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THE HITCHHIKER'S GUIDE TO THE LEAF-CUTTER COLONY

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Abstract: Although the minima caste in the leaf-cutter ants, *Atta,* is primarily involved in nest activities, some of these small sized individuals are found outside the nest "hitchhiking" on leaves carried by workers. Their role may be to deter parasitoid phorid flies. We investigated the purpose of these hitchhikers in *Atta colombica* by observing their distribution along trails, the proportion of hitchhikers in the defensive "head up" position on leaves, and the average size of leaves with and without hitchhikers. The ratio of hitchhikers to leaves was greatest closest to the nest, and hitchhikers were as likely to have their heads up as down. Leaves with hitchhikers had a greater surface area than leaves without hitchhikers. These findings are consistent with the hypothesis that hitchhikers could be defending workers against parasitoid phorid flies, which attack near the nest, and may also initiate cleaning and preparation of larger leaves before they enter the nest.

Key Words: Atta, *minima, phorid flies*

INTRODUCTION

In leaf-cutting ants of the genus *Atta*, ants in the minima caste typically carry out nest duties such as nursing young, tending the fungus gardens, and cleaning and scraping each leaf to prepare it for the gardens (Stevens 1983). Minima are also seen on the trail hitchhiking on leaf fragments carried by workers (Wetterer 1996). It has been hypothesized that hitchhikers (minimas riding on leaf pieces being carried by workers on the ant trails) defend workers against parasitoid phorid flies, which are only active during the day (Linksvayer et al. 2002). The hitchhikers will often assume a "head up" defensive position with head and front legs raised ready to detect and deflect incoming phorid flies. Phorid flies have only been observed attacking ants at the entrance to the nest (D. Matlaga, pers. comm.). Hitchhikers in *A. cephalotes* are equally abundant during the day and night, which suggests a purpose other than protection from parasitoid flies, although during the day hitchhikers spend more time in the defensive "head up" position compared to the night (Linksvayer et al. 2002). It has also been proposed that hitchhikers may prepare leaves by early initiation of the cleaning and scraping process (Linksvayer et al. 2002).

In this study, we tested the hypothe-

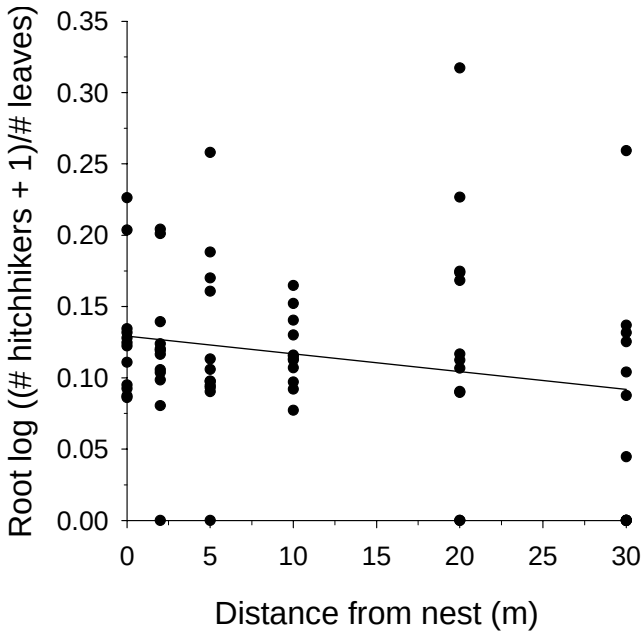

Figure 1. Number of Atta colombica hitchhikers per leaf (normalized) decreased with increasing distance from the nest along the ant trail. y = -0.0013x + 0.13, r^2 =0.044, df = 70, P = 0.078.

ses that the hitchhikers' primary purpose is to protect against parasitic flies, but that they also might initiate leaf preparation while outside the nest. We predicted that hitchhikers should be proportionally more abundant near the nest entrance, should assume the head up position more often than head down, and be present disproportionately on larger leaves.

METHODS

We sampled two trails at each of six *Atta colombica* colonies around Sirena Biological Station in Corcovado National Park, Costa Rica. For 5 min, we counted the total number of leaves being carried and the total number of hitchhikers riding on leaves passing points at 0 m, 2 m, 5 m, 10 m, 20 m, and 30 m from the nest entrance. We calculated the ratio of hitchhikers to total leaves for each location on the trail. At 5 m from the nest, we collected 10 leaves with riding minima and, for each of those 10, the next leaf without a hitchhiker (20 leaves total). For each of the 12 trails, we took the average surface area of one side for the 10 leaves with and without hitchhikers. At 5 m from the nest on each trail we also counted 20 hitchhikers and classified them as head up (defensive posture) or head down (possibly preparing leaf). We were unable to collect data at night, because ants at one trail were disturbed by our headlamps. We normalized the data and used JMP 5.0.1 to perform a one-way ANOVA and a Mixed Model ANOVA.

RESULTS

The ratio of hitchhikers to leaves ranged from 0-0.46 with a mean of 0.083 ± 0.01. In a Mixed Model ANOVA that examined the effects of distance from the nest (fixed effect) and colony (random effect) on the ratio of hitchhikers to leaves, there was a significant effect of colony (F = 5.35, df = 5, 59, P = 0.0004) and distance from the nest (F = 4.27, df = 1, 59, P = 0.04). There was a negative relationship between the ratio of hitchhikers to leaves and distance from the nest (Fig. 1). Of the 20 hitchhikers observed at 5 m from the nest, equal numbers had their heads up as compared to down (Fig. 2). Leaves with hitchhikers had significantly greater surface area than those without hitchhikers (Fig. 3).

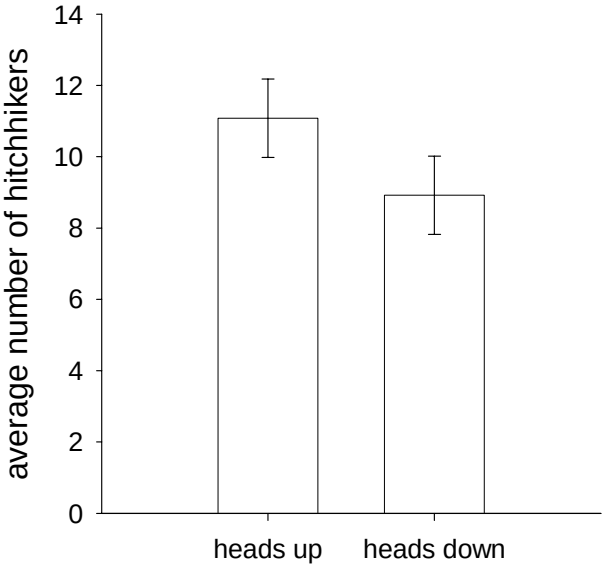

Figure 2. Average number of hitchhikers with heads up and heads down (n = 12 samples of 20 hitchhikers). Hitchhikers were equally likely to have their heads up as down (ANOVA, F = 1.95, df = 1, 22, P = 0.18). Values are means ± 1 SE.

DISCUSSION

The increased ratio of hitchhikers to leaves that we found nearer to the nest entrance is consistent with the hypothesis that these ants may deter parasitoid flies from attacking leaf carriers, as these flies are more active at nest entrances. An alternative explanation for the increased proportion of hitchhikers near the nest is that they are cleaning and preparing leaves; leaves near the nest are not only easier for minima to get to, but also have had more energy invested in them and are thus more valuable to the colony. In addition, the presence of some hitchhikers far from the nest entrance suggests that they fulfill some role in addition to protection, if indeed parasitoid flies only attack at the entryway.

Our finding that hitchhikers are equally likely to have their heads down as up in the defensive position also suggests that their role is not exclusively protective. We only measured "head up" posturing at one point on the trail. Future studies examining whether posture changes with distance from the nest could indicate if hitchhikers change behavior with distance.

The increased presence of hitchhikers on leaves with larger surface area could be because hitchhikers select leaves that require more preparation time before entering the fungus garden. According to Orr (1992), phorid flies have a threshold size for their victims, only attacking larger ants. Hitchhikers may therefore be present on larger leaves because they are protecting larger ants, which carry larger leaves (Wetterer 1994). Or, hitchhikers may simply find it easier to get onto or ride on leaves with larger surface area. Our findings support the suggestion that hitchhikers probably perform multiple functions outside the nest.

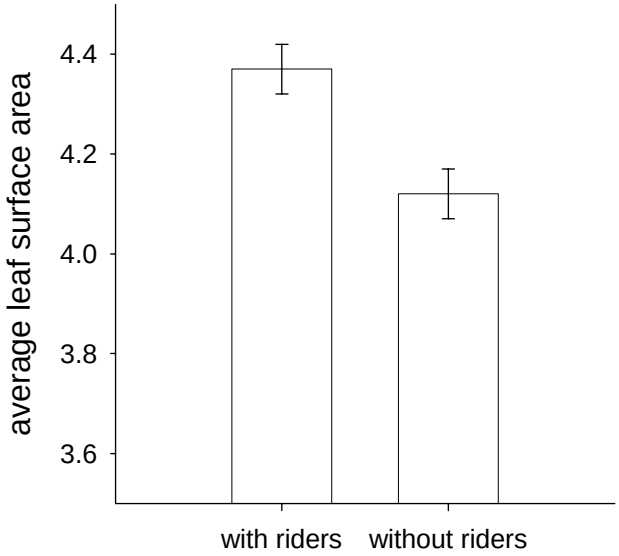

Figure 3. Leaves with riders had greater surface areas than leaves without (ANOVA, F = 13.08, df = 1, 239, P = 0.0004). Values are means ± 1 SE (n = 12 samples of 10 leaves for each category).

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