Discussion

Contrary to predictions, *Eleutherodactylus* frogs in our experiment did not show a significant preference for brown leaves over green and yellow leaves during any of the monitoring periods. During mid-day, however, there was a trend that frogs tended to spend more time on the top of brown leaves. Because the frogs spent only 12% of their time on top of leaves, the sampling time may have been too short to detect a significant difference between time spent on the top of brown leaves and the top of green and yellow leaves.

Crypticity seemed to be accomplished more by frogs hiding under leaves than selection of leaf substrate that matches body color. Frogs spent significantly more time under leaves than on top of leaves during both the morning and mid-day monitoring periods relative to the night monitoring period. We found no significant difference between time spent on top of leaves between morning and mid-day. During both morning and mid-day, light levels were comparable, but temperature was 8°C lower in the morning than mid-day; therefore, temperature does not seem to be a primary factor affecting frogs' choice of leaf position. Frogs' behavior in selecting leaf position during night and day was consistent with our reasoning that hiding under leaves is more important during the day when the majority of their predators are active.

At night, frogs actually spent more time on top of leaves than under leaves. Because we placed the frogs on top of a leaf when first introducing them into the enclosure, moving below the substrate would have required an active choice. For this reason, we do not know if frogs actually prefer sitting on top of leaves during the night or if they have no preference for either leaf position. At night, most frogs hopped a short distance onto a nearby leaf or crawled in short spurts of movement onto adjacent leaves. In daylight, their behavior was markedly different; they actively selected a position under a leaf.

Frogs' behavior during the monitoring periods may have been affected by our experimental design. They may have hidden under leaves because of our presence, though this seems unlikely since it was observed only during the daytime trials. At night, the muted light may have altered their behavior. In other respects, the enclosure appeared to us to closely match their natural environment with its heterogeneous moist litter layer and placement near the forest edge. Frogs rarely attempted escape; one of the frogs even ate an ant during the observation period.

Predator avoidance by *Eleutherodactylus* frogs appears to be accomplished through a variety of behavioral and physiological adaptations. Cryptic coloration could be a passive means of predator avoidance. Even though these frogs do not seem to actively seek out leaves that most closely match their coloration, they are still more difficult to find in the predominantly brown leaf litter than the brightly colored aposematic species, for example. The frogs may, however, exhibit an active means of predator avoidance by hiding under leaves during the day. Our findings indicate that the availability of under-leaf refuges may determine the distribution of *Eleutherodactylus* frogs more than substrate color matching. We do not yet know whether frogs in the field actually forage by hiding under leaves, waiting for prey to pass by, or whether they take refuge under leaves only when threatened. To better understand *Eleutherodactylus* frogs' hiding behavior, future studies should focus on differences between foraging behavior and behavior when confronted with a predator.

Literature Cited

Savage, J. M. and S. B. Emerson. 1970. Central American frogs allied to *Eleutherodactylus bransfordii* (Cope): A problem of polymorphism. Copeia 1970: 623-44. [cited in Janzen 1983.]

Scott, N. J. 1983. *Eleutherodactylus bransfordii* (Rana). Page 399 *in* D.H. Janzen, editor, Costa Rican Natural History. The University of Chicago Press: Chicago, IL, USA.

Scott, N. J. and S. Limerick. 1983. Reptiles and amphibians. Pages 351-363 *in* D.H. Janzen, editor, Costa Rican Natural History. The University of Chicago Press: Chicago, IL, USA.

Woodson, P. S. and B. M. Everett. 1994. Differing foraging strategies of *Dendrobates pumilio* and *Eleutherodactylus* spp. Pages 103-105 *in* J.L. Bykowski, editor, Dartmouth Studies in Tropical Ecology 1994. Dartmouth College: Hanover, NH, USA.

BURNING THE MIDNIGHT OIL: DIEL PATTERNS IN ACTIVITY LEVEL IN *ATTA CEPHALOTES*

Wendy A. Cover, Phuong T. X. Hang, and Grace M. Kim

Abstract. Leaf-cutting ants are one of the major contributors to nutrient cycling in tropical lowland rain forest. Though diurnal movements of leaf-cutting ants to and from the nest have been well studied, very little is known about these activities at night. Several investigators have assumed that movements to and from the nest of leaf-cutting ants decrease during the night. However, we found that ants at Corcovado National Park are active during both day and night, and we also uncovered a cyclical patterns in activity throughout a 24 hr period, with activity peaking at 06:00 again at 18:00 and declining in the periods between. Despite the fluctuations in ant activity, there was a constant influx of leaves throughout the night which indicates continuous foraging. Future studies on leaf-biomass accumulation or diel patterns of *Atta* ants must include night time activities in order to avoid missing a large fraction of the active and efficient foraging time for *Atta*.

Keywords: ant activity, diel patterns, Atta cephalotes

Introduction

Leaf-cutting ants, *Atta cephalotes*, are an abundant and conspicuous component of lowland tropical forests. *A. cephalotes* contributes to nutrient cycling in tropical lowland rain forests by being one of the major herbivory agents - working in concert with fungus to decompose leaf matter in the system (Steven 1983). *A. cephalotes* in the same colony work together to bring back leaves along organized trails to the central nest. Many factors have been found to influence activity patterns of *A. cephalotes*. According to Cover et. al. (1997), sunlight and temperature stimulate leaf-cutting ants to form leaf-piles along the trails. They found that *A. cephalotes* only formed leaf-piles in sunny spots, and that temperature in these spots was higher than those spots without leaf-piles. Another previous study at Corcovado National Park found ants active during daylight hours, with ants moving out of the nest during early morning hours and coming into the nest before dusk (Liebert and Ruel 1994). Mannan et. al. (1996) estimated net leaf biomass intake to a leaf cutter ant colony to be 4.78 metric tons.ha-1.yr-1, based on activity measured during the day. Both Liebert and Ruel et. al. and Mannan et. al. assumed that there would be a decrease in activity of *A. cephalotes* at night. To the contrary, our preliminary observations indicated that leaf-cutting ants were also active at night. Thus, we developed the null hypothesis that there would be no difference in the movements to and from the nest of leaf-cutting ants between day and night, and consequently that the number of leaves coming into the nest would not differ between day and night. Knowing how much leaf-cutting ants forage during the night as well as day provides further insight into the ecological role of leaf-cutting ants in tropical ecosystems, especially nutrient cycling.

Methods

We chose four ant highways, belonging to four different colonies, close to the Estación Biológica Sirena at Corcovado National Park, Costa Rica. They were located < 10 m into the Pavo, Ollas, and Naranjo trails and were of arbitrary size, length, and distance from the nest. At one point along each highway we counted the number of ants moving towards the nest with leaves, the number of ants moving towards the nest without leaves, and the number of ants moving away from the nest, each for a 60 s time period. We took three replicates, and also recorded the air temperature 1 cm above the trail. Data collection continued every three hours for a 24 -hour period. Leaf piles along the highways often form during the day, so we collected data at a point before the incoming ants reached the leaf pile, in order to reduce possible biases in our data.

We defined "activity level" as the total number of ants moving in both directions within the 60 s time interval. We defined "net flow out" as the number of ants moving away from the nest minus the number of ants (with or without leaves) traveling toward the nest. We used paired t-tests to compare day and night data for activity level, net flow out, and number of leaves moving into the nest. We factored out differ-

ences between trails by performing a repeated measures analysis of variance with trail as a blocked factor.

RESULTS

We found that leaf-cutting ant activity was significantly different according to time (repeated measures ANOVA F=17.64, df=28, P<0.001). Activity peaked at 06:00 and precipitously dropped by 12:00, after which it peaked again at 18:00 and declined by 00:00 (Fig. 1). There was considerable variation in ant activity level among trails unrelated to time of day, but the relationship between activity level and time was consistent (repeated measures ANOVA F=7.25, df=3, P=0.001). Overall, however, leaf cutting ant activity levels were not significantly different between the daylight hours (06:00-15:00) and night hours (18:00-15:00) (t-test, t=1.66, df=15, P=0.30).

We also found a significant difference in net flow of ants with time (F=8.11, df=28, P<0.001). We found net flow out of the nest to be highest at 06:00 (Fig. 2). Net flow of ants away from the nest was significantly higher during the day than the night (t=3.45, df=3, P=0.04). During the day the net flux of ants were away from the nest (22.39+10.97 SE) and at night the net flux of ants were towards the nest (-8.06+3.45 SE).

We found that the number of ants carrying leaves towards the nest was significantly different according to time (repeated measures ANOVA, F=13.63, df=28, P<0.001). The influx of leaves was lowest at 06:00 and increased throughout the morning with a peak in the late afternoon (15:00-18:00) and then a positive influx of leaves continued throughout the night (Fig. 3). There was considerable variation due to trail variation that were unrelated to time of day, but the relationship between number of leaves and time was consistent (repeated measures ANOVA, F=5.63, df=3, P=0.004). However, the number of ants carrying leaves towards the nest did not differ between day and night (t=0.384, df=3, P=0.723).

We found temperature to be highest during midday (09:00-15:00; Fig. 4).

DISCUSSION

As predicted, ant activity levels were not significantly different during night and day hours. This pattern of activity can effectively double the foraging rate of ants over the pattern of foraging assumed by previous studies. Continuous night time activity probably maximizes foraging success for the ants, as it increases their leaf input. Ant activity fluctuated strongly within the 24 hour period. There was a significant drop in activity by noon, which other studies have thought to be correlated with the increased temperatures at this time (Liebert & Ruel 1994). We found a trend between high temperature and low noontime activity, but since there is almost no change in temperature throughout the night and ant activity sharply declines again at midnight, factors other than temperature are likely at work. Net flow away from the nest was also at its highest in the morning around 06:00, which coincides with the dawn peak in activity. A possible explanation for the decrease in activity at 12:00 and 00:00 is that the majority of the ants have left the nest and are out actively foraging, therefore not using the highway at that time.

Also, we found that as the number of ants moving out of nest in the morning was high, the number of leaves entering the nest was low. This suggests that ants leave the nest in the morning so that they can forage during the day and continuously bring more leaves back, with a peak during mid afternoon, and maintain a constant flow of leaves in throughout the night. By not including night time activities, previous studies estimating biomass brought in by leaf-cutting ants might not have been accurate. Future studies on leaf-biomass of *Atta* must include night time activities.

LITERATURE CITED

Mannan, A. L.., Taliaferro, E. H., Little, M. K. 1996. Annual and diel harvest rates of leaf-cutter ants. Pages 78-79 *in* A. L. Mannan and D. S. Canny, editors. Dartmouth Studies in Tropical Ecology. Department of Biological Sciences Dartmouth College, Hanover, NH.

Leibert, A. E., and Ruel, J. J. 1994. Diurnal and temperature related patterns in *Atta cephalotes* trail use. Pages 62-65 *in* J. L. Bykowsky, editor. Dartmouth Studies in Tropical Ecology. Department of Biological Sciences Dartmouth College, Hanover, NH.

Stevens, G. C. 1983. *Atta cephalotes* (Zompopas, Leaf-cutting ants). Costa Rican Natural History. Edited by D. H. Janzen. The University of Chicago Press: Chicago.

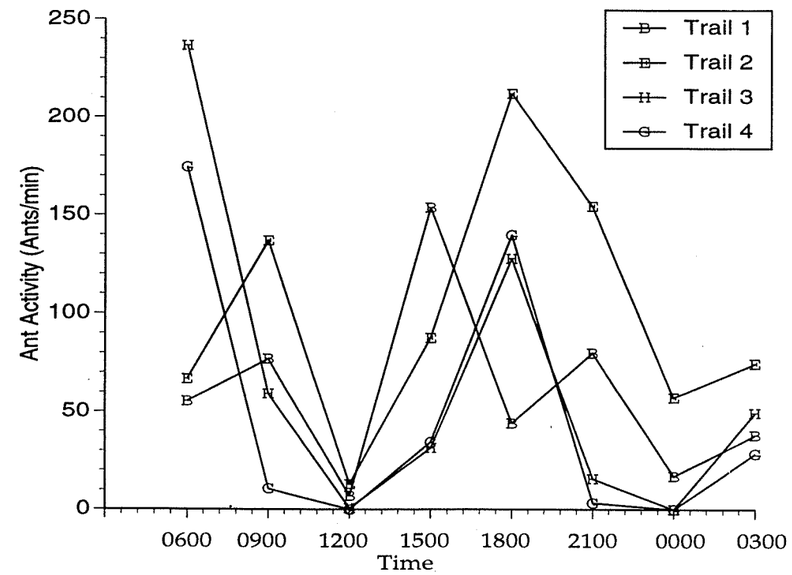

FIG. 1. Diel patterns in ant activity (number of ants moving in either direction past a point on the trail/min) for all four trails. Data points represent means of three samples for each trail at each time.

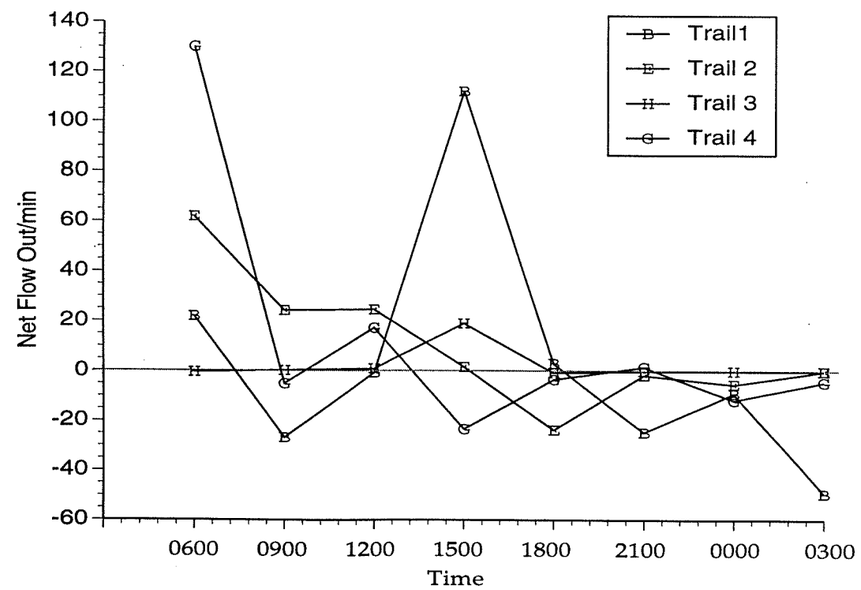

FIG. 2. Diel pattern in the net flow of ants going away from the colony (outgoing ants/total ants past a point on the trail) for all tour trails. Negative numbers indicate a net flow of ant coming toward the colony nest. Data points represent means of three samples for each trail at each time.

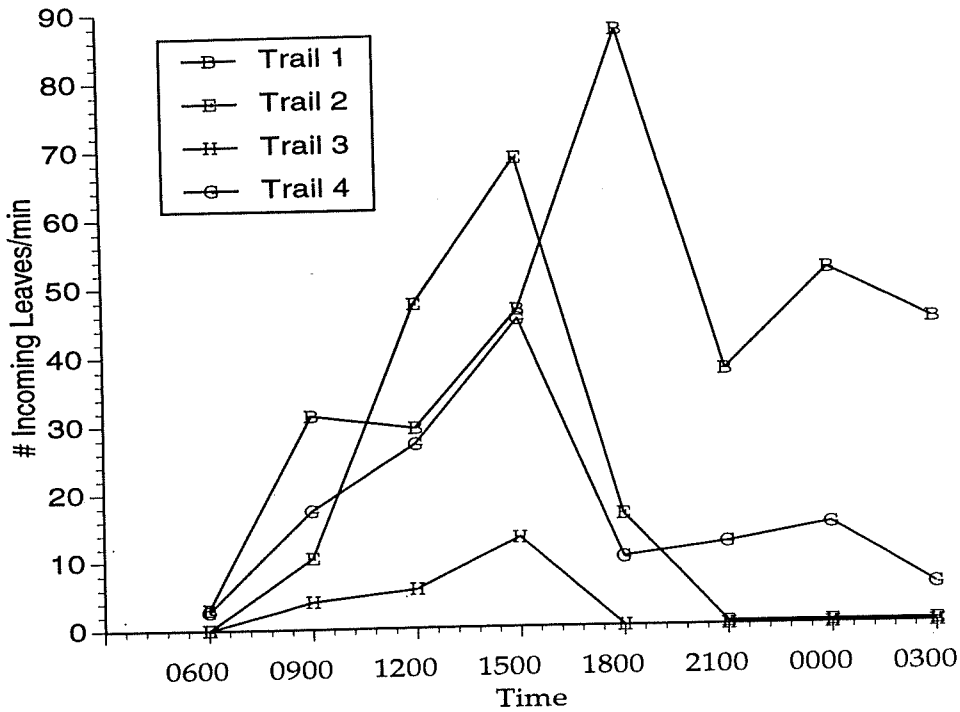

FIG. 3. Diel pattern in number of ants carrying leaves toward the colony nest/min for all four trails. Data points represent means of three samples for each trail at each time.

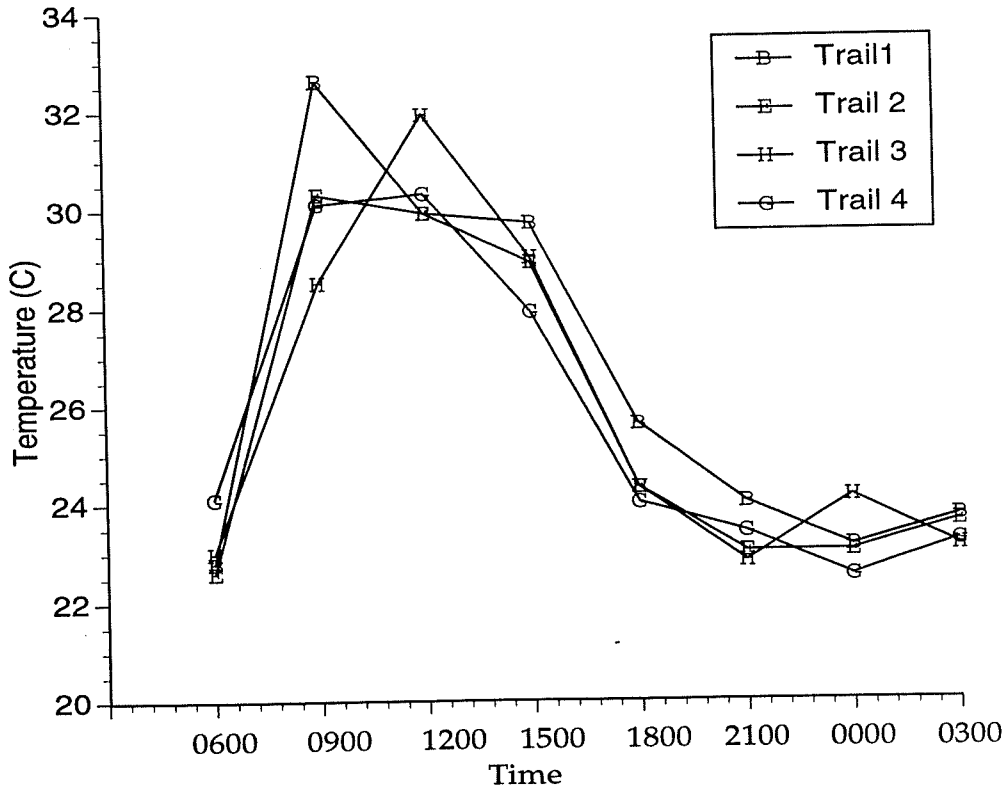

FIG. 4. Diel pattern in temperature(degrees celcius) for all four trails.