ENVIRONMENTAL PREFERENCE AND SHELL SELECTION IN HERMIT CRABS

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Abstract: On the Playa Sirena beach at low tide, there are aggregations of crabs at two locations, one near the water and one near the trees above high tide line. The crabs nearest the trees are larger than those near the water, and also differ in morphology and in the shells they inhabit. We explored patterns in crab size, morphology and shell size between the two aggregations, and used experimental displacements and mark-recapture techniques to investigate habitat preferences. We found that the crabs in each group preferred the habitat in which they were found. The differences in size, morphology and shells between the groups may be explained simply by the tendency of large crabs to move higher on the beach, where resources may be more abundant. Larger crabs are expected to have proportionally larger claws, due to allometric relationships,. A shortage of large shells may explain the tendency for the larger crabs to have shells into which they could not fully retract.

Key Words: habitat preference, Paguridae, Playa Sirena

INTRODUCTION

Hermit crabs (Paguridae) are abundant on the shores of Playa Sirena in Corcovado National Park, Costa Rica. Previous studies have found two aggregations of crabs on the beach at low tide, one close to the forest edge near the high-tide mark and the other approximately 100 m from the tree line near the low-tide mark, with few crabs in between (Dudycha et al. 1992). Furthermore, the crabs higher on the beach are larger than the crabs found in tidal pools near the low-tide mark (Biedron and Theoharides 2003). Previous researchers hypothesized that resource availability and competitive exclusion could account for these trends (Karlsberg and Hubbard 1995). Large crabs could take advantage of high food abundances at the high water mark and exclude smaller crabs, forcing them to scavenge in tide pools (Biedron and Theoharides 2003).

An alternative explanation, that these aggregations represent two distinct populations, is implausible because hermit crabs return to the water to mate and reproduce, so that genetic mixing is likely (although assortative mating remains a possibility). We predicted that crabs from the two zones would not move between them (apart from reproductive events, which we did not observe). We also documented patterns in crab size and morphology, as well as shell size and morphology, between the two groups.

METHODS

To test for movement between the two environments, we distinctively marked 80 crabs near the surf at the low tide mark and 270 crabs at the forest edge, both in 10 m x 2 m plots during low tide, near the outlet of Sendero Naranjos, on 2 February 2005. We recaptured crabs during the following high tide, in the "terrestrial" plot, and low tide, in both the intertidal and terrestrial plots. We also tested environmental preference by placing 20 crabs from the forest edge and 20 from the water's edge (randomly selected) equidistant from the low tide line and forest, and recorded direction of movement for each individual over a 5 min interval.

We haphazardly selected four 1 m^2 plots along the forest edge and six along the low tide line and captured all crabs in each. The two additional plots in the low tide zone were needed to obtain similar sample sizes, because crabs occur at a lower density there. For each crab in our plots, we measured shell width (across aperture), length (laterally, perpendicular to width), and height. We also measured the distal segment of the second pereiopod and recorded the presence or absence of an enlarged cheliped. We recorded how far the crab retreated into its shell (inside, flush with, or partially outside the shell). We recorded shell shape (which we labeled conical, spherical, or "flat"). These were quite distinct. We did not calculate shell volumes because assumptions needed to use simple formulas would confound analyes. (Note, however, that volumes of shells could be measured quite accurately, by sealing apertures and measuring water displacement in a graduated cylinder).

We decided not to report ratios of metrics because this would have required careful assessment of the allometric relations between those metrics, with increase in size of both crabs and shells. Allometric relations typically involve changing ratios among metrics due to size alone (e.g. claw size has been shown to increase greatly, relative to overall crab size), as crabs grow. Because the two crab groups differ substantially in mean size, comparisons between them in the ratios among metrics, would give rise to misleading (spurious) patterns.

Environment preference, shell shape, and distance of retreat into shell were analyzed using Chi Squared tests. Data met or were log transformed to meet the assumptions of parametric tests (JMP 5.0.1).

RESULTS

We recaptured eight of the 270 marked terrestrial crabs within the 10 m x 2 m plot in which they were marked and five more about 20 m into the forest. Twenty-eight of the 80 marked marine crabs were found within the 10 m x 2 m intertidal plot. No marked terrestrial crabs were found in or near the water, nor were any marked marine crabs found near the forest (though we did not quantify that search effort or area). In preference tests, 18 of 20 (90%) of crabs from the forest edge returned to the dunes and two moved to-

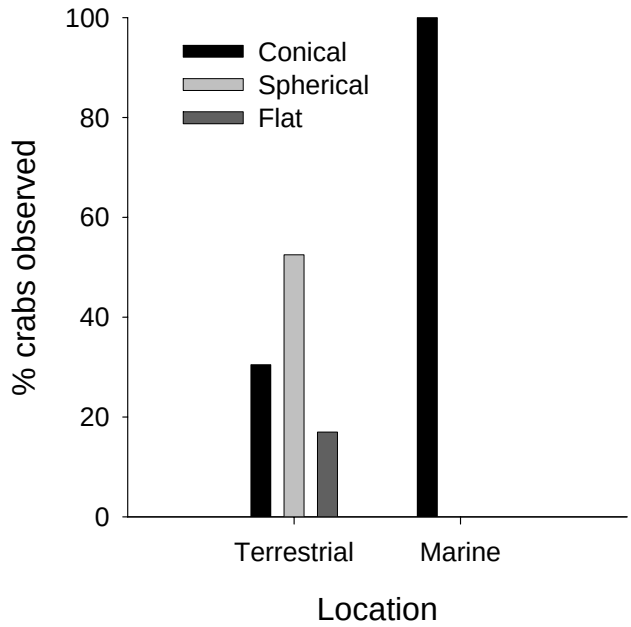

Figure 1. Percent of terrestrial and marine hermit crabs with conical, spherical, and flattened shell types at Playa Sirena, Corcovado National Park, Costa Rica. Terrestrial crabs were found in all shell types, whereas marine crabs were found exclusively in conical shells ($X^2 = 63.611$, df = 2, $P < 0.0001$).

wards the water but did not enter it. Eleven of 20 (55%) crabs from the water's edge moved towards the water and nine did not move ($X^2 = 39.54$, df = 2, $P < 0.001$).

All sampled marine crabs had conical shells (60 of 60), while spherical shells were most common among terrestrial crabs (31 of 59; Fig. 1). Marine crabs also retreated completely into their shells (60 of 60), while terrestrial crabs were often flush with or protruding from their shell aperture (combined 41 of 59; Fig. 2). All terrestrial crabs had an enlarged cheliped (59 of 59), while its presence is rare in marine crabs (10 of 60).

DISCUSSION

Our failure to locate crabs that had been marked near the forest edge near the water, or marked crabs from the water's edge near the forest, suggests that there is little or no movement of individuals between the two aggregations of crabs. Although nine of the crabs from the water's edge did not move in the habitat preference test, this result is consistent with our informal observation that these crabs were less active than those near the forest edge. The lack of large claws in most crabs near the water's edge is consistent with expectations from allometry, as noted above.

Because hermit crabs generally select shells (if available) into which they can fully withdraw, it is likely that large shells appropriate for the large crabs near the forest edge are in short supply. Competition

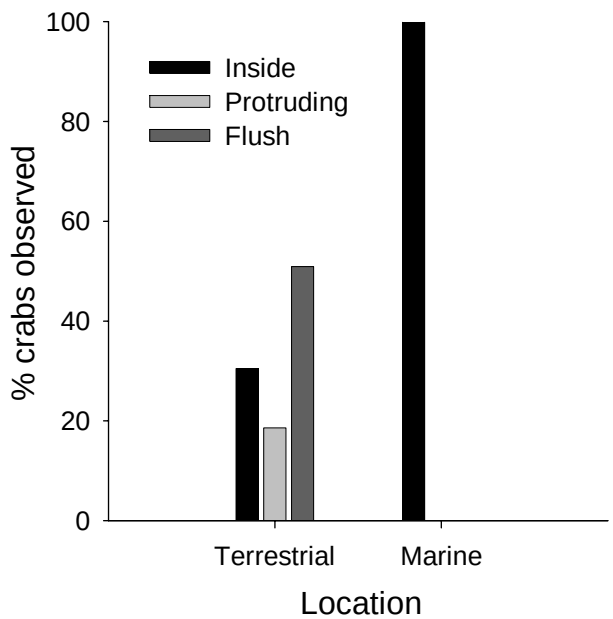

Figure 2. Percent of terrestrial and marine hermit crabs that retreated fully inside of, protruded from, or were flush with their shells. All marine crabs could fully withdraw into their shells, whereas terrestrial crabs exhibited all three behaviors ($X^2 = 63.611$, df = 2, $P < 0.0001$).

among these crabs for large shells may therefore be intense.

Hermit crabs prefer conical shells (Burnaford et al. 1992). Some crabs can sense and locate dying gastropods, whose shells they may then acquire (Small and Thacker 1994). We found crabs at the water's edge exclusively in conical shells, possibly because of this preference, their close proximity to the gastropod resources, and perhaps an abundance of suitably sized shells. Forest edge crabs used all three shell types, which may reflect a limited availability of large shells.

LITERATURE CITED

Beidron, I. S., and K. A. Theoharides. 2003. Habitat partitioning by hermit crabs (Paguridae) at Playa Sirena, Corcovado National Park, Costa Rica. Dartmouth Studies in Tropical Ecology, p. 108-110.

Burnaford, J. L., K. A. Isaacs, and J. V. Ko. 1992. Shell preference in hermit crabs (Paguridae). Dartmouth Studies in Tropical Ecology, p. 93-95.

Dudycha, J. L., J. J. Stachowicz, and S. L. Soucy. 1992. The intertidal zone: Crabs and their community. Dartmouth Studies in Tropical Ecology, p. 88-92.

Karlsberg, S. D., and J. M. Hubbard. 1995. Size distribution and habitat preference in hermit crabs. Dartmouth Studies in Tropical Ecology, p. 76-80.

Simon, K. E., J. P. Casler, and G. M. Ferrie. 2003. Too hot to handle? Diel variation in hermit crab distribution and abundance in beach and forest habitat. Dartmouth Studies in Tropical Ecology, p. 87-89.

Small, M. P., and R. W. Thacker. 1994. Land hermit crabs use odors of dead conspecifics to locate shell sources. Journal of Experimental Marine Biology and Ecology, 182: 169-182.

EFFECT OF NERITID SNAILS ON THE ABUNDANCE OF ALGAE AND PALAEMONID SHRIMP IN A NEOTROPICAL STREAM

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Abstract: In aquatic systems, grazing by herbivores may increase resource availability and structural heterogeneity. In the Rio Claro, Corcovado National Park, Costa Rica, we observed algal and neritid snail abundances, which we hypothesized were inversely related. Through field observations and manipulations, we tested for patterns of abundances and interactions among snails, algae, and palaemonid shrimp. We found that snail abundance was negatively related to algal cover and shrimp abundance. But there were no apparent negative interactions between shrimp and snails over a 24 h period. Snails were patchily distributed throughout the stream, but overdispersed within patches. We speculate that snail effects on resource availability and habitat structure could increase invertebrate abundance in general, as well as exerting positive effects on palaemonid shrimp.

Key Words: herbivory, structural heterogeneity, trophic dynamics, tropical streams

INTRODUCTION

Algal and invertebrate communities are closely coupled in aquatic systems (Poff and Nelson-Baker 1997). Periphyton cover of rocks may provide both food and habitat for invertebrate grazers, which in turn can influence abundance of algae. Invertebrate taxa may also interact directly or indirectly, e.g. by altering shared resources (Pennak 1953).

In the Rio Claro in Corcovado National Park, Costa Rica, there is spatial variation in both algal cover and invertebrate species composition, among nearby sections of the stream. We hypothesized that snail abundance would be negatively correlated with both algal cover and shrimp abundance. Snails are bulldozer grazers of algae (Sommer 2000). Shrimp, as omnivore grazers (Pennak 1953), may compete with snails for food or habitat. We also predicted that interactions with shrimp would reduce grazing by snails.

METHODS

We conducted three experiments on the Rio Claro, approximately 3 km upstream of its estuary near Sirena, Corcovado National Park, Costa Rica on 2-4 February 2005.

First, we measured snail and shrimp abundance and percent algal cover in 22 quadrats (1 m^2) along a 250 m stretch of the Rio Claro. Thirteen quadrats were selected at approximately 20 m intervals, An additional four were selected in a reach with low snail abundance, and five more were in a reach with particularly high snail abundance. To quantify patchiness on the scale of quadrats, we used a variance to mean ratio (VMR) applied to shrimp and snail abundances in the 13 quadrats dis-

tributed at 20 m intervals. A VMR equal to 1 indicates random dispersion, while a value › 1 indicates aggregation and a value ‹ 1 indicates hyperdispersion. We used JMP 5.0.1 to perform linear regressions of the relationships between shrimp abundance, snail abundance, and algal cover in the quadrats. All of our data except algal cover met the normality assumptions of the parametric tests performed. Neither log nor square root transformations were able to normalize percent algal cover.

Second, we tested for the effects of shrimp on snail grazing by excluding shrimp from cages, with three levels of snail abundance (0, 5, and 10 per cage). Thus, cages were exclosures for shrimp, but enclosures for snails. All cages, constructed from half-minnow traps with a diameter of 22 cm, were submerged in the Rio Claro at a site with 100% algal-covered rocks. We prepared two replicates of each snail abundance treatment; one was covered in mesh to prevent any shrimp from entering the cage, while the other was left open so shrimp could enter. After 24 h, we quantified percent algal cover in each cage. We ran a two-way ANOVA to compare the effect of snail abundance and shrimp presence/absence on change in percent algal cover, as well as the effect of shrimp on snail grazing.

Thirdly, we tested for effects of snail presence on shrimp abundance with a container experiment. Containers were plastic storage containers of two different sizes, 1.2 m^3 and 0.5 m^3. Only two of each size container were available, thus limiting the number of replicates. We put 20 shrimp in each large container and 5 shrimp in each small container, and then created a snail treatment by adding 20 and 5 snails, respectively, to one container of each size. We used different shrimp and snail abundances in the two different-sized containers to approximate equal organism:tank volume ratios in all of our enclosures. We measured shrimp abundance after 36 h, and used a one-way ANOVA to compare the abundance of shrimp in treatments with and without snails.

RESULTS

From our quadrat sampling, we found that snail abundance was inversely related to both shrimp abundance (r^2 = 0.41, df = 21, P = 0.0014; Fig. 1a) and algal cover (r^2 = 0.60, df = 21, P < 0.0001; Fig. 1b).

In our measure of snail and shrimp dispersion over 250 m of stream, we found that shrimp were slightly aggregated on a 1 m^2 scale (VMR = 1.53), while snails were more strongly aggregated (VMR = 6.96). Our 250 m transect included four distinct substrate types: pebble-dominated, directly upstream and downstream of a riffle; a sandy area; and an area dominated by cobbles. Within those substrate types, snails were generally overdispersed and shrimp were approximately randomly dispersed (Fig. 2).

In the algal grazer experiment with three levels of snail density, algal cover decreased with greater snail abundance (ANOVA, F = 48.44, df = 1, 2, P = 0.07; Fig. 3). Each snail treatment produced significantly different levels of algal abundance

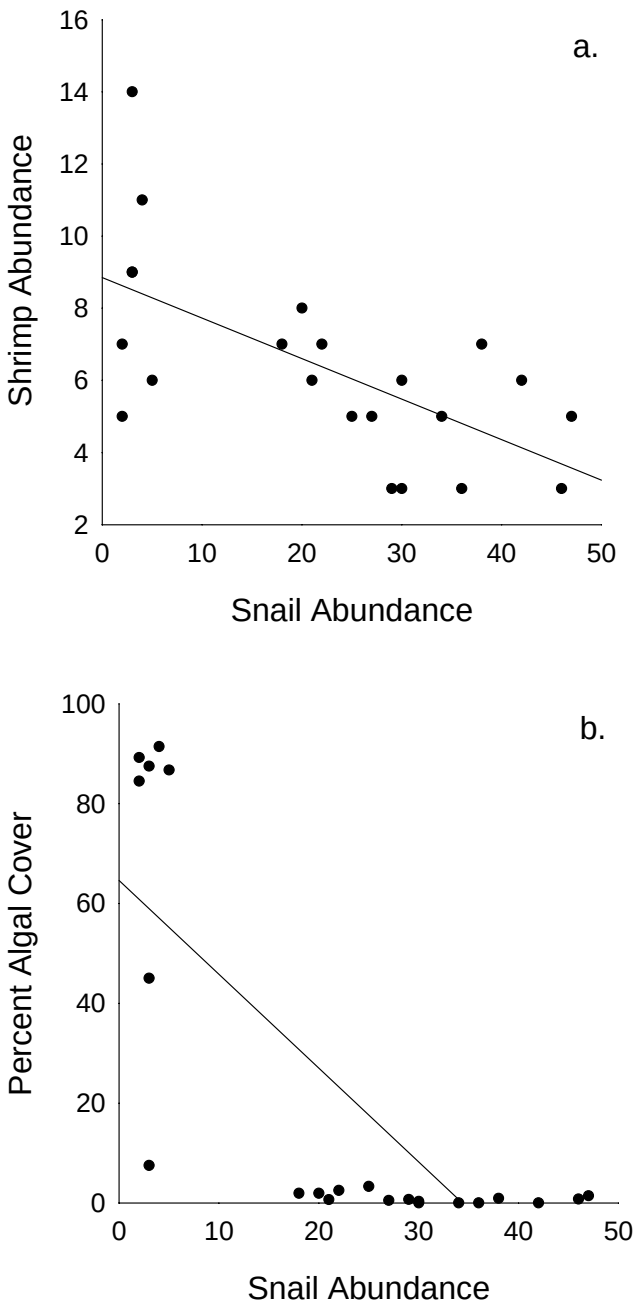

Figure 1. Negative relationship between snail and shrimp abundance (a, Number of Shrimp = 8.8 - 0.1 Number of Snails) and snails and percent algal cover (b, % Algae Cover = 64.6 - 1.9 Number of Snails) in 22 quadrats along a 250 m section of the Rio Claro, Corcovado National Park, Costa Rica.

(Tukey's HSD test, $\alpha = 0.05$). There was no effect of shrimp presence on change in algal cover (F = 0.07, df = 1, 2, P = 0.81).

In our third experiment, we found no change in shrimp abundance over time due to snail presence in our containers (ANOVA, F = 0.00, df = 1, 2, P = 1.00).

DISCUSSION

Our findings indicate that snail distribution may be a key factor in determining local algal abundance in the Rio Claro. Our quadrat sampling over 250 m showed a strong negative relationship between snail abundance and algal cover, and our enclosure experiments showed that increased snail density exerted additional grazing pressure on algae. Sommer (2000) found that snails, as bulldozer grazers, greatly decrease local spatial heterogeneity of microalgal biofilms by removing all algal cover in a patch over a short time period.

Snails were patchily distributed in the Rio Claro, but overdispersed within substrate types, which may be due to intraspecific competition in preferred patches. A possible explanation for the snail patchiness across the 250 m section of stream that we sampled is that juvenile snails may tend to compensate for downstream drift by migrating upstream in aggregated formations (Schneider 1986, 1993).

We found that snail abundance was inversely related to shrimp abundance in the stream. However, neither of our cage and container experiments, which manipulated snail and shrimp presence, revealed any negative interaction between snails and shrimp. This may be because the time

	Downstream		-250 m-		Upstream
Snail dispersion VMR	0.53		0.81	0.00	0.18
	Pebble 1	Riffle	Pebble 2	Sand	Cobble
Shrimp dispersion VMR	0.76		0.23	1.09	1.00

Figure 2. Snail and shrimp dispersion within four patches (Pebble 1, Pebble 2, Sand, Cobble) over 250 m of the Rio Claro, Corcovado National Park, C.R.

interval of our experiments was too short to observe the effects of any negative interaction between snails and shrimp, and/or due to inadequate replication. Further, different results would be obtained depending on how freely organisms were allowed to move in and out of the experimental units. It is also possible that the negative relationship between snail and shrimp abundance is a result of more complex trophic dynamics involving the changes in algal distribution caused by snail grazing. Previous stream studies have shown that a low level of snail grazing may actually increase abundance and diversity of other invertebrates by increasing algal cover heterogeneity, which in turn can provide more diverse food and habitat (Poff and Nelson-Baker 1997, Sommer 2000). This idea is consistent with our finding that shrimp were more abundant in areas of the stream with fewer snails and more algal cover, than in areas of high snail abundance and low algal cover. Although shrimp do not graze on the periphytic algae in our system, shrimp abundance is related to the abundance of other invertebrates, because shrimp scavenge on other invertebrate remains (Pennak 1953). Therefore, it is possible that at low snail densities, algae are abundant and the invertebrates that use those algae provide a food resource for the shrimp. Further research is needed to establish the links between snail grazing and invertebrate abundance, to determine the interactions between shrimp and snails, and to elucidate the causes of snail patchiness in the Rio

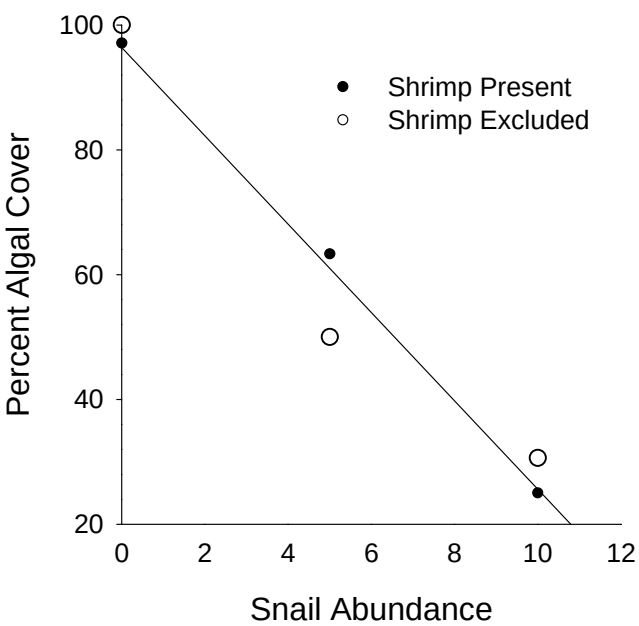

Figure 3. The negative effect of three snail abundance levels (0, 5, and 10 snails) on algal cover of rocks in exclosures submerged in the Rio Claro (% Algae Cover = 96.4 - 7.1 Snail Abundance, r2 = 0.97, df = 5, P = 0.0004). Shrimp presence had no effect on snail grazing.

Claro.

LITERATURE CITED

Pennak, R. W. 1953. Freshwater invertebrates of the United States. Ronald Press Company: New York.

Poff, N. L., and K. Nelson-Baker. 1997. Habitat heterogeneity and algal-grazer interactions in streams: explorations with a spatially explicit model. Journal of the North American Benthological Society, 16: 263-276.

Schneider, D., and T. Frost. 1986. Massive upstream migrations by a tropical freshwater neritid snail. Hydrobiologia, 137: 153-157.

Schneider, D., and J. Lyons. 1993. Dynamics of upstream migration in two species of tropical freshwater snails. Journal of the North American Benthological Society, 12: 3-16.

LITERATURE CITED

Pennak, R. W. 1953. Freshwater invertebrates of the United States. Ronald Press Company: New York.

Poff, N. L., and K. Nelson-Baker. 1997. Habitat heterogeneity and algal-grazer interactions in streams: explorations with a spatially explicit model. Journal of the North American Benthological Society, 16: 263-276.

Schneider, D., and T. Frost. 1986. Massive upstream migrations by a tropical freshwater neritid snail. Hydrobiologia, 137: 153-157.

Schneider, D., and J. Lyons. 1993. Dynamics of upstream migration in two species of tropical freshwater snails. Journal of the North American Benthological Society, 12: 3-16.

Sommer, U. 2000. Benthic microalgal diversity enhanced by spatial heterogeneity of grazing.

ENVIRONMENTAL DETERMINANTS OF SPECIES RICHNESS AND ABUNDANCE IN TROPICAL INTERTIDAL POOLS

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Abstract: Tide pools high in the intertidal zone (i.e., distant from the low tide line) experience more variability in temperature and salinity, because they are isolated from the ocean and exposed to the sun for a longer period of time than lower pools. We hypothesized that few organisms would be able to tolerate the extreme conditions of pools high in the intertidal, and that abundance of organisms and species richness would consequently decrease with increasing distance from the ocean. We assessed abundance and morphotype richness for pools across the intertidal zone. Though abundance and richness decreased with increasing distance from the ocean, it appears that this trend was driven by mobile organisms that move between pools. Furthermore, it appears that the temperature-salinity gradient is probably not the factor driving this trend. Instead, the influence of resource availability may generate the observed patterns.

Key Words: extreme environmental conditions, salinity, temperature, tidal fluctuations

INTRODUCTION

During low tide, variability in tide pool temperature and salinity increases with distance from the ocean (Drake et al. 1993). Tide pools high in the intertidal zone are separated from the ocean and exposed to the sun for the longest period of time, creating high temperatures and rates of evaporation and, consequently, high salinity. This may be particularly pronounced in tropical intertidal habitats. In such environments, some organisms may be unable to tolerate the extreme conditions of these pools and may exhibit a preference for habitat lower in the intertidal zone. Organisms may disperse to these preferred habitats either before the tide recedes or afterwards, by migrating between pools or completely avoiding high pools.

For the clay-underlain intertidal zone of Playa Sirena at Corcovado Na-

tional Park, Costa Rica, we predicted that the pools experiencing more variable and harsh environmental conditions (i.e., those farther from the ocean) would contain fewer organisms and have lower species richness than those pools that are closer to the ocean. We also predicted that this pattern would be less evident at night, when the sun does not drive the temperature-salinity gradient observed during the day.

METHODS

We selected tide pools in a semi-stratified, haphazard fashion at different distances from the tide line in the clay-underlain intertidal zone of the Playa Sirena, Corcovado National Park, Costa Rica. We sampled 25 pools during daytime low tides (1200 - 1600) on 2 and 3 February 2005, and 10 pools during the nighttime low tide (0100 - 0330) on 4 February 2005. No concerted attempt was made to use the same pools for day and night sampling periods, but pools were selected using the same method for both sampling periods. At low tide, all pools were isolated from other pools and from the ocean.

We measured the greatest length, width and depth of each pool to calculate water volume. Pools ranged in surface area from approximately 0.2 to 2.5 m^2 and were between 2.0 and 17.0 cm in depth. Calculated pool volumes ranged from 6 to 220 L. As a reliable proxy for distance from the ocean, which is inherently variable over time, we recorded the distance of each pool from the high tide line, as indicated by the forest edge. We found that tide pool volume did not change with distance from the high tide line for the day ($r^2 = 0.02$, df = 23, P = 0.52) or night ($r^2 = 0.08$, df = 8, P = 0.43) sampling periods. Thus, the sampled pools were comparable in size across the intertidal range.

For each pool, we removed all macro-organisms (i.e., fish, shrimp, snails and crabs) by hand, and counted the number of individuals of each morphotype present. All organisms were returned to their tide pools following counting.

Number of organisms and species richness were log transformed to normalize the data. We examined the effect of time of day on the relationship between organism abundance or morphotype richness and distance from the high tide line using an indicator variables regression. The regression model was:

$$Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_1 X_2 + \varepsilon,$$

where Y is the response variable (number of organisms or morphotype richness), X_1 is distance from the high tide line, X_2 is a binary indicator variable coding for time of day (i.e., for day, $X_2 = 1$, and for night, $X_2 = 0$), β_0 is the intercept for the relationship between the response variable and distance at night, β_1 is the slope for the relationship between the response variable and distance at night, β_2 tests the hypothesis that the intercepts of the relationships are equal for day and night, and β_3 tests the hypothesis that the slopes of the relationships are equal for day and night (Neter et al. 1996).

We performed linear regressions to assess the relationship between distance

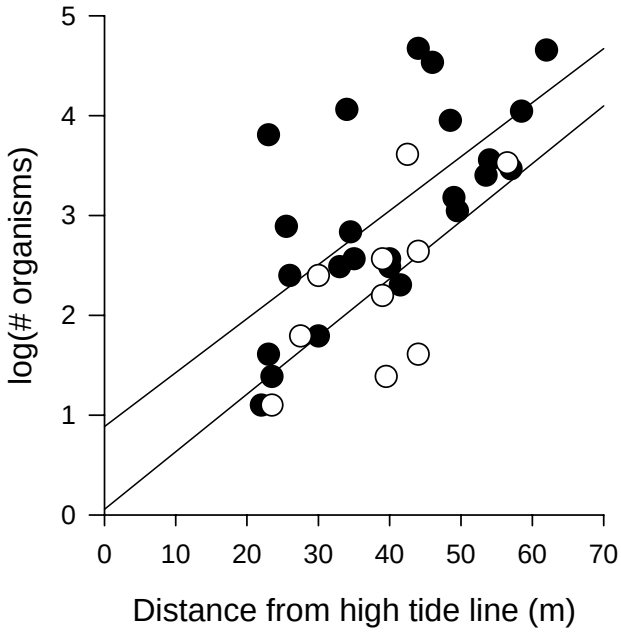

Figure 1. Number of organisms within tide pools increased with distance from the high tide line for day (closed dots) and night (open dots). Lines were fit using least squares linear regression with a binary indicator variable for day and night. Slopes were not significantly different (β_3 = -0.00, P = 0.90), but there was a difference in intercepts (β_2 = 0.68, P = 0.02). $Y_{day} = 0.06x + 0.84$; $Y_{night} = 0.06x + 0.16$.

from the high tide line and the abundance of the six most common morphotypes. Statistical analyses were performed using JMP 5.0.1.

RESULTS

We identified 19 morphotypes in our 35 sampled pools (Table 1). The total number of organisms in each pool increased with distance from the high tide line for both day and night (Fig. 1). Comparisons of this relationship during night and day indicated that slopes were not significantly different. We found a significant difference in intercept between day and night for the relationship between distance from the high tide line and number of organisms (Fig. 1).

Morphotype richness increased with distance from the high tide line during the day and at night (Fig. 2), but the slopes of these relationships did not differ significantly. We found no difference in intercept between day and night for the relationship between distance from the high tide line and morphotype richness (Fig. 2).

We also examined relationships between distance from the high tide line and total abundance (i.e., the sum of abundances for the two sampling periods) for the six most common morphotypes: crab C, crab E, fish A and snails A, B and C. We found a positive relationship between distance from the high tide line and abun-

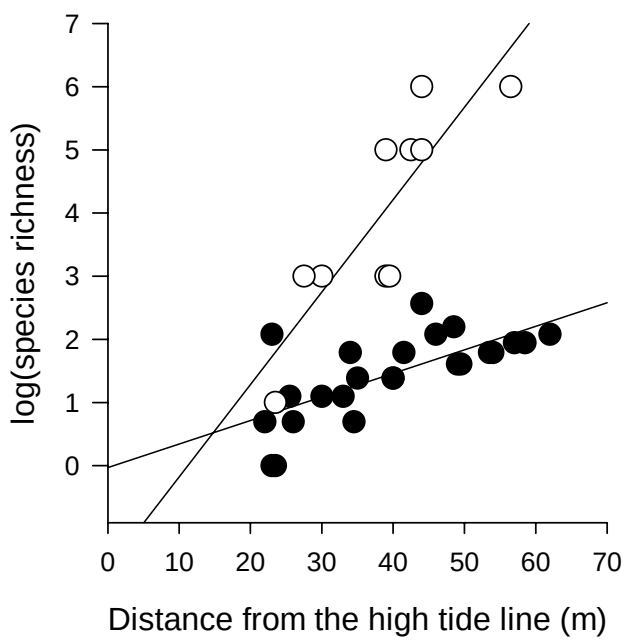

Figure 2. Morphotype richness within tide pools increased with distance from the high tide line for day (closed dots) and night (open dots). Lines were fit using least squares linear regression with a binary indicator variable for day and night. Slopes and intercepts were not significantly different (β_3 = -0.01, P = 0.62; β_2 = 0.12, P = 0.49). $Y_{day} = 0.03x - 0.13$; $Y_{night} = 0.04x - 0.25$.

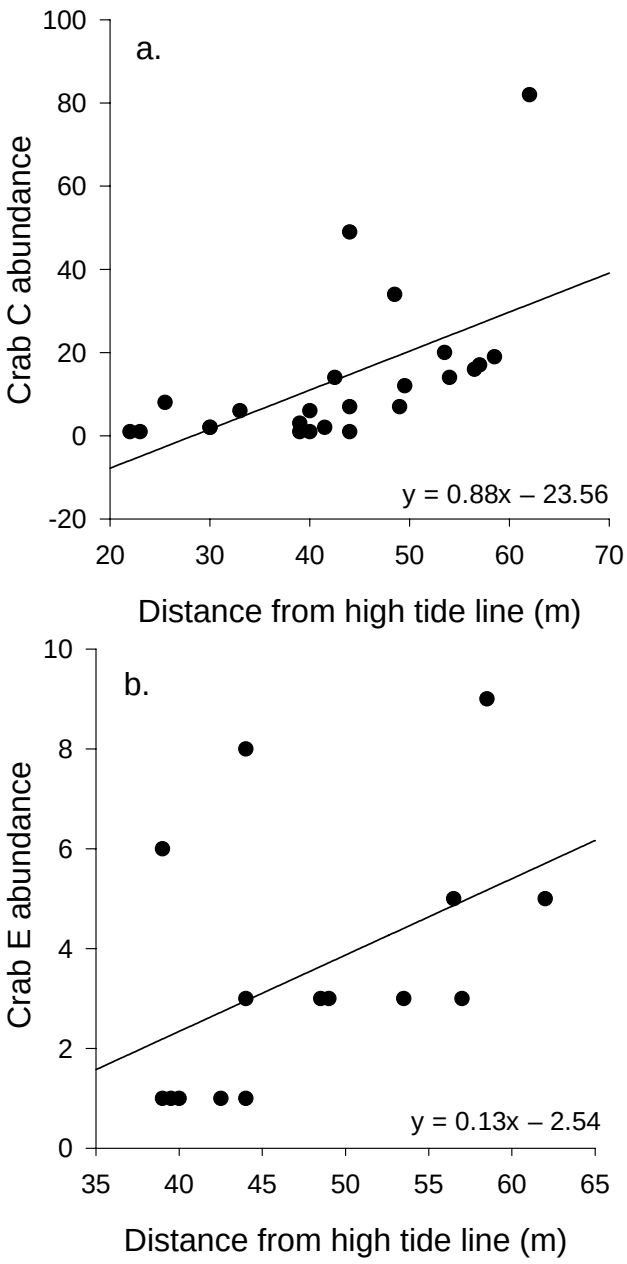

Figure 3. Abundance of (a) crab morphotype C and (b) crab morphotype E increased with distance from the high tide line. Lines were fit using least squares linear regression

dance of crab C (r^2 = 0.33, df = 22, P = 0.01; Fig. 3a) and crab E (r^2 = 0.31, df = 15, P = 0.03; Fig. 3b). There was no relationship between distance and abundance for fish A (r^2 = 0.10, df = 27, P = 0.45), snail A (r^2 = 0.01, df = 12, P = 0.77), snail B (r^2 = 0.04, df = 12, P = 0.47) or snail C (r^2 = 0.19, df = 9, P = 0.18).

Discussion

We found that abundance and species richness of macro-organisms increased with distance from the high tide line during the day. However, contrary to our hypothesis, the same pattern was observed in the night data. Because sun exposure does not differentially affect tide pools at night, an alternative mechanism must drive differences in abundance and species richness across the intertidal zone.

Tides may distribute organisms non-randomly along the intertidal gradient, such that a greater number and diversity of organisms are deposited lower in the intertidal. It is also possible that, during the low tide, when pools are isolated from the ocean, organisms in higher tide pools may die or be preyed upon at higher rates than organisms in lower tide pools. However, these explanations are inconsistent with our observations. We observed very few dead organisms in the sampled pools. We only observed a few bird predators feeding during the sampling period, and these only fed in tide pools outside of our study site. However, it is possible, due to the brevity of the sampling period and the potential influence of our presence on predator behavior, that these observations are not an accurate reflection of actual predation rates in the studied pools.

An alternative explanation is that the more mobile organisms may preferentially distribute themselves along the inter-

tidal gradient, regardless of their original distribution by wave action. This is supported by analysis of the individual distribution patterns of the six most abundant morphotypes and our informal observations of between-pool migration. We found that highly mobile organisms (i.e., crabs C and E) increased in abundance with distance from the high tide line, while organisms with limited mobility between tide pools (i.e., fish A and snails A, B and C) were equally distributed across the intertidal zone. During sampling, we often observed crabs C and E, as well as crabs of other morphotypes, moving from pool to pool. The same observation was never made for fish or snails of any morphotype. This suggests that the more mobile organisms redistribute themselves among pools during low tide. It also suggests that these organisms may prefer pools close to the ocean. The similarity in the patterns of day and night data suggest that this choice is not based upon the extreme temperature or salinity of higher tide pools, but some other factor, such as resource availability.

Table 1. Identification scheme for morphotypes collected in 35 tide pools of the intertidal zone, Playa Sirena, Corcovado National Park, Costa Rica.

Type	Code	N	Diagnostic Features
Fish	A	160	Yellow/tan goby (Gobiidae)
	B	1	Laterally compressed with black longitudinal stripes
	C	1	Laterally compressed with black longitudinal stripes
	D	8	Goby (Gobiidae) with sandy coloration, brown splotches and blue dot below dorsal fin
	E	1	Laterally compressed, round, sandy coloration with brown splotches
Shrimp	A	15	Translucent body, ~ 1-2.5 cm, blue stripes, orange dots on tail
	B	1	Brown with one large claw, < 1 cm
Snail	A	97	Whelk with knobby shell
	B	64	Compressed shell, brown
	C	61	Compressed shell, green spots around spiral, faint red stripes
	D	26	Compressed shell, green spots around spiral
	E	3	Limpet
Crab	A	4	Sandy color, boxy shape
	B	17	Dark color, round shape
	C	360	Hermit crab
	D	23	Dark green color, boxy shape
	E	58	Sandy color, round shape, carapace has 5 teeth, red eyes
	F	8	Purple claws with large bumps
	G	2	Bright orange claws

LITERATURE CITED

Drake, N. L, S. T. Dyhrman and E. D. O'Hara. 1993. A study of fish abundance as a function of tide pool area. Dartmouth Studies in Tropical Ecology, p. 80-83.

Neter, J., M. H. Kutner, W. Wasserman, and C. J. Nachtsheim. 1996. Applied Linear Statistical Models, Fourth Edition. McGraw-Hill/ Irwin: New York.

THE HITCHHIKER'S GUIDE TO THE LEAF-CUTTER COLONY

ANNA R. NOWOGRODZKI, RICHARD W. TRIERWEILER AND S. ALLIE HUNTER

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

Key Words: Atta, *minima, phorid flies*

INTRODUCTION

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

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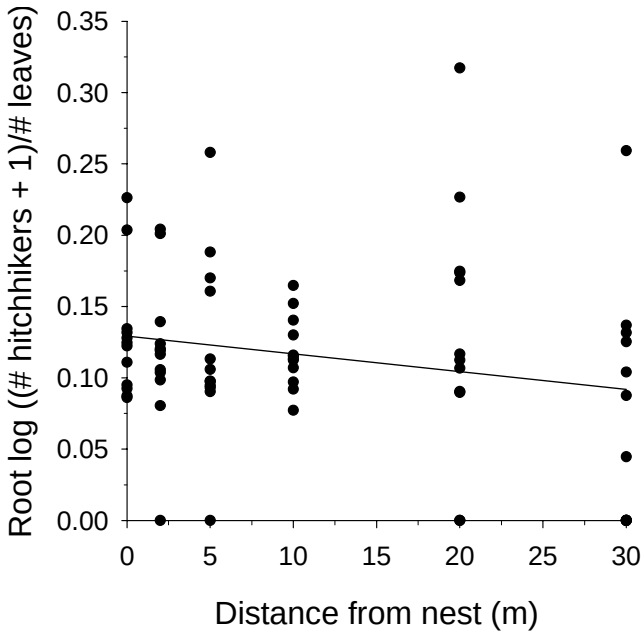

Figure 1. Number of Atta colombica hitchhikers per leaf (normalized) decreased with increasing distance from the nest along the ant trail. y = -0.0013x + 0.13, r^2 =0.044, df = 70, P = 0.078.

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

METHODS

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

RESULTS

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

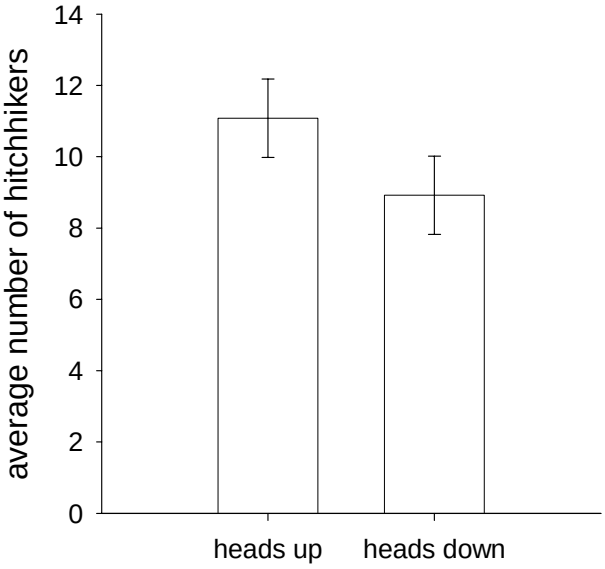

Figure 2. Average number of hitchhikers with heads up and heads down (n = 12 samples of 20 hitchhikers). Hitchhikers were equally likely to have their heads up as down (ANOVA, F = 1.95, df = 1, 22, P = 0.18). Values are means ± 1 SE.

DISCUSSION

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

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

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

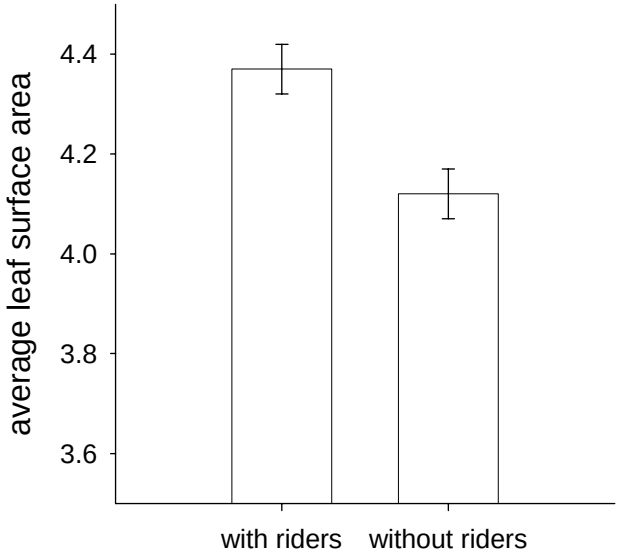

Figure 3. Leaves with riders had greater surface areas than leaves without (ANOVA, F = 13.08, df = 1, 239, P = 0.0004). Values are means ± 1 SE (n = 12 samples of 10 leaves for each category).

LITERATURE CITED

Linksvayer, T. A., A. C. McCall, R. M. Jensen, C. M. Marshall, J. W. Miner, and M. J. McKone. 2002. The function of hitchhiking behavior in the leaf-cutting ant A*tta cephalotes*. Biotropica, 34: 93-100.

Orr, M. R. 1992. Parasitic flies (Diptera: Phoridae) influence foraging rhythms and caste division of labor in the leaf-cutter ant, *Atta cephalotes* (Hymenoptera: Formicidae). Behavioral Ecology and Sociobiology, 30: 395-402.

TREES AS PROVIDERS OF STRUCTURE, PREY CAPTURE, AND PROTECTION FOR WEB-BUILDING SPIDERS

GABRIEL H. CALVI, TIMOTHY R. MATSUURA AND LAKSHMI NARAYAN

Abstract: Large trees and understory plants provide substrate for web-building spiders. We hypothesized that placement and orientation of spider webs affects the type and abundance of prey captured. We predicted that webs built on the buttresses of large trees would have increased prey capture, debris, and less damage than webs built among smaller understory plants. Using simulated webs and observations of natural spider webs, we tested the benefits of building webs in the buttresses of large trees or among understory plants. There was no difference in prey capture between treatments near or far from trees. We found that spider webs on trees accumulated more debris and experienced less damage. Webs built in the buttresses of trees were more often oriented parallel to the ground than were webs far from a tree. Though we did not quantify the costs and benefits of web placement on large trees and understory plants, location and orientation of webs appears to influence the amount of debris accumulated and damage suffered by a web.

Key Words: Arachnida, buttresses, La Selva, web orientation

INTRODUCTION

Web weaving is a common spider strategy for capturing prey (Kaston 1953). Spider webs differ in both shape and placement. Both large trees and understory plants provide the structure for building webs, but they may have different benefits and costs for spiders that build on them.

The vertical relief of a large tree may increase prey capture in horizontally oriented webs. The sturdy nature of tree buttresses, unlike smaller understory shrubs and saplings, provides protection for spider webs from physical stresses such as rain, wind, and animal disturbance. The cost, however, is that these webs may accumulate debris falling from overhead in the tree. Alternately, webs placed away from the base of large trees, especially those with a vertical orientation, might minimize the amount of debris collected while capturing more mobile prey.

We hypothesized that the location and orientation of webs would affect the type and abundance of prey captured. We predicted that horizontally oriented webs near trees would accumulate more debris and capture larger, less mobile arthropods such as beetles and ants compared to webs in the forest understory. We also predicted that webs away from trees that were vertically oriented would accumulate less debris and capture more flying insects than would webs in the buttresses of trees.

METHODS

To examine the relative effectiveness and taxa-specific catch patterns of differently placed webs, we established experimental webs around buttressed trees approximately 15 m apart on opposite sides of the CES trail at La Selva Biological

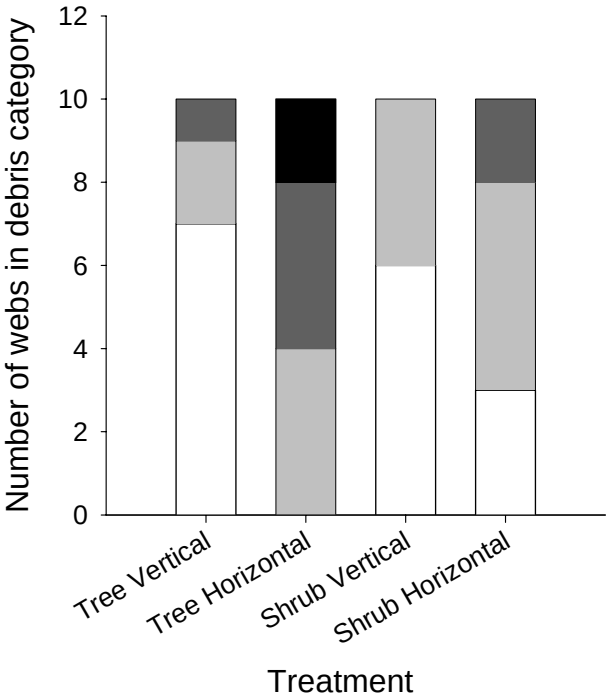

Figure 1. Frequency of different levels of debris in simulated webs, grouped by treatment (substrate type and web orientation). Debris ranges from 1-4, with the lightest bars represent the lowest debris levels (1), and darkest bars highest debris (4). (n = 40).

Station, Costa Rica. We created webs by coating sheets of Ziplock® plastic (each ≈ 18 x 35 cm) with Tanglefoot®, and suspending these traps between 20 and 40 cm above the forest floor. Our four treatments consisted of traps placed horizontally against the tree, vertically against the tree, horizontally approximately 2 m away from the tree on stakes, and vertically 2 m away from the tree on stakes. For each of our 24-h sampling periods (13-14 and 14-15 Feb 2004), we had five replicates of each of our four treatments.

After each 24-h catch period, we counted and identified (to order) all arthropods caught in the experimental webs. We also scored the amount of debris within each web on a scale from 0-4.

We also quantified placement, orientation, damage, and debris collected in naturally occurring spider webs on and around buttressed trees. On 14-15 February 2005, we measured all spider webs encountered on 10 trees and within a 2 m radius of each focal tree, including all webs from the ground up to 2.2 m. We selected focal trees by walking a random number of paces between zero and 100 along the CES, then heading perpendicularly off the trail (randomizing direction) until we encountered a buttressed tree. Our focal trees ranged from 27 to 75 cm in diameter at breast height. For each web present, we recorded the substrate the web was attached to, distance from the ground, web type (three-dimensional or orb), damage on a scale from 0-4, debris on a scale from 0-4, and the presence of any spiders or insects on the web. For all orb webs, we also recorded the angle they made relative to the ground, from 0˚ - 90˚. For the purposes of our analysis, we simplified the substrate variable into two main groups: those attached to our focal tree, and those attached to shrubs and other surrounding objects, heretofore called shrubs.

We used ANOVAs to analyze total and taxa-specific arthropod abundances from our simulated webs. We used an ordinal logistic regression to compare debris level. For observational data, we used contingency analysis to compare web structure, damage, and debris for webs on trees and shrubs. We used a one-way ANOVA to compare angles on trees and shrubs. All data met the assumptions of the statistical tests performed with the exception of the damage and angle measurements in our observational data, which were not nor-

mally distributed. Neither of these data could be normalized using log or square-root transformations.

RESULTS

For the simulated web experiment, we found no effect of substrate, web orientation, or the interaction between these two factors on arthropod abundance (Table 1). Mean insect abundances (± 1 SE) for each treatment were: tree horizontal 10.6 ± 0.9; tree vertical 13.8 ± 3.0; away vertical 9.6 ± 1.9; away horizontal 15.0 ± 3.3. We also tested for effects of substrate, orientation, and an interaction between these factors on the abundance of dipterans, hymenopterans, and coleopterans, the three most abundant arthropod orders in our webs. Our results showed no effect of these variables on arthropod abundance (Table 2.)

The results of an ordinal logistic regression showed that the interaction between substrate and orientation had a significant impact on debris found in the webs (χ^2 = 4.18, df = 1, P = 0.04). Webs placed horizontally against trees had the most debris (Fig. 1).

A logistic ordinal regression of our observational data also showed that debris was greater in spider webs attached to trees (χ^2 = 10.25, df = 4, 125, P = 0.04). A similar analysis on the damage of spider webs showed that webs attached to trees had less damage than those attached to shrubs (χ^2 = 18.16, df = 4, 125, P = 0.001; Table 3).

Analyses of our observational data also showed that shrubs tended to have more orb webs (39) than three dimensional

Table 1. Results of two-way ANOVA tests for the effects of different treatments on arthropod abundance per web. df = 1, 36 for each test (n = 40).

Effect	F	P
Distance	0.00	0.97
Orientation	0.20	0.65
Distance*Orientation	3.12	0.09

Table 2. Results of two-way ANOVA tests for the effects of different variables on abundance of three most abundant arthropod taxa on model webs. df = 1, 36 for all tests. (n = 40).

Order	Mean abundance per web	Effect	F	P
Diptera	8.80			
		Distance	0.22	0.64
		Orientation	0.46	0.50
		Distance*Orientation	1.95	0.17
Hymenoptera	1.33			
		Distance	2.62	0.11
		Orientation	0.01	0.94
		Distance*Orientation	1.00	0.32
Hymenoptera	1.33			
		Distance	0.26	0.61
		Orientation	0.00	1.00
		Distance*Orientation	0.26	0.61

Table 3. Number of webs with different debris and damage levels (0-4) in trees vs shrubs (n = 133).

	Debris					Damage				
Level	0	1	2	3	4	0	1	2	3	4
Shrub	18	25	4	2	0	14	10	12	9	4
Tree	17	38	23	4	2	46	21	12	5	0

webs (10), while webs on trees were evenly distributed between the two types (43 three dimensional webs and 41 orb webs; χ^2= 10.56, df = 1, 131, P = 0.01). The orb webs we found had a higher angle of orientation on shrubs than on trees, with a mean angle of 43.3 ± 5.8° on shrubs compared to 23.1 ± 5.4° on trees (F = 6.55, df = 1, 81, P = 0.01).

DISCUSSION

Though webs on buttresses had more debris than webs in shrubs, our results indicate that spider webs on trees had less damage than webs suspended in shrubs. We also found that horizontally oriented webs caught more debris than vertically oriented webs, and webs that were placed horizontally between buttresses had the greatest levels of debris. The trees and their epiphytes probably provide the source of this debris, but it is unclear how this affects spiders. Increased debris capture may be costly if it damages webs or makes them more visible to predators or prey, but it may be beneficial if increased falling debris is positively correlated with the abundance of falling prey.

Our observational results showed that webs close to trees tended to be positioned at lower angles than webs on shrubs. Since we also observed webs positioned vertically on trees, the differential orientation of webs on trees versus shrubs may be a strategic tradeoff rather than a result of structural limitations. If increased debris catch from horizontal placement were detrimental to spiders, they could both gain protection and minimize damage due to falling debris by building vertically positioned webs close to trees. The prevalence of horizontal webs on trees suggests that some spiders may benefit in some way that outweighs the costs of debris catch, or debris catch may actually benefit spiders by attracting prey that use debris as a food or habitat resource. Also, web destruction, a presumed cost of debris capture, may not affect all spiders equally, as webs of many spider species are ephemeral, lasting no longer than one day (Goodwin 1997).

Contrary to our predictions, our manipulative experiment showed no effect of web orientation or proximity to tree on either the amount or type of prey caught in webs; however, this result may have resulted from methodological constraints, as our sticky traps were unable to catch large insects. We observed large coleopterans crawling off of our traps, and could not determine how the type of prey we were able to catch compared to that caught in real webs. Additionally, overall low prey numbers in real webs that we observed prevented us from quantifying differences in prey capture between real and simulated webs.

Our results also showed differences

in the type of webs placed on shrubs and trees. This could be the result of a structural constraint that limits the ability of spiders to build three dimensional webs on shrubs. However, we observed both types of webs on each substrate, but proportionally more orb webs on shrubs. Additionally, webs tended to be oriented more vertically on shrubs than trees. That web type and angle of placement differ between placement sites suggests that different prey capture strategies may be more effective in different locations. Substrate clearly affects the form and orientation of spider webs, and further studies of building patterns could lead to a better understanding of the effects of site selection and orientation on damage and prey capture efficiency of spider webs.

Literature Cited

Goodwin, S. A. 1997. Web reconstruction and repair by araneid spiders. Dartmouth Studies in Tropical Ecology, p. 134-135.

Kaston, B. J. 1953. How to know the spiders. McGraw-Hill: Boston, MA.

Circadian foraging patterns in *Paraponera clavata*

Jonathon C. Raffensperger

Abstract: Paraponera clavata is a large ponerine ant that feeds on nectar and insects in the understory of tropical forests. Although foraging activity of this ant has been shown to be higher at night than during the day, the mechanism behind this increased rate is unclear. I predicted that individual workers would forage both day and night, becoming more active after dark, and that insect abundance and activity would he higher at night, resulting in a larger percentage of insects in the food brought back to the nest. While I found no difference in the percent composition of food by day versus night, it appears from observations of individually marked ants that daytime workers do remain active and increase their foraging rate at night, but are also joined by a group of exclusively nocturnal foragers.

Key Words: ant foraging, food availability, giant tropical ant, nectar, social organization

Introduction

The giant tropical ant, *Paraponera clavata*, is a common understory forager in the Atlantic coastal lowlands of Costa Rica whose nests are constructed at the bases of large trees and house colonies of 700 to 1,400 workers. This species has been observed to be most active at night, although some workers can be found on foliage and tree trunks during daylight hours (Janzen and Carroll 1983). It is not known, however, whether this nocturnal increase in activity is the result of a general increase in foraging rate, or whether there is some division of labor among workers between day and night, with a larger "night shift" taking over once the sun goes down. Be-