of ants that passed under a 2 cm section of trail during a one minute period was counted.

In the lab, the ants and their respective loads were placed in the freezer. Ant mass and load mass were measured separately using an analytical balance. All mass measurements were taken on the same day that the specimens were obtained. Using the total distance and the time, the velocity of each individual was calculated. A loading index was calculated for each individual using the equation $L = (M_a + M_l)/M_a$, where L is the loading index, M_a is the ant mass in mg, and M_t is the load mass in mg (Rudolph and Loudon 1986). Statistical correlations between pairwise combinations of the variables ant mass, leaf mass, loading index, number of collisions and trail activity were analyzed to determine which variables were appropriate for multiple linear regression analysis with velocity as the response variable. For these correlations, data from all colonies were pooled. If two variables were significantly correlated, only one of them was included in the multiple linear regression analysis. Additionally, colony number was included in the multiple linear regression analysis to determine the effect of colony number on velocity.

Results

Across all colonies, ant mass ranged from 1.0-15.0 mg, with an average mass of 5.0 (± 3.0 mg). Values for load mass ranged from 1.0-188.0 mg, with a mean load mass of 14.5 (± 17.3 mg). The average velocity was 0.9 (± 0.6 cm/s) and speeds ranged from 0.2-3.5 cm/s, although no ants were observed to travel at velocities in the range 1.3-1.5 cm/s (Figure 1). Loading indices ranged from 1.1-15.0, with an average loading index of 4.2 (± 2.3). The number of collisions ranged from 0-18 with a mean of 7.5 (± 4.1). The number of collisions was significantly correlated with relative trail activity ($p<0.001$) and with ant mass ($p=0.001$). As predicted, load mass was significantly correlated with ant mass ($p<0.001$). However, loading index showed no significant correlations with any other variables.

After examining pairwise correlations, multiple linear regression analysis was performed with the following variables: colony number, loading index, and number of collisions. The analysis yielded the following model ($r^2 = 0.266$), where V is velocity (cm/s), L is loading index (mg/mg) and C is the number of collisions:

$$V = 1.705 - 0.0947\,L - 0.0476\,C$$

The model suggests that when the loading ratio is increased by one, either through the adjustment of ant mass or leaf mass, ant velocity decreases by 0.0947 cm/s, which amounts to a 10% reduction from the mean velocity. Similarly, every additional collision corresponds to a 0.0476 cm/s decrease in velocity (5% of the mean velocity). The effects of loading index ($p<0.001$) and collisions ($p<0.001$) are shown in Figures 2 and 3, respectively. Colony number did not have a significant effect on laden ant velocity.

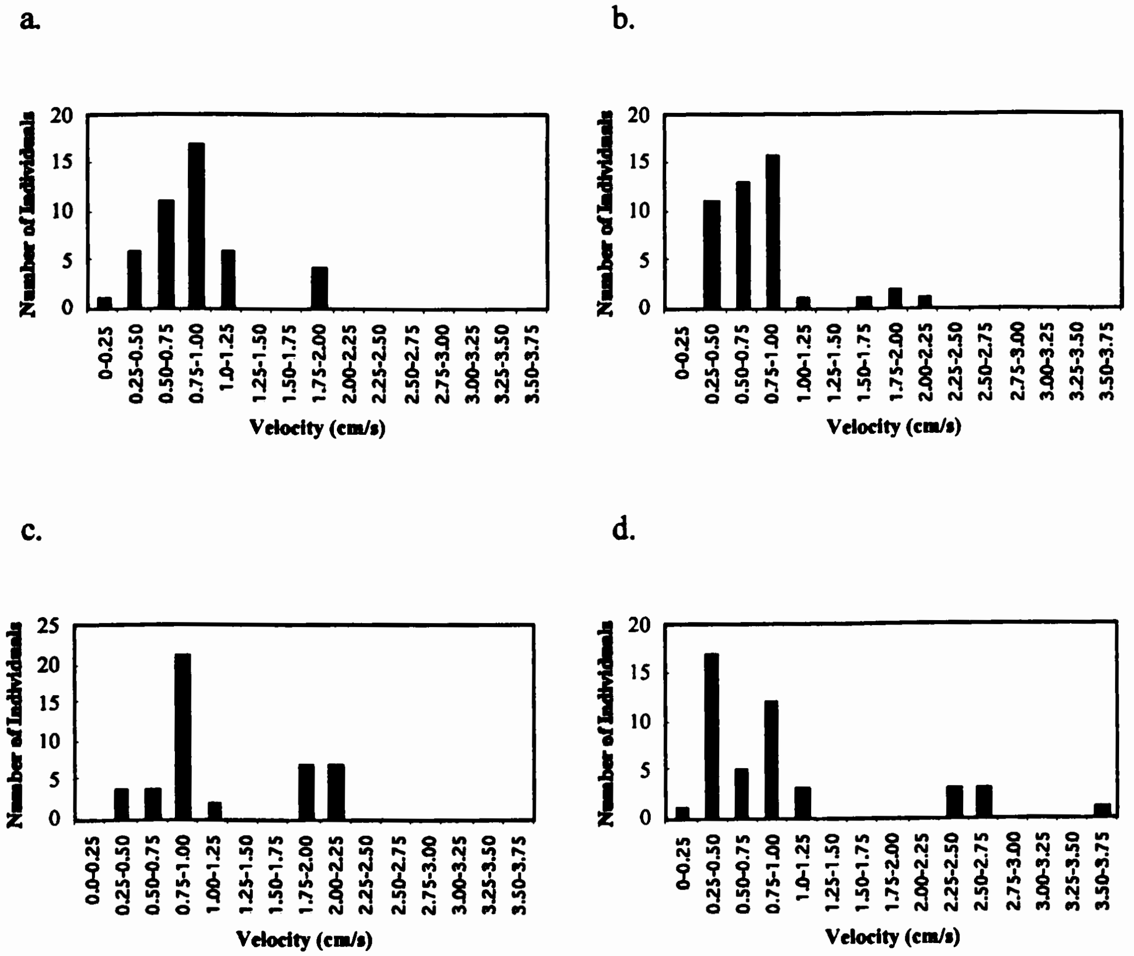

Figure 1: The distribution of velocities (cm/s) for laden *Atta cephalotes* workers from colony 1 (a), colony 2 (b), colony 3 (c), and colony 4 (d). Note that the y-axis scale in panel c differs slightly from the other three panels.

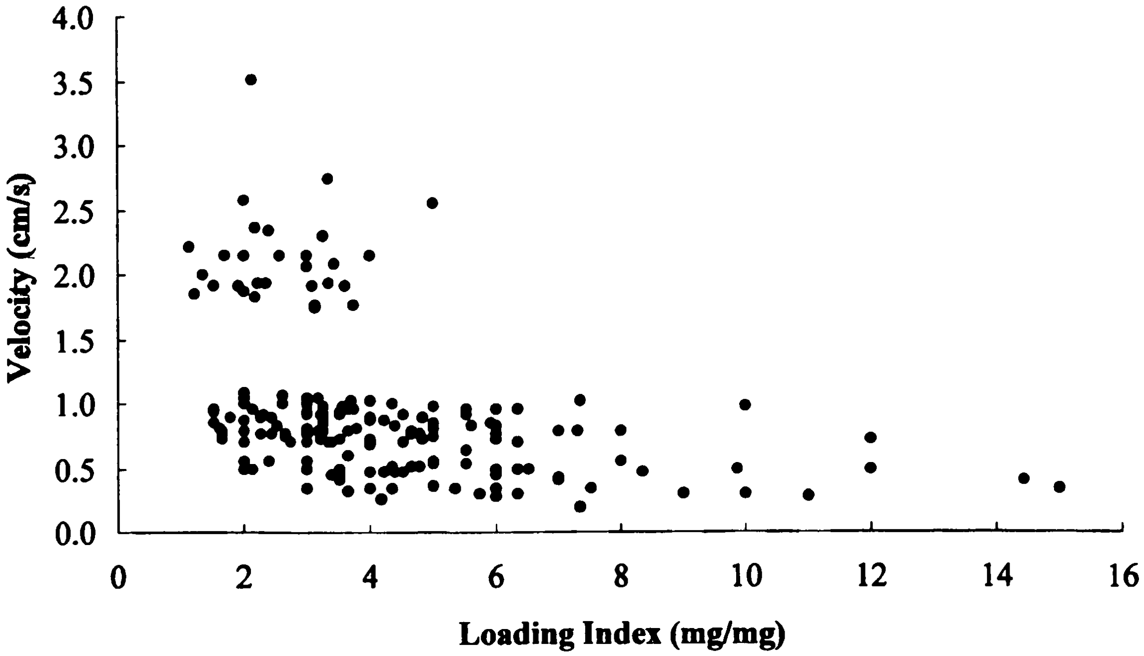

Figure 2: The effect of loading index on laden velocity in *Atta cephalotes*. Data for all colonies are pooled for this figure.

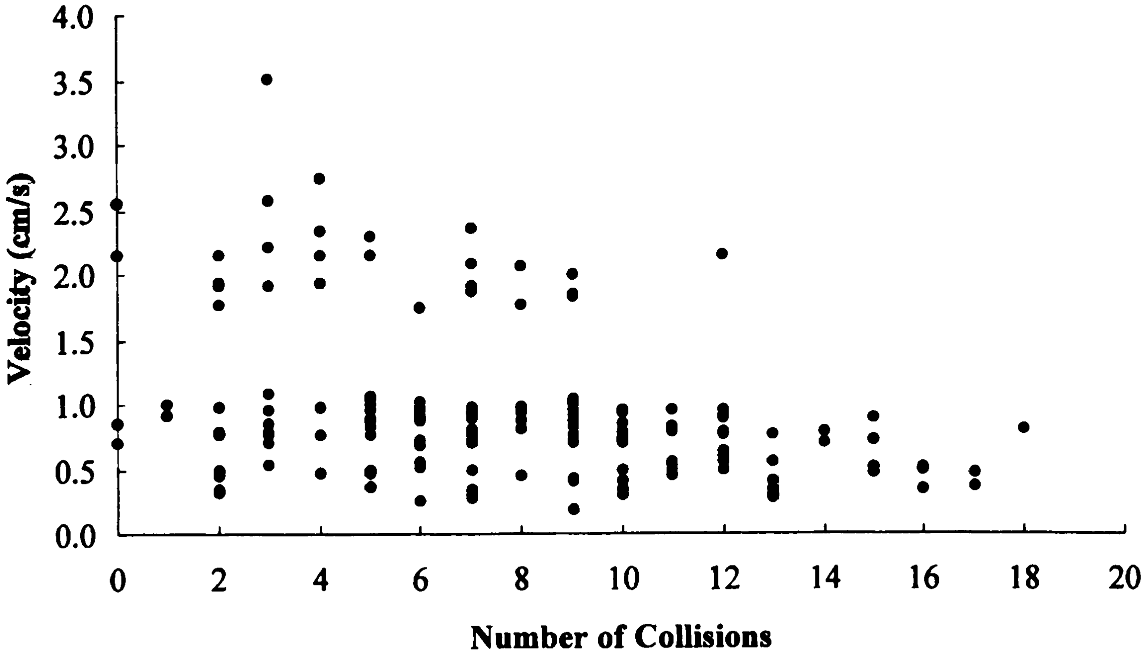

Figure 3: The effect of collisions on laden velocity in *Atta cephalotes*. Data for all colonies are pooled for this figure.

Discussion

The average value for ant mass, 5.0 (± 3.0 mg) is comparable to previously reported measurements. For example, Wetterer (1995) calculated mean forager mass for small and large A. *cephalotes* colonies in Costa Rica and reported values of 3.3 (± 1.0 mg) and 7.3 (± 4.1 mg) respectively. The result for mean load mass reported in the current study, 14.5 (± 17.3 mg), is also similar to values in the literature. Rudolph and Loudon (1986) found a median load mass of 14.0 mg when *A. cephalotes* colonies were studied in Costa Rica. Thus, the colonies studied herein are apparently representative of other colonies of this species, with regard to both ant size and load mass.

My results support previous conclusions that loading index and velocity are inversely related (Rudolph and Loudon 1986; Shutler and Mullie 1991; Burd 1996; Röschard and Roces 2002). Ants that transport fragments which are heavy in relation to their body mass have large loading indices and slower velocities. Contrastingly, ants that select lighter loads are able to move faster (Figure 2). This apparent tradeoff between load size and velocity may set an upper limit to the foraging efficiency of individual ants. Indeed, such a limit is evident upon closer examination of the effects of loading indices on leaf transport rate (see below).

As reported earlier (Burd 2001), the number of collisions an ant incurs while traveling also shows an inverse relationship with velocity (Figure 3). Ants that incur numerous collisions have relatively low velocities whereas ants that incur few collisions have relatively high velocities. At a 5% reduction in velocity per collision, collisions are indeed costly. Soldiers of *A. cephalotes* continually remove debris from the foraging trails so that trails are cleared to bare soil. The soldiers are the largest members of the colony therefore they are energetically expensive for the colony to produce. Because the number of obstacles an ant encounters has a negative effect on foraging velocity, the production of soldiers to clear the trails is advantageous despite the increased energy investment. Although loading indices and collision frequency were the only factors that influenced foraging velocity in my analyses, it is important to note that these two factors only accounted for 27% of the variation in foraging velocity, indicating that other undetermined factors also affect foraging velocities.

Whether or not the ants maximize leaf transport rates with the load sizes they select is an interesting question. Rudolph and Loudon (1986) defined leaf transport rate as the product of load mass and velocity. Leaf transport rate is a measure of the amount of biomass that is transferred to the colony in a given unit of time. They hypothesized that optimal foraging efficiency would be achieved by selection of loads that maximize this rate. For ants of all sizes, it was determined that leaf transport rate is maximized at loading indices of 3.5-6.5. However, a quarter of the ants in their study selected burdens that were well below this range, suggesting that the ants perform sub-optimally. The average loading index of 4.2 (± 2.3) reported in this study is within the optimal range proposed by Rudolph and Loudon. A theoretical analysis was conducted to assess the degree to which the ants in the present study were optimizing leaf transport rate.

Using the regression model, predicted velocities can be estimated for ants spanning the range of body sizes (1.0-15.0mg) and load masses (1.0-190.0mg) observed in this study. These velocities can then be used to determine the relationship between leaf transport rate and loading index. This relationship (assuming no collisions) is shown in Figure 4. Leaf transport rate appears to be maximized at a loading index slightly below 10, regardless of the size of the individual. In order for ants to optimize leaf transport rate, each individual should select a fragment that gives them a loading index approximately equal to 10. Interestingly, the loads actually selected by the ants were roughly half of what is optimal according to the regression model. It is important to note that although collisions would lower the overall transport rates, the peak transport rates would remain at the same loading index.

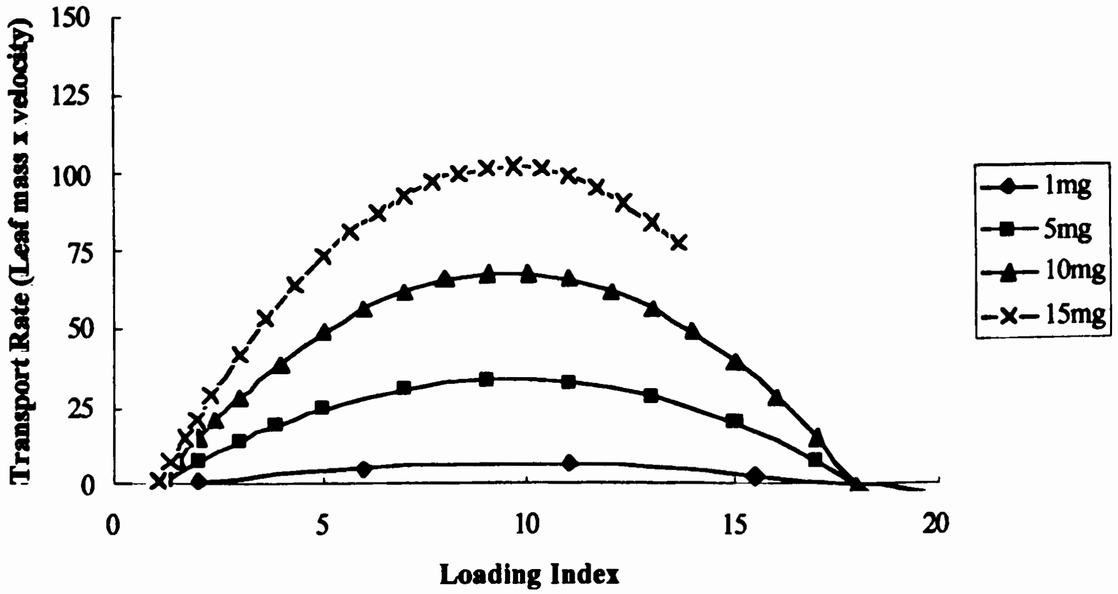

Figure 4: The theoretical relationship between loading index and overall leaf transport rate for individuals of *Atta cephalotes* weighing 1, 5, 10, and 15 mg, bearing leaf fragments of sizes spanning the range observed in this study. This relationship is based on the observed relationship between loading index and laden velocity, assuming zero collisions.

There are several possible explanations for sub-optimal load selection. Perhaps it is more important to minimize travel time than to maximize load size (Burd 1996). While the ants forage, they are exposed to phorid flies, which are parasitoids of the ants (Feener and Moss 1990, in lit.) Rapid return to the colony would decrease exposure time thereby lowering the probability of parasitism. The minima sometimes ride on the leaf fragments to help protect the workers from parasitism. Smaller load sizes might be selected in order to tolerate the additional weight of a rider. However, the minima usually weigh less than 1 mg, therefore this effect alone cannot explain the discrepancy between actual and optimal load sizes (Burd 1996).

Energy is another important consideration when analyzing load size selection, because energy costs may vary nonlinearly with load size. It is possible that extremely high energy expenditures are associated with cutting and maneuvering fragments that are heavier than those the ants select naturally. To perform at the proposed optimal level, the ants might need recovery time between foraging trips (Rudolph and Loudon 1986). Additionally, load size selection by the individual might be dependent on the amount of energy that must be allocated for other tasks (Wilson 1980).

During the foraging process, the ants must transport the load down the vegetation source, to the ground. Other physical factors may constrain loads to a size which can be transported vertically. For instance, the torque exerted on the leaf fragment while the ant is in a vertical position might be overwhelming at larger load sizes (Burd 1996). Since all of my measurements were obtained from ants foraging on horizontal ground, the influence of this factor could not be observed.

The regression model reported here suggests that minimizing the number of collisions may be one strategy for maximizing velocity. By reducing the area of the fragment, the individual might be able to minimize the number of collisions. The reduction in area would yield a lower return of biomass to the colony, however, if smaller fragments allow the ant to travel relatively unimpeded, then smaller fragments may be advantageous.

It is also interesting to note that no ants traveled at velocities in the range 1.3-1.5 cm/s (Figure 1). This gap cannot be attributed to loading index since certain ants with comparable loading indices appear to travel at different speeds (Figure 2). This result has not been reported by previous studies and warrants further investigation. Additionally, further research is needed to determine other variables that affect foraging velocities and to elucidate factors that establish optimal load indices.

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