ENVIRONMENTAL CUES DRIVING THE DIEL ACTIVITIES OF THE TERRESTRIAL HERMIT CRAB *COENOBITA COMPRESSUS*

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Abstract: Hermit crabs at Corcovado National Park, Costa Rica migrate each day from the beach to the forest to seek shelter, and each night from the forest to the beach to forage. We hypothesized that the hermit crabs use environmental cues including beach slope, body temperature, ambient temperature, and light gradients to orient themselves during these diel movements. We used four separate experiments to test our predictions. Our results are inconclusive concerning the effects of slope and temperature, but are strongly supportive of light gradients as cues driving the diel movement of hermit crabs.

Key words: spatial orientation, inter-tidal zone, foraging behavior, behavioral cues, phototaxis, geotaxis

INTRODUCTION

Organisms use environmental cues to orient themselves toward food sources, mating grounds, and shelter. These cues have been extensively studied for many animals; hatchling sea turtles use the light of the ocean to find their way towards the water (Lohmann and Lohmann 1996), songbirds use temperature as a cue to begin seasonal migration (Jenni and Kéry 2003), and snails use geotaxis and phototaxis to move towards the tops of rocks (Warburton 1973). While it has been documented that land hermit crabs (*Coenobita* spp.) spend daytime hours in shelter, and forage after dusk on the beach (Simon et al. 2003), it is unclear what environmental conditions influence this behavior. To determine how land hermit crabs use environmental cues to direct their diel movements, we experimentally tested four hypotheses: (1) depending on the time of day, crabs use the slope of the sand as a cue to orient themselves upslope or downslope; (2) foraging activity depends on the ambient temperature of food sites; (3) the body temperature of crabs influences movement patterns; and (4) crabs use light gradients differently depending on the time of day.

First, we predicted that crabs would move upslope to the nearby forest during the day to seek shelter from the sun, and downslope after dusk to forage along the beach. Second, we predicted that crabs would forage during the day if a shaded pathway was provided toward a food source, but would not

move toward a food source in direct sunlight. Third, we predicted that crabs that had been maintained in a cool, shaded location would spend more time roaming the sand in the sun before returning to the more shaded forest line, compared to crabs that had been left in the sun prior to the experiment. Fourth, we predicted that crabs would orient themselves toward darker areas during the day (i.e. to shady refuges, avoiding overheating) and toward lit areas during the night (i.e. toward the ocean and food sources).

METHODS

We conducted our experiments on 3-5 February 2007, during low tide, on the land hermit crab *Coenobita compressus,* on the Pacific coastline of El Parque Nacional Corcovado, Costa Rica. Crabs were haphazardly selected from forest shelters during the day and from the beach at night. A crab was never used for more than one trial.

Slope Experiment: To determine the effect of beach slope on day and nighttime movements, we constructed a sand pyramid with four slopes (Fig. 1), facing the forest, the ocean, the north beach, and the south beach. We used this arrangement to analyze slope independently of destination (i.e., ocean, forest, north beach, south beach). For each trial, we placed a hermit crab in the middle of the slope and recorded the direction of its movement (up or down slope) after 10 seconds. We also noted the crab's destination, defined as movement towards the forest or the ocean. We conducted 25 trials on each slope of the pyramid, for a total of 100 trials, at both 0900 and 2030.

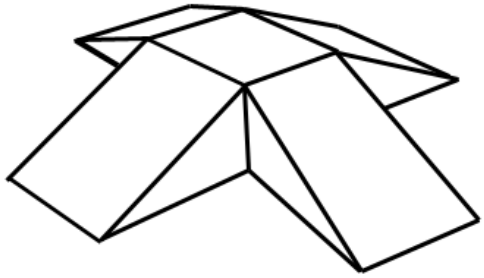

Figure 1. Sand pyramid constructed for the slope experiment, to test response of hermit crabs to slope and slope direction, in day and night trials in Corcovado National Park, Costa Rica. All slopes were approximately 27 degrees, and the four directions were used to control for destination bias (i.e., ocean, forest, south beach, north beach).

Foraging Experiment: To examine the daytime foraging activity of hermit crabs in shade and sun, we constructed an awning covering a 1.75 m-long transect that extended from natural shade onto the sunlit beach. We placed several pieces of coconut and canned tuna, preferred foods of hermit crabs (Hanke et al. 1990), under the awning, and along a similar transect in the sun (Fig. 2). Both the shaded

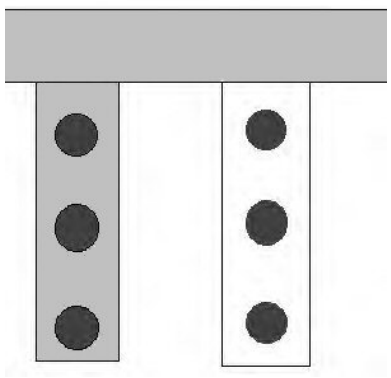

Figure 2. Layout for foraging experiment (not to scale), to determine whether light and temperature affect hermit crab movement toward food sources in Corcovado National Park, Costa Rica. The horizontal gray bar represents a natural crab shelter. The vertical gray bar is the shaded foraging transect, and the white bar is the sunny transect. The three black dots per transect represent places where we placed bait. The transects were 1.75 m long and the distance between transects was 1.75 m.

and sunny transects originated in the same sheltered area and were therefore available to the same population of foraging crabs. We started the experiment at 1030 and counted the number of crabs present at each bait station after 1, 5, 30, 60, and 120 minutes. We simultaneously replicated the entire arrangement using a transect that was naturally shaded by a tree. Because sunlight provides both light and heat, two variables that are difficult to separate in the field, we evaluated them jointly in our experiments.

Pre-heating Experiment: To test for a relationship between initial crab temperature and direction of movement, we placed 20 hermit crabs in a cardboard corral in open sunlight (39.9 ^{o}C sand temperature; hot crabs) and 20 hermit crabs in a shaded corral (31.1 ^{o}C sand temperature; cool crabs) for 1.5 hours. We assumed crab temperatures were similar to sand temperatures in the corrals. We placed each crab in the sand 4 m from the forest and measured the time it took for the crab to move towards the shaded forest. Eighty percent of the crabs in this experiment began moving toward the forest within 5 minutes.

Phototaxis Experiment: To determine the effect of light gradients on crab movements, 8 daytime and 8 nighttime trials were conducted in a 1 x 1 m cardboard corral on the beach, with a cardboard awning shading half of the corral. In daylight trials, unshaded areas were illuminated by sunlight. At night we used a small LED flashlight to simulate moonlight in the unshaded area. For each trial, we placed 10 crabs in the center of the corral and left them for 2 minutes, after which we calculated the percentage of crabs in shaded and unshaded areas. To control for any directional bias, we rotated the cardboard awning after each trial so that it covered a different half of the corral.

Statistical methods: For the slope experiment, we used a Wald Chi-Square test to determine the relative effects of time of day and destination (i.e., ocean, forest, north beach, south beach), and their interaction, on the direction (i.e.,

upslope, downslope, horizontal) that the crab moved on the slope. We used Chi-Square tests to further determine if the effect of destination outweighed the effect of slope on crab movement. Because the data for the foraging experiment were paired between the shaded and sunny bait stations at each time interval, we used paired t-tests to compare the shaded and sunny foraging sites by trial. To determine whether we could combine the number of crabs at the experimental and natural bait stations, we used a t-test to compare the differences between them. For the pre-heating experiment, we used t-tests to analyze the differences in the time that it took until hot and cool crabs headed upslope. For the phototaxis experiment, we used t-tests to compare the number of crabs in the shaded and unshaded areas.

RESULTS

Time of day did not affect the direction of crab movement in the slope experiment (Wald $\chi^2_2 = 0.34$, P = 0.84). However, there were significant effects of destination (Wald $\chi^2_6 = 12.55$, P = 0.051) and time of day x destination (Wald $\chi^2_6 = 28.20$, P = 0.0001) on the direction of crab movement.

During the day, significantly more crabs moved toward the ocean than toward the forest (Pearson $\chi^2_{2,45} = 9.74$, $P < 0.0062$, $r^2 = 0.10$, Fig. 3) and

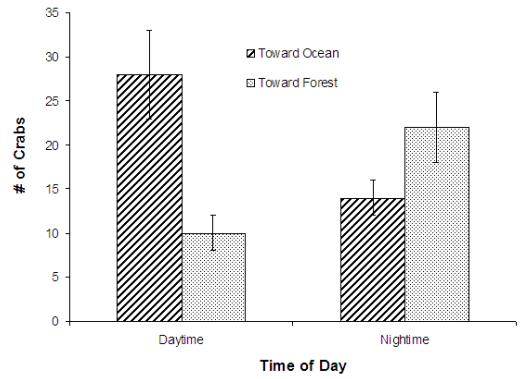

Figure 3. Number of crabs moving toward ocean or forest on the artificial slope (see Fig 1) during both day and night on the beach of Corcovado National Park, Costa Rica. Each crab was placed in the center of a sloping rectangle and the movement toward either destination was recorded after 10 sec. N = 25 individual crabs on each slope for a total n = 100 trials.

significantly more crabs moved toward the south beach than the north beach (Pearson $\chi^2_{2,46} = 28.56$, $P < 0.0001$, $r^2 = 0.33$). There was no significant difference among destination chosen at night, either between ocean and forest (Pearson $\chi^2_{2,44} = 1.86$, P = 0.39, $r^2 = 0.019$) or between north and south beach (Pearson $\chi^2_{2,50} = 2.28$, P = 0.32, $r^2 = 0.021$).

There was no significant difference in the time elapsed before heading upslope between hot and cool crabs ($t_{37} = 0.66$, P = 0.26).

We combined the data from the experimental and natural baits, since there was no significant difference in the total number of crabs at each ($t_8 = 1.39$, P = 0.20). The number of foraging crabs was significantly greater at shaded food (paired $t_9 = 3.39$, P = 0.004) across all

times (Fig. 4). The number of foraging hermit crabs at shaded bait steadily increased over the course of the two-hour observation period, reaching 71 total individuals, while the number of hermit crabs at sunny bait peaked at 10 before decreasing to 0 (Fig. 4). The temperature of the beach in the sun increased by 4.5°C over the two-hour observation period.

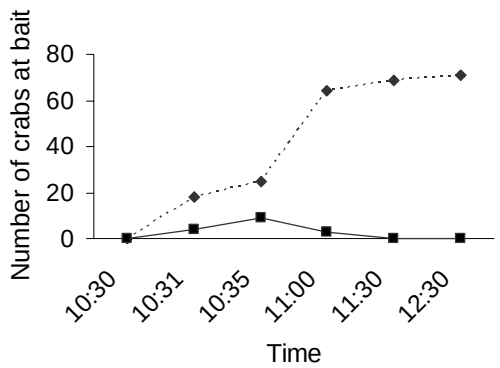

Figure 4. Number of crabs at a foraging experiment (Fig. 2) conducted from 1030 to 1230 on the beach of Corcovado National Park, Costa Rica. The shaded bait station is represented by a dashed line, and the sunny bait station by a solid line.

Crabs showed negative phototaxis (chose shaded habitat) 79% of the time during the day, and positive phototaxis (chose unshaded habitat) 81% of the time at night (t_{14} = 11.40, $P < 0.0001$, Fig. 5).

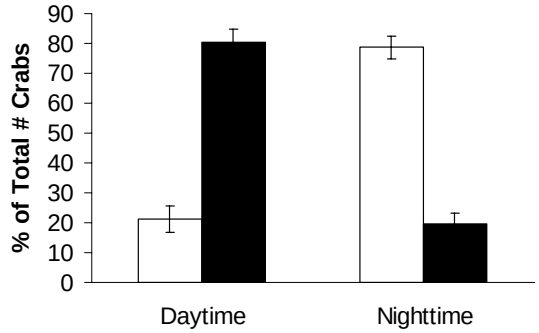

Figure 5. Average percent of hermit crabs in the light or dark half of an experimental corral on the beach of Corcovado National Park, Costa Rica. We conducted phototaxis trials during both day and night. Each trial consisted of ten crabs; N = 8 trials per treatment. White bars represent percent crabs in the light half of the corral, and black bars represent percent crabs in the dark half of the corral.

DISCUSSION

Our results are inconclusive concerning the effect of temperature on crab behavior. The bait experiment showed that crabs foraged less in sunny areas, but we could not disentangle the effects of increased light intensity and ambient temperature. We also found no difference in the behavior of crabs with presumed different body temperatures, despite results from other studies showing that hermit crabs can become heat stressed (Simon et al. 2003). This discrepancy may be due to a failure to induce heat stress in our study.

We found that destination instead of slope was driving crab movement. Because we failed to control for destination, we could not

determine the extent to which crabs use geotaxis. Future studies could analyze the effect of slope on crabs in a more controlled setting.

Hermit crabs oriented themselves using negative phototaxis during the day and positive phototaxis at night, supporting our prediction. Our finding that crabs used negative phototaxis during day was also supported by the bait experiment, in which crabs avoided foraging in sunny transects. Phototaxis in crabs is probably important for avoiding heat stress during the day and finding food at night. While it is likely that the high temperatures of the beach are an important driver in the diel migrations of hermit crabs (Simon et al. 2003), more research is needed for definitive evidence.

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

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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

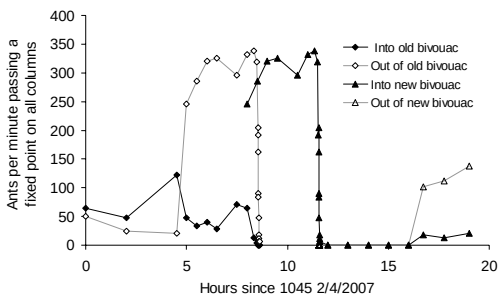

Figure 1. Number of *E. hamatum* ants entering and exiting the old and new bivouacs per minute (averaged across 5 10-second observation periods at each half hour, except during periods of high activity where there was no replication). Immediately before bivouac emigration, the number of ants entering 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

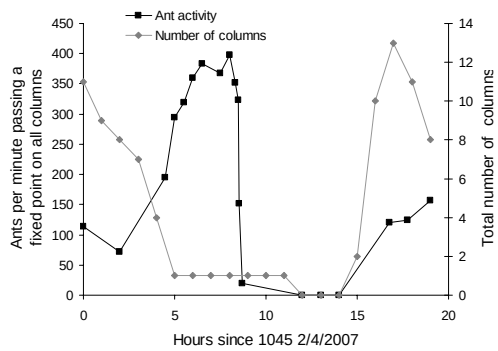

Figure 2. *Eciton hamatum* ant activity (sum of ingoing and outgoing ants) in all columns and total number of columns emanating from the bivouac over a 20 hour period. Hours 0-12 represent the old bivouac and hours 12-20 represent the new bivouac. In the morning of 4 February 2007, the number of columns 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.

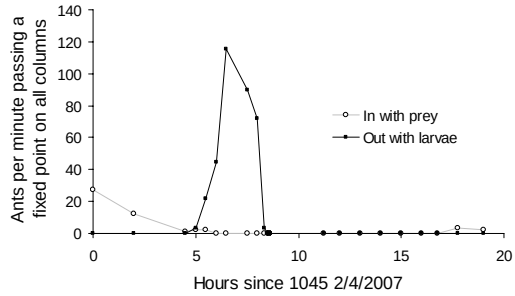

Figure 3. Number of *E. hamatum* ants moving into the bivouac with prey and out of the bivouac with larvae throughout the observation period. The large spike in larvae movement corresponds with bivouac emigration. Immediately before bivouac emigration, the number of ants entering

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.

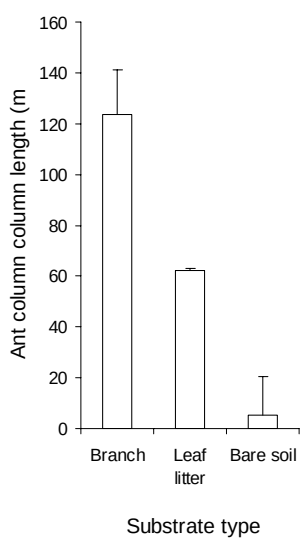

Figure 4: Mean total column length covered by *E. hamatum* ant foragers on each of three substrate types (branches, leaf litter and bare soil) in six replicate mappings, evenly spaced at 2.5 hour intervals over the 20-hour study period, excluding the bivouac dormancy period. There was little dirt available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

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NO NEED FOR SPEED: A STUDY OF THE EFFECTS OF WATER VELOCITY ON *NERITINA LATISSIMA* DISTRIBUTION IN A TROPICAL STREAM

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Abstract: The *Neritina latissima* snail population in the Rio Claro in Corcovado National Park, Costa Rica is found across microhabitats of varying water velocities. We studied the effects of water velocity on *N. latissima*'s distribution within the stream. In an observational study, we measured snail density, size, and location on rocks in various water velocity sites. We found that at higher velocity sites, snail density was lower, smaller snails were present, and snails tended to be at the base of rocks. In a reciprocal transplant experiment, we moved snails from a low water velocity site to a high velocity site and vice versa. When transferred from the low velocity site to the high velocity site, snails either moved to the base of the rocks or fell off. When transferred from the high velocity site to the low velocity site, almost all snails moved to the top of the rocks. Our results suggest that snails seek shelter from strong currents at the base of rocks.

Key Words: snail distribution, Corcovado, snail density, population dynamics

INTRODUCTION

Variation in environmental conditions drives spatial heterogeneity in stream organisms (Cooper et al. 1997). Water velocity is one environmental factor that may influence aquatic populations. Within a stream, velocity is affected by many characteristics such as slope, stream width, and stream depth, and corresponding habitats can be categorized as riffle, run, or pool. A riffle is a part of the stream where water flows rapidly over rocky substrates causing high turbulence. A run is an area of stream with moderate to high water velocity, but water flow is smooth with low turbulence. A pool is an area where the water is still or at a low velocity and has no turbulence.

The Rio Claro in Corcovado National Park, Costa Rica is a large freshwater stream, which contains microhabitats of different water velocities. While some of Rio Claro's organisms are found in riffles and runs, others are found in pools. One population present in all three microhabitats is *Neritina latissima* snails. Due to the snails' prominence within the stream, we wished to understand how water velocity may impact the snails' distribution. We hypothesized that at different water velocities, snail densities would differ, different sized snails would be present, and snail location on its rock would vary. We predicted that snail density would be lower at

higher velocity sites because snails in these environments may have to expend more energy to remain attached to their substrate. We also predicted that smaller snails would be present at higher water velocity sites because they may be better equipped to hold onto rocks due to less force per unit area on their smaller shells (Moore 1964). Lastly, we predicted that in areas with low water velocity, snails would be located on the top of rocks to forage on the area of greater algal growth; and in areas with high water velocity, snails would tend to be at the base of the rocks to seek protection from the strong current.

METHODS

Observational Study. On 4 February 2007, we observed the snail population in the Rio Claro located in Corcovado National Park, Costa Rica. We chose four sites with varying water velocities within a reach of the stream: a separated pool, a pool connected to the stream, a run, and a riffle. In each of the four site-types, we used randomly generated numbers to lay five 1m x 1m quadrats. We measured velocity in each quadrat by dropping a piece of wood on top of the water and timing its movement along the length of the quadrat (1m). We averaged the velocity of the quadrats per site and found a velocity of 0 m/s for the separated pool, 0.1 ± 0.97 m/s (mean ± SD) for the connect pool, 0.69 ± 0.37 m/s for the run, and 1.91 ± 0.43 m/s for the riffle.

In each quadrat, we estimated the percentage of different substrates: ledge (exposed bedrock), boulder (> 25cm), cobble (5-25cm), pebble (1-5cm), and sand (< 1cm). We sampled three rocks from each quarter of the quadrat that were representative of the relative natural abundances of rock sizes in the quadrat. We measured length and width of approximately rectangular rocks and the diameter of approximately circular rocks, and used these metrics to calculate the top surface area of the rock, as an index of rock size. We counted the number of snails on each rock, measured their size from the apex of the shell to the front of the aperture, and noted if each snail was located on the top or base of the rock. We defined the top of the rock as the part that could be seen from above and defined the base as the remainder of the rock. We calculated snail density as total number of snails per rock surface area (cm^2) and calculated an average snail density for each quadrat (n=12 rocks per quadrat).

Experimental Study. On 5 February 2007, we performed a reciprocal transplant experiment in the Rio Claro to test snail behavioral response to changes in water velocity. We chose the two sites with the largest contrast in water velocity,

the separated pool and the riffle sites. We transplanted snails of a range of sizes from the separated pool site to the riffle site, and vice versa. We controlled for rock size by choosing small, medium, and large sized rocks from each site. In each trial, we placed one snail on one of the three rocks from the snail's original habitat, waited for its foot to fully attach to its new rock, and then placed the rock in the other habitat (n = 5 snails per rock size per treatment). Since our observational study showed that snails are generally found on top of the rock in the separated pool and at the base of the rock in the riffle, we placed snails on the top of the rock in the pool-to-riffle transplant and at the base of the rock in the riffle-to-pool transplant. For both treatments, we recorded whether the snail fell off the rock, moved to a new location on the rock, or stayed where it was originally placed on the rock, at the end of a five minute period.

Statistical Analysis. We used a MANOVA to determine whether there were differences in snail density [square-root transformed (cm^{-2})], snail size [log- transformed (mm)], and percent of snails at the base (arcsine square-root transformed) among the four sites. We used separate one-way ANOVAs to determine if snail density, size and location on rocks (transformed as above) varied among sites. To determine differences of snail density, size and location on rocks among sites, we used a Student's t-test. We used a Chi-squared analysis to determine whether the reciprocally transplanted snails moved non-randomly.

RESULTS

Overall, at higher velocity sites, snail density was lower, snail size was smaller and snail location was on top of their rocks. We found that there were differences in snail density, size, and percent of snails at the base among the four sites (Wilks' Lamba = 0.16, $F_{9,34}$ = 4.33, P = 0.0008). We found that snail density was four times higher at the separated pool and the connected pool sites than at the run and the riffle sites ($F_{3,18}$=6.72, P=0.0038, Figure 1). We found that snail size was 54% smaller at the run and the riffle sites than at the separated pool and the connected pool sites ($F_{3,18}$=18.92, P <0.0001, Figure 2). We found that the percentage of snails at the base of rocks in the run and the riffle was twice as great as that of the separated pool and the connected pool ($F_{3,18}$ = 6.36, P = 0.0054, Figure 3).

In our transplant experiment, we found that when moved from the separated pool to the riffle, 60% of the snails moved to the bottom and 40% fell off the rock. When moved from the riffle to the separated pool, 20% stayed on the bottom, 80% moved to the top, and none fell off

($\chi^2_{2,28}$= 21.00, P = 0.0001).

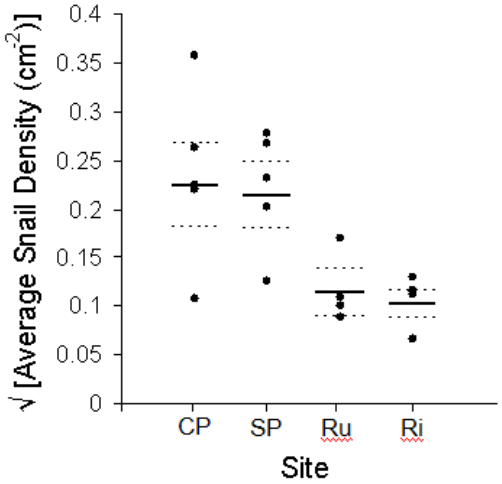

Figure 1. Density of snails (square-root transformed) in the connected pool (CP), separated pool (SP), run (Ru), and riffle (Ri) along the Rio Claro in Corcovado National Park, Costa Rica. Each point represents a quadrat. (n=5 per site).

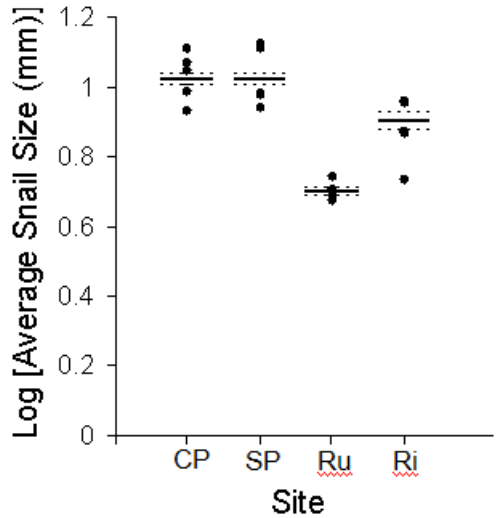

Figure 2. Size of snails (log-transformed) in the connected pool (CP), separated pool (SP), run (Ru), and riffle (Ri) along the Rio Claro in Corcovado National Park, Costa Rica. Each point represents a quadrat (n=5 per site).

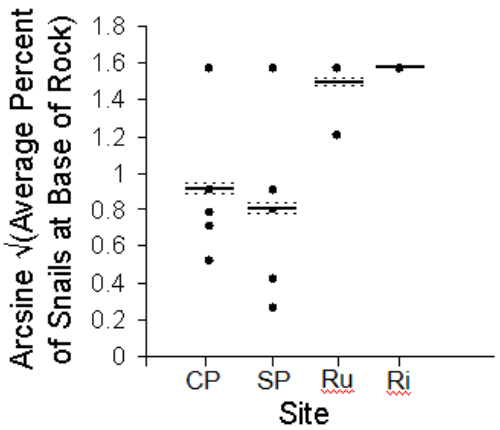

Figure 3. Percent of snails at the base of the rock (arcsine square-root transformed) in the connected pool (CP), separated pool (SP), run (Ru), and riffle (Ri) along the Rio Claro in Corcovado National Park, Costa Rica. Each point represents a quadrat (n=5 per site).

DISCUSSION

We focused on the effect of water velocity on snail density, presence of different sized snails, and location of snails on rocks in a neotropical stream. In our observational study, our first prediction, that snail density would be lower at higher water velocity sites was supported: snail density was lower in the riffle and the run sites than the separated pool and connected pool sites. It is possible that snails are more abundant in the lower velocity sites because they do not have to expend energy to remain attached to the rock in a strong current. Instead they are able to allocate their energy to activities such as foraging.

Our second prediction, that there would be more small snails at

higher water velocity sites was supported: snails at the riffle and run sites were smaller than snails at the separated pool and connected pool sites. Smaller sized snails may be more prevalent in high velocity waters because they experience less force per unit area on their shells, affording them a better hold on rocks (Moore 1964).

Our third prediction, that snails would be located on the top of rocks in areas with low water velocity and at the base of rocks in areas with high water velocity was also supported: snails in the separated pool and connected pool were found on the top of their rocks, and snails in the riffle and the run were found at the base. It is possible that snails in high velocity waters seek shelter from the current by hiding at the base of the rocks where water velocity is lower and where the rock impedes the current. In the higher velocity sites, the location preference of the snails could have negative effects on their foraging success: we observed less algae, presumably the main food for the Rio Claro snails, at the base of the rocks.

Our experiment further confirmed the results of our third observational prediction: the position of snails on rocks depended on water velocity. We found that 80% of snails transplanted from the riffle to the pool moved to the top of the rocks, while 20% remained on the bottom. On the other hand, 60% of the snails transplanted from the pool to the riffle moved to the bottom of the rocks, and the other 40% fell off the rocks. The large proportion of the pool-to-riffle snails that could not remain attached suggests that fewer snails are capable of remaining attached in these environments, which would lead to decreased snail density.

Future studies could replicate our transplant experiment using a range of snail sizes to test for an interaction between the effects of snail size and water velocity, i.e. are larger snails more likely to be detached from rocks in high currents? Another study could evaluate differences in snail foraging success on the tops and bases of rocks. We have shown that snails preferentially remain on certain parts of rocks depending on the water velocity of their environment and that within environments with higher water velocity, there tends to be a lower snail density and smaller snails. These population distribution patterns contribute to a better understanding of population dynamics of this prominent species in the Rio Claro.

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THE PONERINE PARADOX: FORAGING INEFFICIENCIES IN THE GIANT TROPICAL ANT, *PARAPONERA CLAVATA* (HYMENOPTERA: FORMICIDAE: PONERINAE)

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Abstract: Bullet ants, *Paraponera clavata* (Formicidae: Ponerinae), are one of the oldest phylogenetic groups of ants and display the primitive trait of solitary foraging. When a prey item is too large for a single ant to carry, *P. clavata* will recruit other workers to segment pieces for transportation back to the colony. Our study examined how a primitive, eusocial ant responds to varying prey biomass. We predicted that the time required to segment and carry insect prey to the nest would increase as prey biomass increased and that single bullet ants would have higher biomass movement rates than groups. We measured ant responses to insect prey presence, including time to take the prey item into the nest, number of prey segments, and total ant recruitment. Our results supported our predictions, showing that total processing time increased with mass and that prey biomass movement rates (g/min and g/min/ant) were faster for individuals than for groups. Our findings suggest solitary foraging in *P. clavata* is much more efficient than group foraging because *P. clavata* has not evolved efficient social foraging methods for larger prey items.

Key Words: bullet ant, social insects, foraging efficiency

INTRODUCTION

The bullet ant, *Paraponera clavata* (Hymenoptera: Formicidae: Ponerinae), is a primitive ant species that acts as a top-down regulator in some neotropical ecosystems (Dyer 2002; Janzen 1983). Bullet ants build subterranean nests at the base of trees, though they have also been shown to nest arboreally (Thurber et al. 1991). Sources of mortality include parasitic phorid flies (Brown and Feener 1991) and competing conspecifics from nearby nests (Breed et al. 1991). *P. clavata* have also been shown to be over-dispersed, indicating strong competition between colonies (Thurber et al. 1991).

P. clavata use both visual cues and pheromones to map trails to food sources (Ehmer 1999), which include nectar, arthropods, and occasionally small vertebrates (Fewell et al. 1996). High contrast areas (e.g., light gaps) are key to bullet ant vision (Ehmer 1999), and may be more important than pheromone trails in guiding bullet ants. Although they are capable solitary foragers, *P. clavata* will recruit others from its colony to nectar or food sources depending on the amount available and the distance from the colony (Breed et al. 1996). When prey is too large for a single

ant to carry back, multiple ants will segment the prey outside the nest, carrying it to the colony in pieces.

Although one of the most widespread and oldest living phylogentic assemblages (Wilson and Holldobler 2005), ponerine ants remained socially primitive. Because bullet ants are a primitive, eusocial species with only basic social capacities, their communications (e.g., pheromone trails) are relatively undeveloped (Wilson and Holldobler 2005). Confused and disoriented ants are seen frequently once a prey item is located by a forager (*personal observation*). Unlike other more socially developed ants, such as the subfamily Ecitoninae, they are unable to synchronize their efforts to bring prey back to the nest (Wilson and Holldobler 2005).

Despite these primitive characteristics and apparent foraging limitations, bullet ants maintain important effects on arthropod populations. For example, bullet ants prey upon leaf-cutter ants (Dyer 2002), one of the dominant herbivores in the neotropics (Hölldobler and Wilson 1990). Because they have the ability to indirectly influence plant biomass, understanding their foraging behaviors is important to understanding forest dynamics (Dyer 2002). Although many previous studies have looked at foraging rates, recruitment, and behaviors (e.g. Nelson et al 1991; Breed et al. 1996; Baader 1996), none have looked specifically at prey segmentation, subsequent movement, or foraging efficiency of both individual and groups of bullet ants.

Our study investigates patterns of prey biomass processing in *P. clavata*. We hypothesized prey processing and movement rates would vary depending on the mass of the prey item and recruitment. We predicted segmentation and overall processing time would increase with prey biomass. Because of the primitive foraging characteristics described above, we also predicted that single bullet ants would have higher prey biomass movement rates than both groups and individual ants within groups (both grams/min and grams/min/ant).

METHODS

Study System:

We collected data throughout the day on 13 and 14 February, 2007, at the La Selva Biological Station, Costa Rica. All but two trials were performed during daylight hours. We used one *P. clavata* colony located approximately 450 m into the Sendero de Arboleda trail, approximately 25 m east of marker 550, 900 on the trail map.

Field Methods:

We collected 19 *P. clavata* prey items (eight grasshoppers, five katydids, five crickets, and one praying mantis) from the grassy area

surrounding La Selva Biological Station. We used one massed prey item per trial. We severed the prey's muscles, preventing it from flying away. The prey item was placed at the base of the *P. clavata* colony, *c.* 10 cm from a colony entrance. We presented one ant from the colony with the prey item. Timing began when the ant first stung the prey item. We recorded the total number of segments into which the prey was divided, the number of segments that were taken to the nest, the time at which each segment was brought into the nest, and the total time until all of the segments had been brought into the nest. Every two minutes we counted the number of *P. clavata* on the prey item and the total number of ants outside of the colony (i.e., on the prey item, ground, and tree) in order to determine maximum number of ants on the prey item and maximum number of ants out of the colony at any one time during the trial. Once all the segments had been brought to the nest, we continued to count the number of ants every two minutes until all ants had returned to the colony. We waited at least five minutes between trials.

We performed a correlation between prey mass (log-transformed) and total segments (log-transformed). Because these were highly correlated (r^2=0.79, $F_{1,16}$=61.70, P<0.0001), we chose to analyze the effect of mass in order to focus on biomass movement rates. We performed a simple linear regression to test the effect of prey mass (log-transformed) on total processing time (log-transformed). T-tests assuming unequal variances were used to compare rates of biomass movement by a single ant with rates of biomass movement by a group (i.e. ≥2 ants) for both g/min and g/min/ant. Using g/min and g/min/ant allowed us to analyze group prey biomass movement at both group and individual levels.

A Levene's test was used to analyze the variance in total biomass movement (g/min) between individuals and a group. One outlier was excluded from all statistical analyses because the single ant displayed a prey biomass movement rate (1.77 g/min) that was 984% greater than the mean prey biomass movement rate for a single ant. The mass of this prey item (0.85 g) was also the maximum processed by an individual ant. Data were analyzed using JMP 6.0.

RESULTS

Total processing time increased with prey mass (Log (time) = 2.9568519 + 1.3264649 Log (mass); r^2=0.88, $F_{1,16}$=118.80, P<0.0001; Fig. 1).

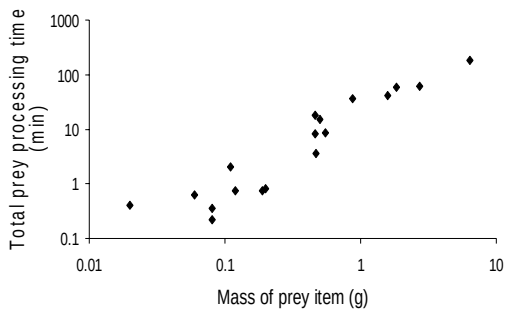

Figure 1. Total prey processing time (time from initial sting until all prey pieces arrived in the colony) increased with prey mass during 18 feeding trials of *Paraponera clavata*. *P. clavata* from a single colony were sampled 13-14 February at La Selva Biological Station, Costa Rica.

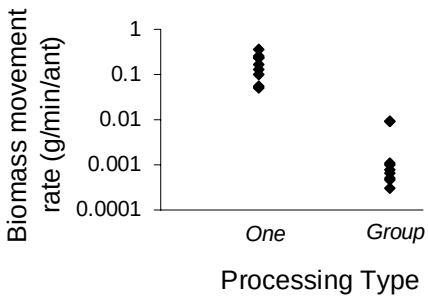

Figure 2. Mean prey biomass movement rate (g/min/ant) for processing by one bullet ant (*Paraponera clavata)* was approximately 7020% higher than mean prey biomass movement rate for ants in a group. N=9 for one ant (single ant moving prey item), N=9 for group (two or more ants working to move prey item). Prey was massed before each feeding trial, and time of movement was defined as time from first sting until final prey pieces arrived in the colony. Total number of ants in a group was the maximum number of ants processing the prey item at any given moment. Mean and SE are not shown due to distortion of these values when using a log scale. *P. clavata* from a single colony were sampled 13-14 February at La Selva Biological Station, Costa Rica.

The mean prey biomass movement rate (non-transformed) into the colony by a single ant (mean ± SD = 0.18 ± 0.10 g/min) was 447% greater than the total mean prey biomass movement rate by an ant group (0.04 ± 0.01 g/min; $t_{11.43}$=5.28, P=0.0002 for log-transformed data). The mean prey biomass movement rate per individual (non-transformed) for a single ant (0.18 ± 0.10 g/min/ant) was 7020% greater than the mean prey biomass movement rate per ant individual within a group (0.0026± 0.0038 g/min/ant; $t_{12.54}$=10.16, P<0.0001 for log-transformed data; Fig. 2). The variance of prey biomass movement rate (log-transformed; g/min) for a single ant was significantly higher than for a group ($F_{1,16}$=5.25, P=0.0358).

All whole prey items under 0.46 g were handled by a single ant. Between 0.46 and 0.85 g, processing type (i.e. single ant or group) varied. Above 0.85 g, all prey items were handled by a group and broken into segments.

DISCUSSION

Our data support our two predictions, (1) that *P. clavata* segmentation of prey and total prey processing time would increase with biomass and (2) that individual ants would have higher per ant biomass movement rates than groups of ants.

Prey processing time:

As prey size increased, the total processing time necessary to cut up a prey item and bring it into the nest also increased (Fig. 2). Although large prey items require both more workers for transport and more time to cut and transport prey, these larger prey items may be necessary to support the energy demands of the colony.

Biomass movement rate:

An important aspect in the survival of any ant colony is the rate at which its foraging workers can transport prey. Solitary ants were faster on average (0.14 g/min faster) at moving biomass into the nest than an entire group of ants (Fig. 2). A single worker was extremely efficient at moving prey biomass (0.18 grams/minute/ant faster) compared to ants foraging in groups. This much lower per-ant group foraging rate was due to four major social foraging inefficiencies. When foraging in groups, recruited ants (1) fought over prey items and (2) failed to locate prey accurately using pheromone trails of the recruiting ant. (3) *P. clavata* tended to over-recruit ants for prey processing and transport, leaving many ants without prey processing tasks. (4) In many cases, ants cut and transported leaves back to the colony. Ants apparently discovered later that the leaves were not food items and dropped them. More derived species have overcome these inefficiencies through complex pheromones, associated sensory systems, and divisions of labor (Brady 2003). The relative chaos of *P. clavata* social foraging is in stark contrast to the highly organized social foraging of many eusocial ant species.

Wilson and Hölldobler (2005) describe the "ponerine paradox" as "globally successful yet socially primitive." *Paraponera clavata* is a perfect example of this paradox: it is evolutionarily less derived and lacks the complicated social foraging strategies (e.g., complex pheromone communication, cooperative transport of prey) of other more developed ant lineages, such as the subfamily Ecitoninae (army ants; Wilson and Hölldobler 2005). Yet the high efficiency of *P. clavata* as solitary foragers may explain why they have persisted relatively unchanged for 100 million years (Wilson and Holldobler 2005). The long term availability and stability of the ecological niche occupied by *P. clavata* has allowed *P. clavata* to remain successful while other ants with more complex behaviors have diversified. Thus, *Paraponera clavata* may not have experienced strong natural selection for more complex foraging organization.

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POPULATION STRUCTURE AND DISTRIBUTION OF *COCOS NUCIFERA* ALONG A STRETCH OF PACIFIC COAST, PARQUE NACIONAL CORCOVADO, COSTA RICA

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Abstract: The spatial distribution of a plant species can speak to conditions affecting growth, survival, and seed dispersal. The coconut palm, *Cocos nucifera*, is found along coastlines in tropical climates throughout the world. We studied a population of *C. nucifera* on a Pacific beach at Parque Nacional Corcovado, Costa Rica. We hypothesized that patchiness due to dispersal, and environmental limitations to establishment and growth, would influence the distribution of *C. nucifera* trees. Specifically, we predicted that (1) more *C. nucifera* would be found near reproducing adults than along the rest of the beach, (2) younger *C. nucifera* would be found farther from parent trees than older offspring, and (3) *C. nucifera* distribution would vary with shade and distance from water and would therefore be restricted to a zone of relatively constant width along the beach. Our results supported prediction 3 but failed to support predictions 1 and 2. Given the unique study system and the potential ease of experimental manipulations, we hope that our findings stimulate further research into the growth, survival, reproduction, and dispersal of *C. nucifera*.

Key Words: coconut, palm, population dynamics

INTRODUCTION

Habitat conditions, seed dispersal, competition, and predation determine the spatial distribution of plant species (Richardson and Bond 1991). Examining the distribution and size structure of a population can provide insights into the historical processes that may have shaped the establishment, survival, and growth rates of individuals in the population.

The coconut palm, *Cocos nucifera* (Arecaceae), has a pan-tropical coastal distribution. Once *C. nucifera* ovules are fertilized, the fruit (coconut) may take up to a year to mature to its full length of about 30 cm. When the fruit falls, it may be washed into the ocean and spend months traveling up to several thousand kilometers before being deposited on a beach (Zuchowski 2005). From personal observations, we noted that *C. nucifera* either occur in clusters, with one reproductive adult surrounded by immature offspring (henceforth called a "neighborhood"), or as solitary individuals.

Because the species is easy to recognize at all life stages, including the obvious, large seeds, and because it has a clearly defined coastal

distribution (apart from planting by humans), it may be well suited to a long-term study of its population dynamics. While we attempted to lay the foundation for such a long-term study, we focused on the following short-term questions: (1) How are different size classes of *C. nucifera* distributed along the beach, and (2) What factors might determine the species' spatial distribution? We hypothesized that the distribution of *C. nucifera* would be primarily determined by local dispersal from reproductive adults and by environmental factors that influence growth and survival following seed dispersal.

We made three short-term predictions, based on the assumption that size class and age are positively correlated. First, we expected to find more immature *C. nucifera* in neighborhoods than as solitary individuals, because we assumed input rates from a nearby parent plant would be higher than input rates from the ocean. Second, within each neighborhood we expected to find larger *C. nucifera* closer to the parent tree and smaller *C. nucifera* farther away, because individuals that establish close to the parent could competitively inhibit growth, and exclude later cohorts to more distant microsites. Third, we predicted that the distribution of *C. nucifera* would be consistent with shading limiting its landward range and wave action limiting its seaward range.

METHODS

We carried out our study on 4 and 5 February, 2007 at Parque Nacional Corcovado, Costa Rica. The park was partially cleared for agriculture until 1975 and is still recovering. Also, from c. 1975-1990, guards harvested almost all coconuts present in the study area, so seed input fell to near zero during that time.

We censused all of the *C. nucifera* that had germinated and survived along approximately 520 m of the beach (1114 steps at a mean of 46.9 cm/step), from the end of the airstrip at the Estación Biológica Sirena north to Rio Sirena. While one researcher paced the beach, others recorded location and relevant data for each *C. nucifera*. We placed each *C. nucifera* into one of five size classes: < 1 m tall, 1-3 m tall, > 3 m tall but non-woody, woody adult, and reproductive adult (tree with maturing coconuts). "Woody" refers to the emergence of the woody stem from the ground. Flowering adults without coconuts were placed in the "woody adult" category.

For each tree, we recorded its horizontal and vertical distances from that day's high tide mark, the amount of crowding vegetation at the level of the individual's leaves (low, medium, high), and the

amount of shading by the canopy above that individual (low, medium, high). At the beginning of our sampling, we reached consensus on levels of crowding and shading, which we assessed visually. High crowding was reserved for cases where the *C. nucifera* leaves were in close contact with surrounding vegetation, and high shading was reserved for cases where canopy cover above the individual approached the levels characteristic of the closed forest immediately inland from the study area. Vertical distances above high tide level were estimated by one researcher standing at the high tide mark, while another stood at the *C. nucifera* individual. They then estimated the vertical distance above high tide, in 0.5 m intervals, usually by approximating where a horizontal line from the eyes of one intersected the body of the other, accounting for height differences among researchers. Horizontal distances from the high tide mark were also estimated visually, after having paced several early samples. In spite of inherent measurement error in visual estimates (e.g., errors may be up to 0.25 m in vertical estimates, and up to 2 m in horizontal distances), we chose to maximize sample size and therefore sacrificed measurement precision for speed of sampling.

We characterized each neighborhood in the following manner. For each reproductive adult, we recorded the number of maturing coconuts present on the tree and whether or not a later cohort of younger, much smaller coconuts was developing above the maturing fruits. We also recorded the number of non-reproductive sprouted *C. nucifera* found in neighborhoods surrounding reproductive adults, and their distances from the central adult, estimated by pacing. Juveniles at successively greater distances from the reproductive adult were included in its neighborhood if they were within 5 m of that adult, or within 5 m of another juvenile that had already been included in that neighborhood. This criterion defined four neighborhoods around four reproductive adults.

We observed five very tall reproducing adults situated 15 m or more inland from the high tide mark, beyond the dense underbrush that covers the shoreline. We did not include these trees in our results because their size and location suggest they were likely planted by humans when this area was under cultivation and thus were not dispersed naturally. There was no evidence of offspring from these adults extending as "neighborhoods" into the shoreline habitat of our study area.

Combining all individuals from the four coconut palm neighborhoods, we tested for differences among size classes in mean distance to the nearest

reproductive adult with an ANOVA, using log-transformed data to achieve normality (N = 9 for < 1 m, N = 6 for 1-3 m, N = 8 for > 3 m, N = 2 for woody adult). We then repeated the analysis, excluding the woody adult category due to the small sample size. Next, we grouped our estimates of distances vertically and horizontally from the high tide mark into classes of low and high, and performed four 2-way contingency tests to evaluate correlations between two sets of categorical factors (shading and crowding vs. elevation above tide and distance from tide).

RESULTS

Within neighborhoods, the mean distance to the parent plant did not vary among age classes either with or without the woody adult category included in the analysis (With woody: $F_{3,20} = 0.93$, $P = 0.45$, Without woody: $F_{2,20} = 1.20$, $P = 0.32$, Table 1).

Table 1: Along a 520 m stretch of the Pacific coast at Parque Nacional Corcovado, Costa Rica, *Cocos nucifera* occurred as solitary individuals or within neighborhoods of offspring centered around a reproducing adult. We categorized all *C. nucifera* into size classes (as a proxy for age, which we could not determine). Within each neighborhood, we recorded the distance of each individual tree to the single reproducing adult.

Size Class	Mean distance to parent (m)	± 1 SE
< 1 m	1.37	0.21
1-3 m	1.36	0.25
> 3 m, non-woody	0.95	0.22
> 3 m, woody	1.61	0.62

Of the 72 individuals we censused, 39% occurred as members of a neighborhood, and 61% occurred as solitary individuals. Overall, the population of coconut trees on the stretch of beach we surveyed appeared skewed in favor of the youngest size class, with fewer individuals present in each successively larger size class (Fig. 1). This skew appeared stronger in the solitary trees than in the neighborhood trees (Fig. 1).

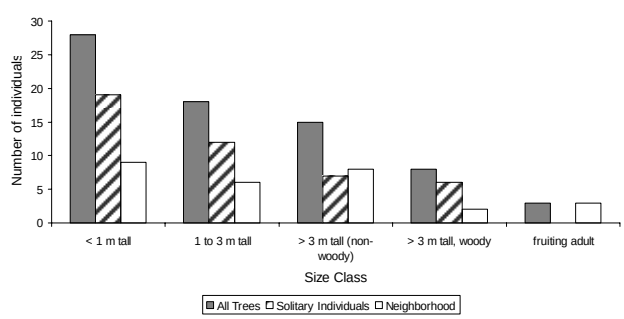

Figure 1: The population size distribution of *Cocos nucifera* individuals along a 520 m stretch of the Pacific coast at Parque Nacional Corcovado, Costa Rica consists of 44 solitary individuals and 28 trees in neighborhoods around reproductive adults.

For all trees observed, 49% experienced low crowding, 46% medium crowding, and 5% high crowding. For all trees observed, 47% experienced low canopy shading, 36% medium shading, and 17% high shading. Plants higher above the high tide mark experienced more shading ($\chi^2_{2,68}$ = 6.715, P = 0.0348). There was a similar tendency for greater shading with increasing distance from the high tide line that was marginally significant ($\chi^2_{2,68}$ = 4.959, P = 0.0838). In contrast to canopy shading, there was no tendency for crowding around coconut plants to vary with vertical height above, or horizontal distance from, the high tide mark ($\chi^2_{2,68}$ = 0.319, P = 0.8525; $\chi^2_{2,68}$ = 2.241, P = 0.3261). In relation to the height of the high tide line, *C. nucifera* ranged from -0.5 m to 1.0 m (mean ± 1 SE = 0.2 ± 0.05 m), in our estimates. Estimated horizontal distance from the high tide ranged from 0 m to 12 m, with a mean of 4.4 ± 0.3 m.

DISCUSSION

C. nucifera growing along the beach of Parque Nacional Corcovado are not distributed randomly. All but five of the observed *C. nucifera* were within 12 m (horizontally) from the high tide mark, reflecting the limitations of wave action as a dispersal vector. The degree of canopy shading may be a significant limitation to the landward range of *C. nucifera*. As expected, canopy cover was greater over coconut plants higher above high tide, reflecting a general increase in canopy cover from the beach to the well developed forest canopy inland. However, there was no corresponding trend in crowding by vegetation at the level of coconut foliage. Ground vegetation is well-developed just above high tide; this may be due in part to the sparse canopy cover which allows light to penetrate.

Both elevation above high tide and horizontal distance from high tide reflect limitations on oceanic transport of coconut seeds. Even waves of high amplitude cannot transport coconuts high above the tide level (except perhaps during storm events), and dense vegetation, even on a gently sloping shoreline, can physically restrict water-borne dispersal of coconuts inland.

The smallest size class contributed the highest proportion of individuals to the population, and the numbers of individuals per class declined with increasing size (Fig. 1). This size class distribution corresponds to the typical age structure found in tree populations that are either growing or stable. In contrast, the reverse trend (i.e., most individuals in large size classes), or an even size class distribution, would suggest that the population was in decline, since mortality occurs at each stage and larger size classes

are derived from smaller ones in the past. However the limitations of static data must be recognized explicitly. To infer dynamics, even from age structure data, one must assume constancy of seedling recruitment. If size class distributions are used in place of age distributions to infer population dynamics, interpretations must be made even more cautiously, in part because time intervals required to transition from one size class to the next may vary.

The unexpected finding that the majority of the *C. nucifera* occur as solitary individuals could be explained by the fact that after the high human harvesting of coconuts decreased in the late 1990's, larger cohorts of seedlings may have established. Before that time, human consumers may have removed coconuts that were near or on adult *C. nucifera* trees more frequently than solitary coconuts, because fruiting trees would be easier to find. Therefore, solitary coconuts may have had a greater per capita chance of germinating than would coconuts under their parent trees, resulting in the current high proportion of *C. nucifera* that exist as solitary individuals. We did not estimate the rate of input of coconut fruits from the ocean, and it is possible that some coconuts delivered outside the neighborhoods, by wave action, were derived originally from local adults.

A final goal of our study was to provide initial observations and hypotheses to help in the design of a future long-term study of the population dynamics of *C. nucifera* along the Pacific coast of Parque Nacional Corcovado. To that end, our dataset has been archived and will be available for future use. From our findings, we hypothesize that light, nutrient availability, water availability, wave action, and beach topography all contribute to the spatial distribution of *C. nucifera*. Mapping and permanently marking individuals (including ungerminated fruits), and monitoring survival, reproduction, and growth rates, would supply the information necessary to complete a life table and project *C. nucifera*'s population structure and growth rate. Experimental manipulations with coconut fruits would not be difficult, and may be used to test the effects of some of the hypothesized factors affecting the growth and survival of *C. nucifera.*

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