DIEL EMIGRATION AND FORAGING BEHAVIORS OF THE ARMY ANT, *ECITON HAMATUM* (SUBFAMILY ECITONINAE)

SAMUEL J. HAYNOR, CHAD S. GORBATKIN,
SARAH C. ISBEY, AND ZACHARY A. MAYER

Faculty Editor: David R. Peart

Abstract: As predators of many social insects and larger arthropods, army ants are a key component of tropical forest ecosystems. Specifically, their foraging behaviors and food preferences can affect forest invertebrate abundance and composition. To better understand army ant behavior, we observed foraging and movement patterns of *Eciton hamatum* for a continuous 20 hour period. We measured movement rates in and out of the bivouac and mapped changes in foraging column and bivouac locations. We also characterized substrate use by foraging columns. The number of columns and movement rates varied with foraging status (e.g. active foraging or zero foraging). *Eciton hamatum* moved only in dense columns (~ 4 ants wide), showing no swarm foraging behavior. *E. hamatum* workers foraged during the morning hours and only on larvae of social insects, including wasps, ants, and termites. From the evening into the night , the ants spent seven hours (1600-2300) emigrating from their old bivouac to their new bivouac, approximately 90 meters away (column distance). Army ants were more commonly found traveling on branches than on leaves or bare soil. *Eciton hamatum* may have considerable effects on the reproductive success and colony structures of their primary prey sources (social insects).

Key Words: bivouac, foraging column, Corcovado

INTRODUCTION

In many tropical and subtropical forests, army ants are important predators of social insects, large arthropods, and small vertebrates (Brady 2003; Powell and Franks 2005). Army ants can influence tropical biodiversity through two mechanisms: (1) migrating army ant colonies can alter arthropod community composition and abundance (Boswell et al. 1998) and (2) army ants can create niches for approximately 200 obligate and facultative associate species, including 50 neotropical bird species, phorid flies, parasitic beetles, and mites (Kistner 1982). Recent genetic and fossil evidence suggests that the 298 ant species with the 'army ant adaptive syndrome' (i.e. obligate social foraging, nomadism, and dichthadiigyne queens (i.e., blind queens with large gasters and ovaries)) evolved from a common subterranean ancestor in the subfamily Dorylinae (Brady 2003; Berghoff 2003). Some non-army ant species display two of the three characteristics of army ant adaptive syndrome, but only true army ants

display all three. Many army ant genera have remained partially or completely subterranean, but some exhibit derived epigaeic (above-ground) foraging behaviors. Certain lineages also differ in foraging strategies, ranging from swarm feeding to the specialized raiding of termite, ant, or wasp colonies in columns (Berghoff 2003; Kaspari and O'Donnell 2003). Many species also exhibit diel and/or seasonal variation in prey selection, raid formations, and emigration cycles (Forsyth and Miyata 1984).

We studied the foraging and emigration behavior of *Eciton hamatum* (Subfamily Ecitoninae), a species of epigaeically and arboreally foraging army ant in the tropical moist forests of Corcovado, Costa Rica. We aimed to better understand the ecological roles of *E. hamatum* as arthropod predators by measuring the ant's diel foraging behavior, movement patterns, and interactions with other species. We hypothesized that the colony would have different periods of maximum biotic interaction (e.g. intense foraging) and minimum biotic interactions (e.g. retraction of all ant columns to the bivouac). Based on previous field observations of a different army ant species at Corcovado on 3 February 2007, we predicted that maximum foraging would occur during daylight while bivouac emigration and rest would occur at night.

METHODS

We observed one army ant colony continuously from 1045 on 4 February to 0630 on 5 February in Corcovado National Park, on the Osa Peninsula of Costa Rica. As soon as we located the colony on 4 February, we began recording rates of movement of ants both in and out of the bivouac, and mapping all columns leaving the bivouac. Natural history data (personal observations and notes about the surroundings and ant activity) were collected throughout the day and night.

We recorded five categories of ant movement rates (number of ants per min in and out of the bivouac) every half hour. During periods of highly fluctuating movement (e.g. during bivouac dismantling and relocation), we recorded movement rates continuously. When the bivouac contained more than one column, we recorded the rates for each column. Ant movement rates were estimated by counting the number of ants crossing a designated point on the substrate in a ten second interval. Specifically, for each ten second count, we recorded the number of ants: (1) moving into the bivouac, (2) moving out of the bivouac, (3) carrying larvae, and (4) carrying larval prey. In all cases but those where ant activity was

changing at an interval of 10 seconds or less, we recorded movement rates for each of the four movement types for five replicate 10-second sampling intervals per half-hour time period. In times of high activity fluctuation, we did not replicate rate samples because ant movement was changing rapidly between replicates. The only prey items we observed ants carrying were larvae of other social insects (i.e. wasps, termites, and ants), which we were able to differentiate from their own larvae based on size and direction of movement (ants moved prey into the bivouac, while they only moved their own larvae out of the bivouac).

Bivouac emigration occurred from 1600-2300 on 4 February 2007. We mapped the columns of the colony every 2.5 hours throughout the study, except during times of bivouac dormancy from 2215 on 4 February to 0345 on 5 February. We measured the lengths of all ant columns (main foraging columns plus side branches). For each distinct column segment, we recorded the substrate type (sticks/twigs, bare soil, or leaves), the total number ants carrying food sources, the number of ant body-bridges, and the length of the column segment. For each of the six replicate mapping periods, we measured the proportion of each substrate type used, summing across all columns and column branches sampled. A bridge was noted any time one or more ants served as a connector between two objects on the path. Army ants link together to form these bridges, which expedite movement by other individuals in the colony.

Analyses

To characterize the diel patterns of ant movements in and out of the bivouacs, we plotted average movement rates (four types: with and without larvae by direction (in and out of the nest)) over the entire 20 hour period (averages of five replicate 10-second counts per movement type in each 30-minute time interval and single rates from periods of rapid change in movement rates). To calculate the rate of ants moving into the new bivouac, data from the ants moving out of the old bivouac were shifted forward three hours (lag time between departure from old bivouac and arrival at new bivouac). Here, we assumed that all ant velocities were equal to the velocities of the final departing ants (used for lag time calculations). We compared the mean percent of total column length of different substrate types used by the ants with a one-way ANOVA (n = 6 mapping periods for the entire colony).

RESULTS

Diel Patterns

During the 20-hour observation period, we observed the

army ants foraging and moving their bivouac. When we found the army ant colony on 1045 4 February 2007, they had an established bivouac and three foraging columns. At 1300, the ants from the foraging columns began to return to the nest, and at 1600, activity on one column greatly increased (Fig. 1). At this point, the

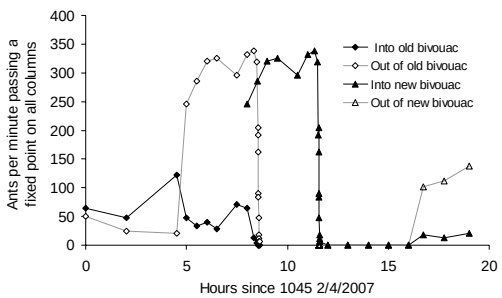

Figure 1. Number of *E. hamatum* ants entering and exiting the old and new bivouacs per minute (averaged across 5 10-second observation periods at each half hour, except during periods of high activity where there was no replication). Immediately before bivouac emigration, the number of ants entering the old bivouac greatly increased. The increase in activity between hours 16 (0345) and 20 (0630) shows foraging from the new bivouac after it was established.

ants began to carry their larvae towards the new bivouac along this column (Fig. 2). We discovered a new bivouac at the end of this column and, as the movement of larvae towards the new bivouac increased, the number of foraging ants returning with prey items to the old bivouac decreased (Fig. 2). By the time ant activity on the column moving towards the new bivouac had increased greatly, all other columns had disappeared (Fig. 3). There was an approximately three hour time lag between the time when the old bivouac was entirely deserted (1937) and the time when the entire column of ants had reached the new bivouac (2216, Fig. 1). After the new bivouac was

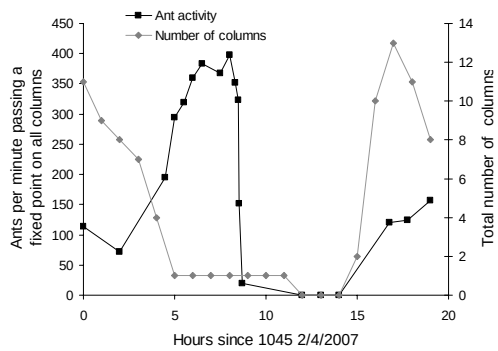

Figure 2. *Eciton hamatum* ant activity (sum of ingoing and outgoing ants) in all columns and total number of columns emanating from the bivouac over a 20 hour period. Hours 0-12 represent the old bivouac and hours 12-20 represent the new bivouac. In the morning of 4 February 2007, the number of columns was declining, as the foraging columns were eliminated and activity focused on a single bivouac emigration column. After the number of columns dropped to one, bivouac emigration intensified and ant activity spiked. After the bivouac emigrated, the colony was dormant for several hours. At 0345, multiple foraging columns formed and ant activity increased.

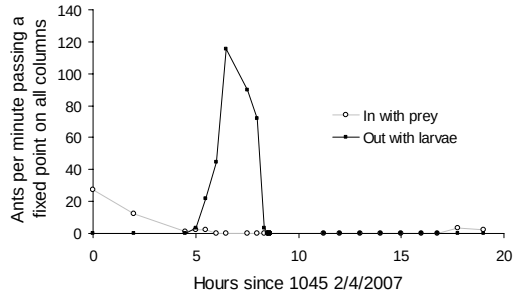

Figure 3. Number of *E. hamatum* ants moving into the bivouac with prey and out of the bivouac with larvae throughout the observation period. The large spike in larvae movement corresponds with bivouac emigration. Immediately before bivouac emigration, the number of ants entering

with prey decreased greatly. Increases at hour 18 (0430) and 19 (0520) represent the reestablishment of foraging.

established, activity ended for approximately 5.5 hours until 0345 on 5 February, when the ants established three new foraging columns (Fig. 1).

Foraging Columns

Throughout the six replicate mapping periods, we surveyed a total of 1159 meters of ant columns on three different substrates. The ants did not use substrate types equally (ANOVA, $F_{(2,15)} = 17.00$, $P = 0.0001$, Fig. 4). For all column lengths studied throughout the entire 20-hour sampling period, 65% was on branches and twigs, 32% was on leaf litter, and 3% was on bare soil.

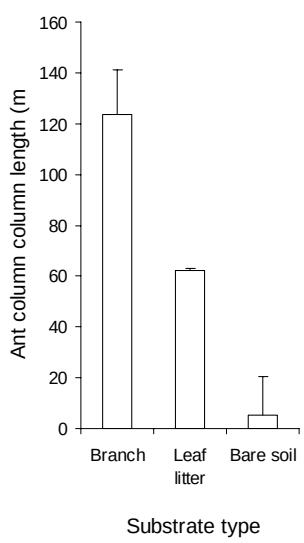

Figure 4: Mean total column length covered by *E. hamatum* ant foragers on each of three substrate types (branches, leaf litter and bare soil) in six replicate mappings, evenly spaced at 2.5 hour intervals over the 20-hour study period, excluding the bivouac dormancy period. There was little dirt available for ant travel. Error bars represent 1 SE.

Early morning ant foraging activity was much lower than ant activity during bivouac emigration (Fig. 1). The maximum number of columns (13) was recorded when foraging recommenced at the new bivouac (Fig. 2). These columns extended as far as 200 meters away from the bivouac and typically ended with raids of arboreal insect nests (Fig. 3). We calculated that the longest foraging columns would require a three hour round trip from the bivouac to their prey location (0.0025 hour/m x 400 m of column). Finally, we found that *E. hamatum* would not consume live or dead adult arthropods that we placed in their foraging columns, and the ants would notice and collect prey larvae only if larvae were placed within seven centimeters or less of the foraging column.

Bivouac movement

Bivouac emigration took place over seven hours, followed by a 5.5 hour dormancy period after the entire colony had reached their final destination (Fig. 1). The ants moved their bivouac to a fallen log that was 90 m along a foraging column from the original bivouac location (71 m absolute distance). Prior to bivouac emigration, this column had reached a length of 140 m. It then retracted in the early afternoon before bivouac

emigration. After we observed soldier ants near the bivouac that appeared to be erasing foraging paths using anally-transmitted pheromones, only a single column remained, extending from the old bivouac site to the new bivouac (Fig. 2). Flanked by soldiers on the sides of the column, ants transported larvae in a narrow (3-4 cm wide) column through the forest floor at sunset. During the 7-hour emigration period (including preparation time), we observed no foraging activity. In total, the *E. hamatum* colony did not prey on any insects in the trees or in the leaf litter for almost 12 hours, from 1600 on 4 February to 0345 on 5 February.

DISCUSSION

Army ant foraging strategies and their subsequent ecological effects can vary both among species and among seasons (Kaspari and O'Donnell 2003). While approximately seven-week cycles of either bivouac dormancy or nomadism have been recorded in many army ant species (Boswell et. al. 1988), we found evidence for shorter diel behavioral cycles in *E. hamatum.* As predicted, peak foraging occurred in the early morning, and bivouac movement occurred in the evening and early night. These diel foraging and movement patterns might be adaptive if they reduce parasitism rates by diurnal phorid flies (primary parasites of many army ant species). In addition to their direct lethal effects, some phorid flies elicit alarm pheromones from both sedentary and nomadic ants, which greatly decrease foraging and movement efficiency (Braganca et al. 1998). Because *E. hamatum* bivouac emigration occurs in a single column, alarm pheromone release could devastate emigration attempts. Additionally, the individuals directly linked to colony fitness (larvae and the queen) would be exposed to parasitism if they moved the bivouac during the day. Experimental manipulations of phorid fly density during different foraging and emigration stages would help isolate the effects of phorid flies on *E. hamatum* diel behavior patterns.

Foraging Columns

Army ants are obligate social foragers, requiring pheromones to maintain colony-scale efficiency. Without pheromone trails, ants that we experimentally displaced rarely found their way back to foraging columns, and often did not return to the bivouac. Pheromones may also be necessary to recruit enough ants to overcome adult prey arthropods that are defending their colony's larvae.

Army ants are selective foragers, in contrast to the more generalized swarming army ant species (e.g. *Eciton burchellii)*, which

entirely clear leaf litter of adult arthropods and even small lizards (Powell and Franks 2005). The distinct foraging columns we observed are likely to affect the terrestrial invertebrate community differently than mass foraging swarms characteristic of some other army ant species, such as the well-studied *E. burchelli*. Columnar foraging is extremely selective, as foragers ignore nearby food sources to raid large larval caches farther away. Instead of creating large changes in invertebrate community composition and abundance, *E. hamatum* reduces reproductive success of a few social invertebrate species.

Even though the forest floor we studied consisted mostly of leafy material (*personal observations*), *E. hamatum* foraging columns primarily moved on woody substrates (Fig. 4). Therefore, they may also be spatially removed from most of the terrestrial invertebrates that live only in the leaf-litter, such as the prey harvested by swarming army ant species. Because *E. hamatum* forages in columns on woody substrates without flushing out leaf litter arthropods, they do not create niches for ant-following birds which feed on flushed-out arthropods (Boswell et. al. 1988).

Bivouac Movement

Foraging and bivouac emigration periods occurred at different times of day, and we documented the transition between the two. Because foraging occurred in columns, retraction of the day's raid was rapid, sometimes at a rate of two meters per minute. Immediately before the colony moved their bivouac, workers formed bridges with their bodies to span gaps in the leaf litter. In foraging columns, bridging behavior was only observed when movement rates were high. The occurrence of bridges in high-traffic columns suggests that bridging is important for efficiently transporting large numbers of ants across broken terrain. The army ant body-bridges we observed were composed of as many as 90 bodies per bridge, and bridges sometimes occurred in densities greater than ten bridges per meter of column. All bivouac emigration was concentrated in a single four centimeter-wide column with many ant body bridges. Therefore, larger colonies may spend a greater proportion of their time transporting their bivouac, which could cut into overall foraging time. Single column emigration may limit *E. hamatum* colony size. Further research should investigate emigration patterns of different size colony population and how this relates to the colony energy budget.

Ecological Impacts

Army ants can influence tropical forest biological diversity

through two mechanisms: predation leading to changes in arthropod community composition and abundance (Boswell et al. 1998; Brown and Feener 1998) and facilitation of obligate and facultative associates (Kistner 1982). In addition, the selective larval predation exhibited in *E. hamatum* may affect the evolution of life history strategies in their arboreal social insect prey. For example, when an *E. hamatum* worker successfully communicates the location of a potential food source to the rest of the colony, forager recruits proceed to remove larvae from that source until it is depleted. Therefore, column army ant predation may select for small, well-hidden colonies in its prey (e.g. wasps), while leaving colony size strategies of litter-dwelling arthropods relatively unaffected. Thus, column-foraging species of army ants may have concentrated, species-specific effects on invertebrate communities. In contrast, a mass swarming foraging strategy might create changes in invertebrate communities that affect more invertebrate individuals and species, which could subsequently influence invertebrate competition and diversity in tropical ecosystems (Boswell et al. 1998).

Compared to the swarming foragers such as *E. burchelli*, the intensity of *E. hamatum* foraging is be mitigated by both its propensity for selective foraging as well as the time required for bivouac emigration in columns. However, *E. hamatum's* effects on its individual prey species are still likely very strong, removing the majority or all of larvae from a given nest (*personal observation*). Social insects, such as those targeted by *E. hamatum*, are ecologically important species who make up a large portion of forest biomass and perform essential ecosystem functions (Wilson and Holldobler 2005). By preying upon these ecologically important species, *E. Hamatum* may have strong indirect effects on the forest ecosystem.

LITERATURE CITED

Berghoff, Stefanie. 2003. Army ants: and evolutionary bestseller? Current Biology 23: R676-R677.

Boswell, G.P., Britton, N.F., and Franks, N.R. 2005. Habitat fragmentation, percolation theory, and the conservation of a keystone species. Proceedings: Biological Sciences 265(1409): 1921-1925.

Brady, Seán G. 2003. Evolution of the army ant syndrome: the origin and long-term evolutionary stasis of a complex of behavioral and reproductive adaptations. Proceedings of the National Academy of Sciences USA 100: 6575-6579.

Bragnaca, M. A., A. Tonhasca, and T.D. Lucia. 1998. Reduction in the foraging activity of the leaf-cutting ant *Atta sexdens* caused by the

phorid *Neodohrniphora sp.* Entomologia Experimentalis et Applicata 89.3: 305-311.

Brown, B. and D. Feener. 1998. Parasitic phorid flies (Diptera: Phoridae) associated with army ants (Hymenoptera: Formicidae: Ecitoninae: Dorylinae) and their conservation biology. Biotropica 30.3: 482-487.

Couzin, I.D. and Franks, N.R. 2003. Self-organized lane formation and optimized traffic flow in army ants. Proceedings of the Royal Society of London 270: 139-146.

Forsyth, A. and K. Miyata. 1984. Tropical Nature. Charles Scribner's Sons: New York, NY.

Kaspari, M. and O'Donnell, S. 2003. High rates of army ant raids in the Neotropics and implications for ant colony and community structure. Evolutionary Ecology Research 5: 933-939.

Powell, S. and N.R. Franks. 2005. Caste evolution and ecology: a special worker for novel prey. Proceedings of the royal society B 272: 2173-2180.

Wilson, E.O. and B. Holldobler. 2005. The rise of ants: A phylogenetic and ecological explanation. Proceedings of the National Academy of Science USA 102: 7411-7414.

Witte, V., and U. Maschwitz. 2000. Raiding and emigration dynamics in the ponerine army ant leptogenys distinguenda (Hymenoptera: Formicidae). Insectes Socieoux 47: 76-83.