to higher-quality forage. There are two alternatives that may explain the great variation in trail quality: poorly-cleared trails may represent paths that are slowly being abandoned as foraging routes by an ant colony, or poorly cleared trails may represent scouting paths that have yet to be fully developed. To separate the effects of trail age and forage preference on trail quality, future studies should consider the change in the degree of clearing and quality of forage transported over the entire "life" of an individual trail.

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DIFFERENTIAL FORAGING OF *ATTA CEPHALOTES* IN THE PRIMARY AND SECONDARY FOREST

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Abstract. We tested for differences in the foraging behavior of leaf-cutter ants (*Atta cephalotes*) between primary and secondary forest in Corcovado National Park, Costa Rica. We hypothesized that because leaf quality tends to be lower in the primary forest as a result of higher chemical and physical defenses, ants in the secondary forest should show more discrimination when foraging than ants in the primary forest. When presented with an array of leaves varying in quality, ants from the secondary forest harvested mostly from one leaf while ants from the primary forest harvested equally from all leaf types. Habitat-specific differences in the foraging discrimination of ants may contribute to differences in regeneration patterns and diversity between primary and secondary forest.

Key Words: Atta cephalotes, *habitat, leaf-cutter ants, optimal foraging*

Introduction

Leaf-cutter ants, *Atta cephalotes*, harvest a wide variety of plant species in both primary and secondary forests. However, the species composition in these two forests differs considerably. Trees that dominate the secondary forest have adapted to their competitive environment with rapid growth rates, and thus tend to have tender leaves with few chemical defenses. Long-lived, primary forest species devote significantly more resources to defenses (Coley, 1983).

It is well known that leaf-cutter ants prefer leaves with fewer secondary chemicals that can limit fungal growth (Nichols-Orians, 1990). Lab ant colonies have also been shown to be less selective when there is a shortage of suitable substrate (Nichols-Orians, 1990). If attine ants are foraging optimally, those in the primary forest should be less selective because the probability of finding high quality leaves with few secondary chemicals is relatively low, and the costs of searching for such leaves is high. On the other hand, optimally foraging ants in the secondary forest can afford to be more discriminatory because costs of searching for high quality leaves is low. We tested this hypothesis by offering standardized arrays of leaves to ants from the primary and secondary forest and by comparing their tendency to discriminate among different leaf tissues.

Methods

On 31 January 1996 we collected leaves from three unidentified plant species growing in the vicinity of the Sirena Biological Station, at Corcovado National Park, Costa Rica. Based on their relative leaf toughness as measured by a penetrometer, the species were ordered from least tough (Plant 1) to most tough (Plant 3). Leaves were grouped into arrays consisting of one leaf from each of the three species arranged in haphazard order. Four leaf-cutter trails, two trails each in primary and secondary forest, were selected for experimental manipulation. Five leaf arrays were placed at 2 m intervals along each trail, and each was monitored at 5 minute intervals for a total of 30 minutes. The number of leaf fragments cut and removed from each leaf species was recorded. We compared the foraging preferences of ants inhabiting primary and secondary forest with a Chi-square testing the null hypothesis that each plant species was harvested equally. Thus, the size of the Chi-square statistic represents the extent of discrimination by the ants. Ratios of chi-square values approximate an F-distribution, so we tested the null hypothesis that ants from the two habitats were equally discriminating with an F-test (where F = secondary forest Chi-square/ primary forest Chi-square).

Results

Ants in both primary and secondary forest reacted immediately to begin harvesting the introduced leaves in their trail. A. cephalotes from the primary forest did not discriminate among the three plant species ($X^2 = 2.54$, df = 2, $P > 0.05$; cuts from plants 1, 2, and

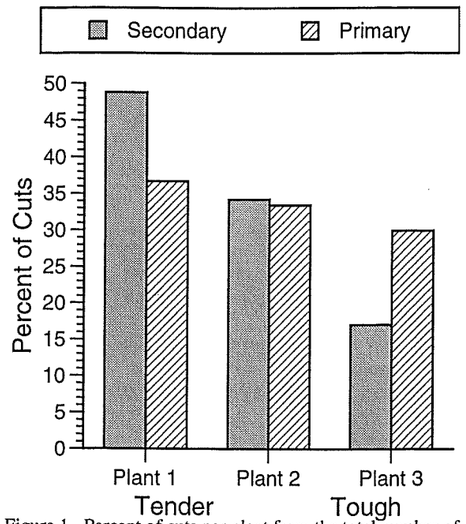

Figure 1. Percent of cuts per plant from the total number of cuts on *Atta cephalotes* trails in both secondary and primary forest in Corcovado National Park, Costa Rica.

3 = 135, 123, and 110). In contrast, leaf-cutters from the secondary forest were highly discriminating in their leaf selection ($X^2 = 63.63$, df = 2, $P < .0025$; cuts from plants 1, 2, and 3 = 204, 143, and 71). Thus, ants from the secondary forest preferred the most tender leaves (plant 1) almost 50% of the time, and cut the toughest leaves (plant 3) only 17% of the time (Figure 1). Overall, ants in the secondary forest were more discriminating in their leaf selection than ants in the primary forest ($F = 25.05$, df = 2, 2, $P < 0.05$).

Discussion

Ants in the secondary forest were more discriminating in their leaf selection than ants in the primary forest. The preferences of ants in the secondary forest showed decreasing preference for leaves with increasing toughness. Other studies have similarly indicated that leaf-cutter ants select against tough leaves (Nichols-Orians, 1990). These results suggest that leaf quality is a mechanism affecting leaf choice as well as foraging strategies of *A. cephalotes*. Optimally foraging ants in the secondary forest can be more discriminating in their foraging habits due to low costs associated with search time and high potential returns due to the abundance of high quality leaves.

Conversely, the relatively low abundance of suitable leaf substrates in the primary forest implies that ants should search less for high quality leaves because the chances of finding them are low, while the costs of looking are high. Consistent with this, ants in the primary forest did not discriminate between tender and tough leaves. Additional tests might compare search time as a function of habitat quality in leaf-cutters.

Differences in foraging behavior between ant colonies in primary vs. secondary forest may be the result of differences in resource quality as we originally hypothesized. However, our sampling design suffered from limited independence among samples (individual leaf cuttings). Initial cuts on a given leaf could determine the frequency of cuts to follow if ants rely on pheromone cues in determining the acceptability of a leaf. This would represent a violation of the assumption of independence required by our chi-square analyses. These deficiencies could be eliminated by using a design that treats colonies as the experimental units, with trails nested within colonies, and leaf arrays nested within trails. In this design, percent of cuts from each leaf type could be treated as the (continuous) dependent variable

Optimal foraging patterns based on relative resource quality and availability may affect forest dynamics. Leaf-cutters have been estimated to remove approximately 5% of gross plant primary productivity per year (Little et al., 1996). Secondary forests would be particularly affected by leaf-cutter biomass harvesting, due to the greater abundance of *A. cephalotes* colonies in secondary forests than primary forests (pers. obs.). Leaf harvesting by ants may affect future plant recruitment, thus altering the composition of secondary forest. If leaf-cutter ants are more discriminating in their host choices in the secondary forest than in the primary forest, and if the variance in leaf quality among tree species is similar in the two habitats, leaf cutter ants would tend to reduce diversity in the secondary forest more than in the primary forest.

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