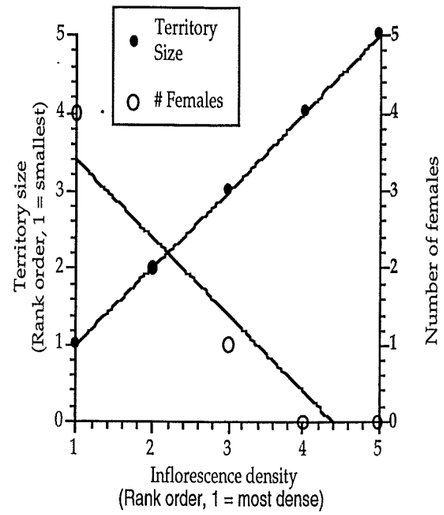

Figure 1. Territory size and number of females as a function of inflorescence density at Cuerici Biological Preserve, Costa Rica.

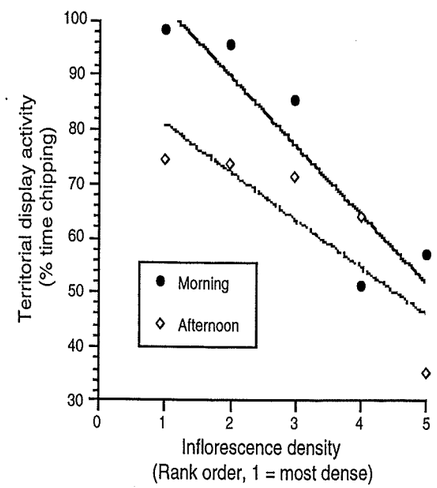

Fig. 2. Territorial display activity by fiery-throated hummingbirds as a function of inflorescence density at Cuerici Biological Preserve, Costa Rica.

range of flower densities, males spent approxi mately 20% less time chipping in the afternoon than in the morning ($t = -7.09$, $df = 4$, $P = 0.002$; Fig. 2). In addition, interspecific interactions appeared to be more frequent on high-quality than on low-quality territories, although we were unable to quantify this.

Discussion

Fiery-throated hummingbirds are a highly territorial species whose breeding success depends on the quality of their territories, as measured by flower density (Stiles 1983). At Cuerici Biological Preserve, males with flower-rich territories spend more time chipping than males with flower-poor territories, perhaps because the high flower density allows the males to ingest adequate nectar in less time and to call for more time than males on low quality territories. Additionally, males with flower-rich territories might spend more time chipping due to increased interspecific and intraspecific competition.

Temporal variation in chipping (Fig. 2) might be due to diurnal variation in territory quality. Because daytime nectar production is highest in the morning, males may spend more time defending nectar-rich flowers during the morning than after nectar resources are depleted. Greater defenses could also be a reflection of typical weather conditions in which clear morning skies often give way to heavy clouds and afternoon mists. Perhaps, both territory holders and potential competitors are more active in the morning than in the afternoon when energy expenditures might be greater due to wet, cool conditions.

Flower density apparently also affects the presence of females, intraspecific competitors, and interspecific competitors. Females were only observed in the three highest quality territories. Similarly, interspecific competitors such as the slaty flower piercer (Diglossa plumbea) and the volcano hummingbird (Selasphorus flammula) were more abundant in the two most flower-rich territories. Nevertheless, the male hummingbird's defenses indicate that despite additional interspecific competition, it may be beneficial for males to defend the best territories due to increased mate attraction.

Our results support the hypothesis that territory quality affects chipping rates, territory size, and number of visits by females. The population dynamics of fiery-throated hummingbirds appear to be heavily resource driven, and future studies might center on the hummingbird's susceptibility to decreased resource abundance. This might aid the preservation of this species by highlighting the extent to which flower resources dictate fiery-throated hummingbird populations.

Literature Cited

Stiles, F.G. 1983. *Panterpe insignis*. Pages 593-594 *in* D. H. Janzen, editor. Costa Rican Natural History. University of Chicago Press, Chicago, Illinois, USA.

EFFECTS OF FORAGE PREFERENCE ON TRAIL QUALITY AND TRANSPORT EFFICIENCY IN *ATTA CEPHALOTES*

Jon S. Beadell, Christy Hansel, James W. Hourdequin

Abstract. Variation in the clearing of trails created by *Atta cephalotes* may be a function of different ant densities on trails leading to different quality forage. Ant density was highest on trails leading to high-quality forage. These trails were better cleared and allowed ants to travel faster than on poorly-cleared trails. This suggests that responses to forage of variable quality may be governed by the ant colony (numbers of ants retrieving forage) and not individual ants (behavioral shift).

Key Words: Atta cephalotes, *leaf toughness, trail quality, transport rate*

Introduction

Leaf-cutter ants, *Atta cephalotes*, create small trails through leaf litter in lowland tropical forests to transport leaves from forage sites to the fungal gardens that feed their larvae. The ants form the trails by removing litter and pushing it to the side or carrying it back to their colony (Canny et al. 1996). Numbers of traveling ants and the amount of clearing varies considerably among trails. Nichols-Orions and Schultz (1990) found that ants preferentially select leaves of low toughness because they are easier to cut and transport back to the colony. We hypothesized that opportunities for high quality forage attract a greater number of ants, which results in more clearing, and consequently, faster movement of high quality forage.

Methods

We observed leaf-cutter ant activity on 31 January 1996 on the Sendero Rio Sirena at Parque Nacional Corcovado. We selected two high and two low quality trails based on the amount of debris present and measured trail width, an indicator of clearing, at five points spaced 1 m apart. The total number of ants moving in both directions ("flux") across a line in the trail was recorded over a two-minute period. We collected 20 leaves from each of the four trails and measured leaf toughness using a penetrometer. Leaf toughness was ranked on an ordinal scale based on natural groupings of penetrometer readings. On each trail we marked 12 leaves carried by ants, measured ant travel time over a 5 m segment of trail, and recorded incidences of dropped leaves. Linear regressions were used to compare leaf toughness to ant flux, flux to trail width, and trail width to travel time.

Results

Ant flux was highest on trails leading to low toughness forage ($r = -0.94$, $P = 0.08$; correlation between leaf toughness and ant flux). Trails with more ants were better cleared than trails with fewer ants ($r = 0.92$, $P = 0.05$; correlation between ant flux and trail width). Travel time was significantly lower on trails appearing well-cleared (mean ± SE = 247 ± 18 vs. 550 ± 34 sec; $t = 2.06$, $df = 24$, $P < 0.001$), and there was a strong negative correlation between trail width and travel time ($r = -0.64$, $P < 0.001$). Leaves were not dropped by ants on either class of trails.

Discussion

Ant colonies appear to respond to high quality forage by producing wide, well-cleared trails that allow for efficient transport of the foliage. Trails leading to high quality forage were wider and better cleared, and travel time decreased with increased clearing. If individual ants allocate a similar proportion of time to clearing regardless of the quality of the trail (Canny et al. 1996), then the mechanism behind increased clearing of trails may be an increase in the number of ants clearing trails and not a behavioral shift in individual ants. It is not clear, however, whether different castes are responsible for different activities given that ants carrying leaves and ants clearing trails were morphologically similar. Nonetheless, as a consequence of clearing, the colony accumulates high-quality leaf tissue more rapidly. Leaf retention did not vary with trail quality; thus, the increase in rate of forage transport may be the greatest benefit of trail clearing.

The results of this study suggest that poorly-cleared trails lead to poor-quality forage and that these trails may only exist if an ant colony does not have access

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.

LITERATURE CITED

Canny, D., J. Ruben and P. Shelby. 1996. Trail clearing behavior in *Atta cephalotes*. Pages 69-71 *in* A. L. Mannan and D. S. Canny, editors. Dartmouth Studies in Tropical Ecology. Dartmouth College, Hanover, NH, USA.

Nichols-Orion, C. and J. C. Schultz. 1990. Interactions among leaf toughness, chemistry, and harvesting by attine ants. Ecological Entomology **15**: 311-320.