Trail Length and Nutritional Value for *Atta cephalotes*

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ABSTRACT

The leaf-cutter ant *Atta cephalotes* has a complex society including workers who forage for leaf fragments used to grow fungus for food. The purpose of this project was to find *if A. cephalotes'* head size and foraged leaf fragment size and quality changes with trail length. Twelve trail lengths were measured and fifty leaf fragments and ant head measurements were collected per trail. The leaf fragments and whole leaf samples were measured for nitrogen content and toughness. Results showed negative relationships between trail length and wet weight (simple regression, P=.0083) and trail length and dry weight (simple regression, P=.0007). Increasing trail length led to increased leaf toughness (simple regression, P=.2008) and nitrogen content (simple regression, P=.2250). Results relating foraging trail length to ant head size showed a negative relationship (simple regression, P=.0199). These trends suggest that A. *cephalotes* are able to selectively choose both workers and plants on different trails to increase foraging efficiency.

RESUMEN

El cephalotes de la hormiga del cortador de la hoja Atta tiene una sociedad compleja inclusive trabajadores que se adentran para fragmentos de hoja utilizó para crecer el hongo para el alimento. El propósito de este proyecto debía encontrar si A. cephalotes' el tamaño de cabeza y se adentró el tamaño del fragmento de hoja y cambios de calidad con la longitud del rastro. Doce longitudes del rastro se midieron y cincuenta fragmentos de hoja y medidas de cabeza de hormiga se reunieron por el rastro. La hoja fragmenta y las muestras enteras de hoja se midieron para el contenido de nitrógeno y dureza. Los resultados mostraron las relaciones negativas entre la longitud del rastro y mojaron el peso (el retroceso sencillo, P = .0083) y la longitud del rastro y secan el peso (el retroceso sencillo, P = .0007). La longitud creciente del rastro llevó a la dureza aumentada de hoja (el retroceso sencillo, P = .2008) y el contenido de nitrógeno (el retroceso sencillo, P = .2250). Relacionar de resultados que adentra la longitud del rastro al tamaño de la cabeza de la hormiga mostró una relación negativa (el retroceso sencillo, P= .0199), Estas tendencias sugieren que A. cephalotes es capaz de escoger selectivamente tanto los trabajadores como las plantas en rastros diferentes aumentar adentrándose la eficiencia.

INTRODUCTION

The leaf-cutter ant *Atta cephalotes* has a complex society specialized to live in forest gaps (Holldobler and Wilson 1990). They have a caste system that includes a queen, workers, soldiers, minima, and reproductive males. The workers cut and collect plant parts while the minima ride atop, protecting the colony from parasitic flies with their mandibles and hind legs (Wilson 1971). Leaf-cutters collect and utilize fresh leaves, flowers, fruit, and tubers from as far as one hundred meters away from their nest in order to cultivate fungus for food in underground chambers called "fungus gardens" (Huxley and Cutler 1991).

Holldobler and Wilson (1990) reported that higher selectivity for greater nutrition should occur the farther away the food item. This is due to the fact that those ants expending more energy to travel farther should be compensated for this energy loss with a greater nutritional reward. For example, A. *cephalotes* have been found to collect plant species with a below-average water content, since water is of no nutritional value to the fungus or the ants (Holldobler and Wilson 1990). However, the complexities of the foraging preferences of these ants are just beginning to be examined (Janzen 1983).

This project focused on the comparative benefits of food items selected by A. *cephalotes* closer to and farther from their nest. Leaf fragments with greater nutritional content should be those that are larger (containing more nutrients) with lesser water content (and therefore proportionately more nutrients) and greater nitrogen content (important nutrient for cultivating fungus) (Holldobler and Wilson 1990). Leaves that are less tough should also have greater overall nutritional benefits since they would take less energy and time to be cultivated into fungus. It was hypothesized that leaf-cutters venturing farther from the nest and expending more energy to do so will need to supplement their energy expenditure with a greater nutritional reward. Therefore it was believed that A. *cephalotes* foraging farther from their nest would choose leaf fragments greater in size and lower in toughness with lesser water content and greater nitrogen content. Additionally, it was believed that larger ants would be foraging farther away from the nests than smaller ants. Larger ants would be stronger, and therefore able to travel longer distances than smaller ants.

MATERIALS AND METHODS

The study site was the Ecological Farm in Cerro Plano, Monteverde, Costa Rica. It is a fairly open site, which made identification of leaf-cutter ant nests and trails easier to identify and follow.

This project began by finding seven A. *cephalotes* nests and measuring a total of twelve trail lengths from the entry point of each nest to the end of each trail with the tape measure. Colonies generally had one to three trails, forcing trails from different colonies to be chosen. Therefore, separating colony effects from within each colony was important for the results. Each trail ended with a tree from which the ants were collecting leaf fragments, and the measurement ended at the base of each. The head size of fifty ants (workers who were carrying leaves) was measured with calipers at the ends of each foraging trail, and fifty samples of their leaf fragments were collected per trail. This was necessary to see if larger ants (measured by head size) are found farther from the nest.

Each leaf fragment was weighed to see if larger leaves are collected from longer trails. Ten whole leaf samples were collected (by shooting leaves down with a slingshot) per foraged plant from each trail in order to measure leaf toughness with a penetrometer, and nitrogen content with a soil test kit. Nitrate nitrogen was measured in pounds per acre with a La Motte Soil Test Kit After mixing collected leaves with an extraction solution; a color developed which was compared with colors coordinated with nitrate nitrogen values, ranging from ten to twenty. This was done to see if more tender leaves are collected farther away, providing better nutrients as they would break down more quickly for fungus growth. These whole leaf samples were also used to measure nitrogen content, since leaves gathered farther away should contain more of this important nutrient.

RESULTS

Trail Length

Across Colony

Figure 1 shows that trail length is negatively correlated with wet weight of leaf fragments by a significant amount. This is an important graph because it shows higher selectivity for leaf fragments that are easier to carry longer distances. Figure 2 shows that trail length is negatively correlated with dry weight of leaf fragments by a significant amount. This is an important graph because it emphasizes the fact (in addition to the results for wet weight) that there is higher selectivity for leaf fragments that are easier to carry longer distances. Figure 3 shows that head size is negatively correlated with trail length by a significant amount. This graph is important because it shows that significantly smaller ants forage on longer trails, despite previous assumptions. A simple regression (Fig. 4) showed that trail length is negatively correlated with leaf toughness, although not significantly. Despite these results, it is important to note that toughness is in fact selected against on longer trails. Figure 5 shows that nitrate nitrogen content is positively correlated with trail length, although not significantly. Despite these results, it is important to note that greater nitrogen content in leaf fragments is selected for on longer trails.

Within Colonies

Toughness

There was not a significant difference (P=.5524) in mean leaf toughness between the two trails of Colony A. The penetrometer showed Trail One (22.5 m) had a mean leaf toughness of 248.604 mL (+/- .316) and Trail Two (15.3 m) had a mean toughness of 296.604 mL (+/- .404, t=-4.298, p<.0001. n=50 for each trail).

There was a significant difference (P=.0071) in mean leaf toughness between Trails Four (24.4 m) and Six (27 m) of Colony C. Mean toughness of Trail Four was 234.104 mL (+/- 63.430) and mean toughness of Trail Six was 482.595 mL (+/- 260.858). It is important to note that these results show higher selectivity against toughness on longer trails. There were not significant differences (P=.3811 and P=.0533, respectively) between Trails Four and Five (33 m, mean toughness of 310.104 mL +/-192.913. n=50 for all trails in Colony C) and Trails Five and Six.

There was a significant difference (P=.0188) in mean leaf toughness between the trails of Colony D. Trail Seven (16.5 m) had a mean toughness of 332.604 mL (+/-127.585) and Trail Eight (24 m) had a mean toughness of 178.104 mL (+/-139.686, t= 2.583. n=50 for each trail).

There was a significant difference (.0446) in mean leaf toughness between the trails of Colony F. Trail Ten (15.4 m) had a mean toughness of 94.104 mL (31.990) and Trail Eleven (65 m) had a mean toughness of 225.604 mL (+/-189.890, t= -2.159. n=50 for each trail). It is important to note that this colony shows selectivity against toughness while foraging longer distances.

Wet Weight

There was not a significant difference (P=.3735) in mean leaf fragment wet weight between the trails of Colony A. Trail One (22.5 m) had a mean wet weight of .025 g (+/- .012) and Trail Two (15.3 m) had a mean wet weight of .027 g (+/- .006, t= -.894. n=50 for each trail).

There was not a significant difference (P=.2134) in mean leaf fragment wet weight between Trail Four (24.4 m, mean wet weight of .024 g +/- .009) and Trail Five (33 mm, mean wet weight of .021 g +/- .009) of Colony C. There was a significant difference (P=.0017) between Trails Four and Six (27 m, mean wet weight of .030 g +/- .012. n=50 for each trail). There was also a significant difference (P<.0001) between Trails Five and Six. These significant results show selectivity for lighter leaf fragments that are easier to carry longer distances.

There was not a significant difference (P=.6094) in mean leaf fragment wet weight between the trails of Colony D, yet this colony still followed the trend of being negatively correlated with trail length. Trail Seven (16.5 m) had a mean wet weight of .028 g +/- .012 and Trail Eight (24 m) had a mean wet weight of .027 g +/- .009 (t= .513, n= 50 for each trail).

There was a significant difference (P<.0001) in mean leaf fragment wet weight between the trails of Colony F. Trail Ten (15.4 m) had a mean wet weight of .034 g +/- .014, and Trail Eleven (65 m) had a mean wet weight of .025 g +/- .007 (t= 4.228, n=50 for each trail). This is important because this colony shows selectivity for easier to carry leaf fragments on longer foraging trails.

Dry Weight

There was a significant difference (P<.0001) in mean leaf fragment dry weight between the trails of Colony A. Trail One (22.5 m) had a mean dry weight of .006 g +/- .004 and Trail Two (15.3 m) had a mean dry weight of .010 g +/- .004 (t= -5.299, n= 50 for each trail). This is important because it emphasizes results of selectivity for lighter leaf fragments.

Colony C did not show a significant difference (P=.8629) in mean leaf fragment dry weight between Trail Four and Trail Six. Trail Four (24.4 m) had a mean dry weight of .011 g +/- .009 and Trail Six (27 m) had a mean dry weight of .011 g +/- .012. There were significant differences between Trails Four and Five (mean dry weight of .008 g +/- .009, P=.0167. n=50 for each trail) and between Trails Five and Six (P=0101). These results show selectivity for lighter leaf fragments.

There was not a significant difference (P=.1021) in mean dry weight between the trails of Colony D. Trail Seven (16.5 m) had a mean dry weight of .010 g +/- .006 and Trail Eight (24 m) had a mean dry weight of .009 g +/- .003 (t= 1.650, n= 50 for each trail).

Colony F showed a significant difference (P<.0001) in mean leaf fragment dry weight between trails. Trail Ten (15.4 m) had a mean dry weight of .015 g +/- .007 and Trail Eleven (65 m) had a mean dry weight of .007 g +/- .003 (t= 7.835, n= 50 for each trail). This is important because this colony emphasizes results of selectivity for lighter leaf fragments.

Head Size

Across Colonies

Figure 6 shows that head size varies significantly with trail length. Three pairs out of twenty-one did not have significant differences between mean head sizes across colonies. (Standard deviations = +/- .316 (a), .249 (b), .167 (c), .206 (d), .218 (e), .218 (f). These results are important because they show strong evidence for colony selectivity for sending smaller ants' longer distances.

Within Colonies

Colony A showed a significant difference (P<.0001) in head sizes between its two trail lengths. Trail One (22.5 m) had a mean ant head size of 2.016 mm +/- .316, while Trail Two (15.3 m) had a mean ant head size of 2.328 mm +/- .404 (t= -4.298, n=50 for each trail). Colony C showed a significant difference in mean ant head sizes between Trails Four (24.4 m) and Five (33 m), with a P-value of .0002, and Four and Six (27 m), with a P-value of .0003. These results show colony selectivity for sending smaller ants on longer trails. There was not a significant difference (P=.8996) in head sizes between Trail Five and Trail Six. Mean head size for Trail Four was 1.957 mm +/- .181, Trail Five was 1.836 mm +/- .140, and Trail Six was 1.840 mm +/- .151 (n=50 for each trail). Colony D did not show a significant difference (P=.5683) in mean ant head sizes between trails, although it continued the trend of decreasing head size with increasing trail length. Trail Seven (16.5 m) had a mean head size of 1.908 mm +/- .168 and Trail Eight (24 m) had a mean head size of 1.888 mm +/- .181 (t= .573, n= 50 for each trail). Colony F showed a significant difference (P<.0001) in mean ant head sizes between trails. Trail Ten (15.4 m) had a mean head size of 1.726 mm +/- .218 and Trail Eleven (65 m) had a mean head size of 1.564 mm +/- .018 (t=4.461, n=50 for each trail). Colony F also shows that colonies send smaller ants foraging farther distances.

DISCUSSION

Results from across colonies comparing trail length to every other factor of nutrition in leaf fragments collected by A. *cephalotes* consistently followed my hypothesis that greater nutritional value (lower wet and dry weight, lower toughness, and greater nitrogen content) would come from foraged leaf fragments of longer foraging trails. This would compensate for expending more energy by traveling longer distances. Wet weight and dry weight of leaf fragments showed a significant negative correlation with trail lengths, showing that ants traveling farther collect leaves with lower water content, making them easier to carry these longer distances.

Nitrate nitrogen content results agreed with the hypothesis by increasing with trail length. Nitrogen is an important nutrient to A. *cephalotes* and the growth of their fungus (Huxley and Cutler 1991) and therefore the ants traveling farther would collect leaves with greater nitrogen content. Although it followed this trend, it did not show significant results, possibly due to low sample size.

Leaf toughness was also negatively correlated with trail length, because the ants traveling farther that should be collecting more nutritious food items would take leaves that could be broken down more quickly to make their fungus (Huxley and Cutler 1991). Tougher leaves are more fibrous and therefore would be slower to break down and would not have the room for nutrients less fibrous leaves would have. Tougher leaves may also be heavier, and therefore the ants traveling farther would carry less tough leaves to save energy for compensation of their energy expense.

Within colony comparisons of leaf toughness partially supported the hypothesis that tougher leaves would be taken from shorter trails. These results were not significant, probably due to the method of using the penetrometer. This device made it difficult to obtain equal measurements between leaves. Placement of leaf in the device and placement of water on the unbalanced top of the device made it impossible to measure leaf toughness uniformly for each leaf. This probably resulted in the scattered measurements that were made.

Within colony comparisons of mean wet weight tended to support the hypothesis that lower wet weight in foraged leaf fragments would be found on longer trails. The majority of these results show that ants traveling longer distances select for easier-to-carry leaf fragments. Within colony comparisons of dry weight also tended to support the hypothesis that lower dry weight in foraged leaf fragments would be found on longer trails. Results tended to show that lighter leaf fragments were often selected for.

Additionally it was hypothesized that larger ant head size would be found on the longer trails due to greater strength (and ability) to travel farther. Results did not support this, which may be because larger ants are kept closer to the colony but make more trips back and forth to forage. Smaller ants may be sent on longer foraging trails since they are only making one trip, and are collecting lighter leaf fragments. Leaf fragments lower in wet weight, dry weight, and toughness would be easier for smaller ants to carry. The smaller ants would also be better suited to carry the smaller leaves that are found farther from the nests. The trend found between head size and trail length is probably not the result of an error due to small sampling size, because the same trend was found within each colony among the majority of trails.

Results show that A. *cephalotes* are a complex species able to select food sources for nutritional content. They are somehow able to choose trees with leaf fragments that are higher in nutritional value and easier to carry. This species is also organized in its ability to select for which size ants to send on which length of trail in order to be most productive. How these ants are able to choose certain beneficial food items should be examined in future studies relating leaf-cutter ant foraging trail length and leaf fragment nutrient content.

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FIGURES

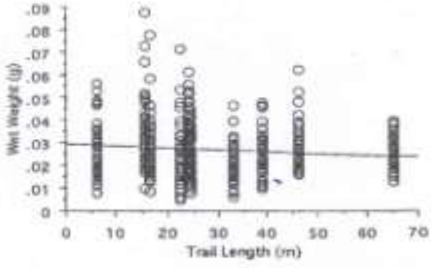

Figure 1. Simple regression for wet weight of leaf fragments for each trail length (Y = .029 - 7.9E-5 * X; R^2 = .013, P=.0083).

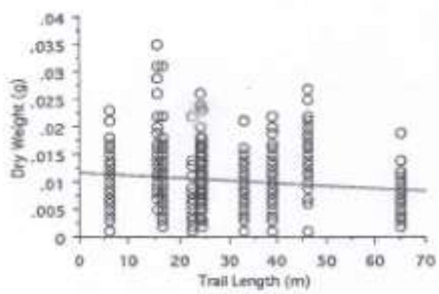

Figure 2. Simple regression for dry weight of leaf fragments for each trail length (Y = .012 - 4.81E-5 * X; R^2 = .021, P=.0007).

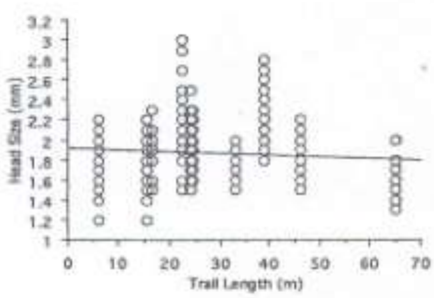

Figure 3. Simple regression for head size of *A. cephalotes* for each trail length (Y = 1.914 - .002 * X; R^2 = .01, P=.0199).

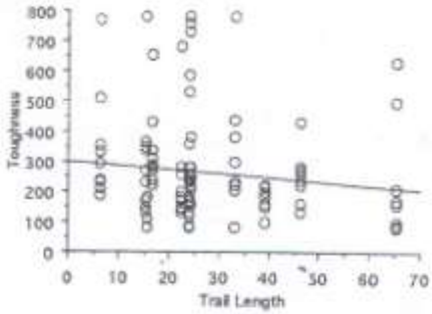

Figure 4. Simple regression for leaf toughness for each trail length (Y = 300.835 - 1.334 * X; R^2 = .014, P=.2008).

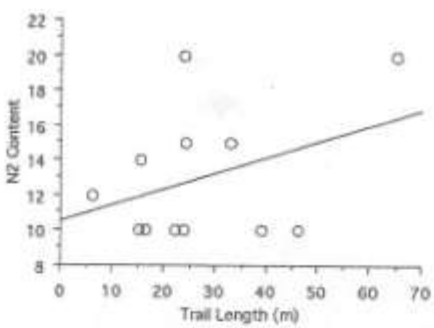

Figure 5. Simple regression for nitrate nitrogen for each trail length (Y = 10.502 + .09 * X; R^2 = .143, P=.2250).

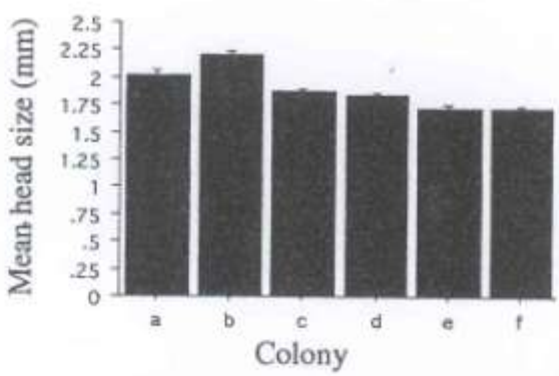

Figure 6. One-way ANOVA test and interaction bar plot for *Atta cephalotes* head size versus Colonies.