COMPARISON OF FORAGING BEHAVIOR BETWEEN HOWLER MONKEYS, SPIDER MONKEYS, AND SQUIRREL MONKEYS

KATHERINE R. AMATO, D. DÜNYA ÖNEN,
SARAH L. EMEL, AND CHRISTINA H. MAY

Research advisors: Faculty and graduate students. Faculty editor: Matthew P. Ayres

Abstract: Different monkey species have different foraging behaviors based on their preferred food and its availability. We compared foraging behavior of focal individuals of 3 monkey species: *Alouatta palliata* (howler monkey; a folivore), *Ateles geoffroyi* (spider monkey; a frugivore) and *Saimiri oerstedii* (squirrel monkey; an omnivore on fruits and insects). We predicted that howler monkeys would spend a larger proportion of time foraging, and a smaller proportion of time moving, than the other two species. We found that squirrel and spider monkeys spent the greatest proportion of time foraging, the greatest proportion of time moving, and traveled farther than howler monkeys. Proportion of time spent moving, and the total distance traveled by each species, appear to be driven by food availability. However, proportion of time spent foraging appears to depend on overall energy demands and not food quality. We suggest that specific energetic demands and food availability be considered in explaining mechanisms that drive monkey foraging behavior.

Key Words: foraging, Alouatta palliata, Ateles geoffroyi, Saimiri oerstedii

INTRODUCTION

Monkeys spend a large proportion of their time foraging to obtain energy for other activities. However, different species of monkeys prefer different food types. *Alouatta palliata* (howler monkey), *Ateles geoffroyii* (spider monkey) and *Saimiri oerstedii* (squirrel monkey) are three species of New World monkeys commonly found in Corcovado National Park, Costa Rica. Each species has different food preferences: howler monkeys are selective folivores (Mittermeir and Coimbra-Filho 1977), spider monkeys are selective frugivores, and squirrel monkeys consume a wide variety of foods such as fruits, insects, and nectar (Carrillo et al. 1999).

In this study, we compared foraging behavior of these three species. We hypothesized that each species would exhibit different foraging behaviors based on differences in food quality and availability, which we expect to be inversely related. In general, leaves (a low-quality food) are abundant, while fruit (a better-quality food) is less abundant, and insects (a high-quality food) are the least abundant. If we were to assume an inverse relationship between food quality and quantity, we would predict that: (1) time spent foraging is lowest in howler monkeys and highest in squirrel monkeys; (2) time spent moving is lowest in howler monkeys and highest in squirrel monkeys.

However, food availability might not vary according to food quality since we know that not all leaves and fruit are equally edible, and monkeys are discriminating foragers. Then we would not predict the same patterns in time spent foraging, moving, or distance traveled, among the three monkey species.

There is also a relationship between food quality and metabolic rate of the consumer, where low food quality may be associated with lower metabolic rates. Thus, species that depend on high-quality food should be more active, or spend less time resting, than species with lower metabolic rates. Under this hypothesis, howler monkeys would rest the most, and squirrel monkeys would rest the least. We acknowledge that this hypothesis may be too simple, as metabolic rates may be reflected in rate of movement and activity as well as (or instead of) resting time.

METHODS

We observed howler, spider, and squirrel monkeys on 1 - 4 February 2006, along Naranjos, Rio Claro, Espaveles, Ollas, Guanacaste, and Pavo trails in Corcovado National Park, Costa Rica. We observed the monkeys intermittently between 07:30 and 17:30 during two 3-hour intervals on each day. We recorded number of individuals per troop, haphazardly chose focal individual monkeys within troops, and observed them for five minutes. Although we made an effort to choose in an unbiased manner, focal individuals were usually the most visible individuals in the troop. Using five one-minute increments, we categorized animal behavior as foraging (searching for and manipulating food), watching (scanning surrounding ground and vegetation), resting (sitting, lying, or sleeping without any other activity), moving (walking and climbing not accompanied by other activities), or performing other activities (behaviors not fitting into the above categories). We also estimated the total distance each individual moved during the observation period. We collected and identified samples of each species' food resource when possible (Appendix A).

We examined species differences in proportion of time spent foraging, moving, watching, resting, and other behaviors, and total distance traveled using a two-way ANOVA, with troop nested within species. We examined the directionality of results using general linear contrasts. Also, we recorded the number of individuals in each troop and tested the effects of species on troop size using a one-way ANOVA (Appendix B). We performed all analyses with JMP 5.0.1.

RESULTS

During the 5-day sampling period, we observed 99 focal individuals from 39 monkey troops (6 howler, 24 spider, 9 squirrel) varying in size from 2 - 25 individuals. The three species spent similar proportions of time foraging (Fig. 1). Squirrel monkeys spent a greater proportion of time moving than spider monkeys, which spent a greater proportion of time moving than howler monkeys (Fig. 2). Squirrel monkeys and spider monkeys moved further than howler monkeys (Fig. 3). No one species spent a significantly greater amount of time resting than another, but a linear trend in the data suggested that howler monkeys spend the

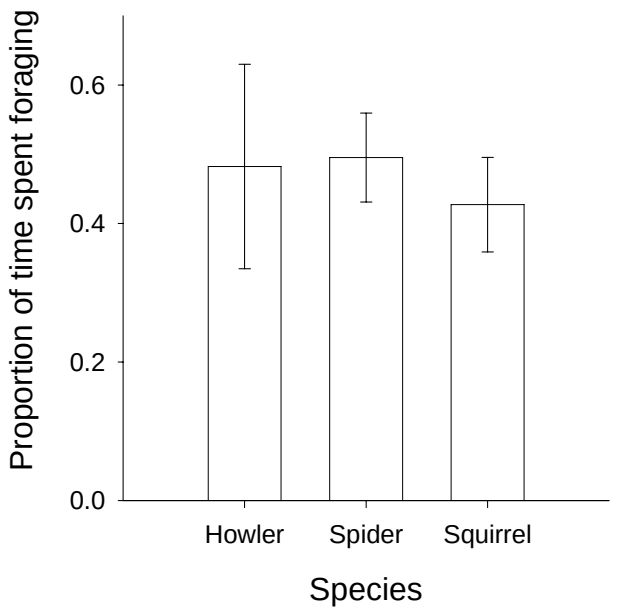

Figure 1. Proportion of time spent foraging during a 5-minute interval (mean ±1 SE) did not differ among monkeys species in Corcovado National Park, Costa Rica ($F_{2, 25} = 0.09$, P = 0.91).

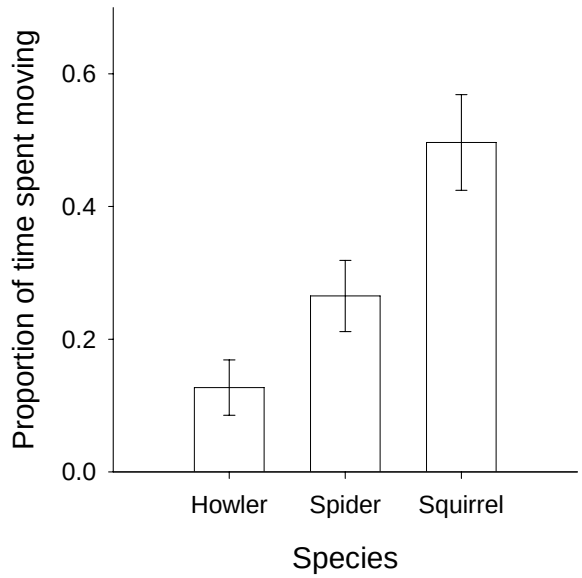

Figure 2. Proportion of time spent moving during a 5-minute interval (mean ±1 SE) for individuals of three monkey species in Corcovado National Park, Costa Rica ($F_{2, 25} = 5.61$, P = 0.011; P = 0.0028 for linear trend).

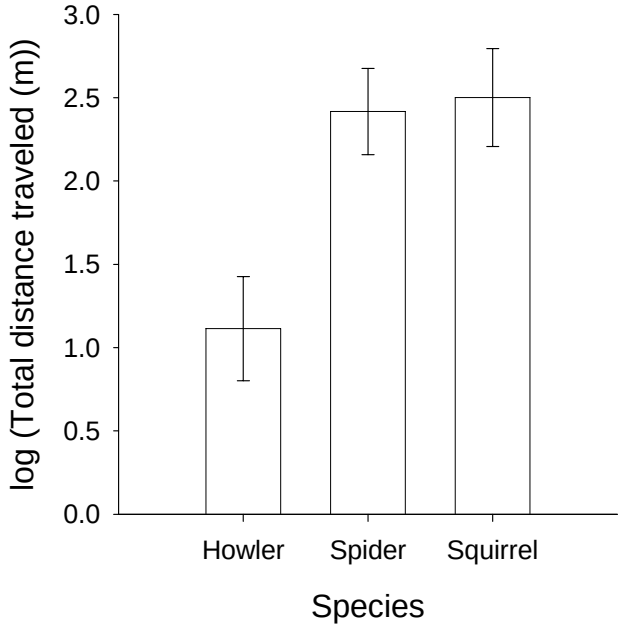

Figure 3. Log of total distance traveled during a 5-minute interval (mean ±1 SE) for individuals of three monkey species in Corcovado National Park, Costa Rica ($F_{2, 25} = 4.57$, P = 0.02; P = 0.03 for linear trend).

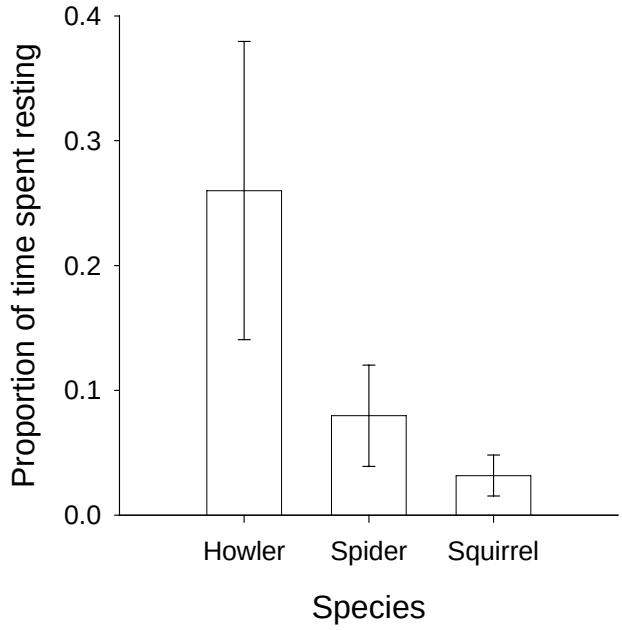

Figure 4. Proportion of time spent resting during a 5-minute interval (mean ±1 SE) for individuals of three monkey species in Corcovado National Park, Costa Rica ($F_{2, 25} = 2.37$, P = 0.012; P = 0.077 for linear trend).

most time resting, while squirrel monkeys rest the least (Fig. 4). No one species spent a greater proportion of time watching or performing other activities than another (all $P > 0.57$).

Troop size varied significantly across species (Appendix B). Food resources collected for all species matched the literature (Carrillo et al. 1999; Mittermeir and Coimbra-Filho 1977; Appendix A).

DISCUSSION

As predicted, the proportion of time spent moving (and the total distance traveled by each species), was associated with food quality. Squirrel monkeys must search for food more than spider monkeys, while howler monkeys apparently search (move) the least. Squirrel monkeys spent a larger proportion of time moving than spider monkeys, yet the total distance traveled is similar to that of spider monkeys. This may simply be a function of body size; squirrel monkeys (0.5 - 1 kg) are much smaller than spider monkeys (5 - 9 kg; Carrillo 1999) and are likely not able to move at the same rate.

Food quality does not appear to be the primary factors influencing the amount of time each species spends foraging. Howlers appear to spend more time resting than either of the other species, and therefore expend less energy searching for food. It is also possible that foraging time is distributed differently throughout the day for different species. For example, because they use fermentation to digest leaves, howler monkeys may spend more time foraging in the earliest part of the day, and less time later in the day. Because we did not observe the monkeys over a wider time range, such as continually from daybreak to sundown, our methods were not designed to detect schedules of foraging behavior.

We believe that our data fairly represent the general foraging behaviors of each species, although our visual estimates of total distance traveled were rough. We suggest that energetic demands and actual food resource availability be examined in more detail for each species to better understand the physiological mechanisms behind foraging behavior. Although we used proportion of time spent watching to evaluate predator avoidance behavior, proportion of time spent moving may also be associated with predator avoidance.

Foraging behavior determined by food quality and availability may influence the distribution of monkey species within an area such as Corcovado National Park. In general, if howlers need to move less to find food, they may have lower space requirements than other monkey species. However, this would depend on the distribution of preferred leaf species.

The monkey community within the park may be dynamic. Lief et al. described spider monkeys and white-faced capuchins (*Cebus capucinus*) as the two most abundant species in Corcovado National Park (1996), but we observed only one troop of white-faced capuchins. It is unclear whether such changes are due to resource availability, space requirements, predation, or disease. However, both our samples and those of Lief et al. (1996) were small, so differences may be due to chance.

LITERATURE CITED

Carrillo et al. 1999. Squirrel Monkey, Mantled Howler Monkey and Geoffroy's Spider Monkey in Costa Rica Mammals. Institute Nacional de Biodiversidad: Santo Domingo de Heredia.

Lief, G.M. et al. 1996. Foraging strategies and niche partitioning in *Ateles geoffroyi* and *Cebus capucinus* in Dartmouth Studies in Tropical Ecology 1996. Dartmouth College: Hanover, NH.

Mittermeier R.A. and Coimbra-Filho A.F. 1977. Primate Conservation, H.R.H. Prince Rainier III and G.H. Bourne (eds.), New York Academic Press.

APPENDIX A. Food resources we observed individuals of each species consuming 1-4 February 2006, in Corcovado National Park, Costa Rica.

Monkey Species	Plant Family	Species	Portion of Plant Consumed
Howler monkey	Morphotype A		Leaf
Spider monkey	Anacardiaceae	*Spondias purpurea*	Fruit and leaf
	Annonaceae	*Guatteria amplifolia*	Fruit
	Arecaceae	*Astrocaryum standleyanum*	Fruit
	Malpighiaceae	*Byrsonima crispa*	Fruit
	Moraceae	*Ficus spp. 1*	Fruit
		Ficus spp. 2	Fruit
Squirrel monkey*	Meliaceae	*Guarea pterorhachis*	Fruit
	Moraceae	*Ficus costaricana*	Fruit

*Squirrel monkeys were also observed consuming insects which we were unable to identify.

APPENDIX B. Maximum, minimum and mean (± SE) troop size for each of three monkey species. Troop size was significantly different across species ($F_{2, 38} = 6.83$, $P = 0.0029$). Data were recorded on 1-4 February 2006, Corcovado National Park, in Costa Rica.

Monkey Species	Maximum	Minimum	Mean
Howler	16	4	7.75 ± 1.88
Spider	12	2	4.25 ± 1.08
Squirrel	30	5	11.78 ± 1.77

RESOURCE PREFERENCE AND FORAGING EFFICIENCY IN LEAF-CUTTER (*ATTA COLUMBICA*) ANTS

KATHRYN M. SULLAN, CATRINA A. LINDGREN, ABIGAIL ADAMS

Research advisors: Faculty and graduate students. Faculty editor: Matthew P. Ayres

Abstract: Leaf-cutter ants (*Atta spp.)* move enormous amounts of woody and herbaceous biomass in neotropical forests. We examined *Atta columbica* plant preference across 5 colonies by presenting four different leaf and flower types on primary and secondary foraging trails. We examined (1) whether plant resource preference varied across colonies, (2) whether trail type affected foraging preference and efficiency, and (3) whether the least desirable plant resources were removed (dumped) from the foraging trail. Our results suggest that *Atta columbica* has about the same rank preference of plant resources across all colonies. Of the four species samples, tougher plant species were preferred over less tough species. All plant resources were picked up faster on primary trails than secondary trails and dumping rate was highest for the least tough, least preferred resource. Although clearing a well-defined primary trail requires additional energy expenditure by the ants, the benefit to the colony appears to be a faster, more efficient return of resources to the nest.

Key Words: leaf-cutter ants, foraging preference, foraging trails, Atta columbica

INTRODUCTION

Leaf-cutter ants (*Atta spp.*) are important herbivores in neotropical forests. Mannan et al. (1996) estimated that *A. columbica* in Corcovado, Costa Rica, can consume roughly 4.78 tons of leaves/ha/yr which presumably has broad impacts on forest structure and composition. Vegetation is cut and carried back to the nest to support fungal gardens which feed the colony. Although leaf-cutter ants are generally regarded as highly selective foragers (Stevens 1983, Grace et al. 1997), there is limited knowledge on plant preference within and across colonies. We investigated the tendency of *A. columbica* to pick up non-target plant resources (ie not being used by the colony at that time) on primary and secondary foraging trails. Primary trails are wider, well-cleared, and have higher ant activity than secondary trails, which may directly affect the costs and benefits of picking up non-target resources on each trail type.

We examined how resource preference varied across colonies and how costs and benefits are weighed in picking up non-target resources on different trail types. We tested whether preference differed between colonies, predicting that toughness of plants may influence preference.

A. columbica colonies invest much energy clearing and maintaining primary trails, which may benefit the colony by increasing the efficiency of workers. We hypothesized that non-target resources would be picked up faster on primary than secondary trails.

There may be a benefit to removing undesired plant resources from foraging trails to prevent the resource from accidentally being brought back to the colony. Thus, we hypothesized that the rate of dumping (when a plant fragment is

moved off a trail) would be highest for the least preferred plant species.

METHODS

We examined 5 leaf-cutter ant colonies (*Atta spp.*) on 2-3 February 2006 in secondary forest near the Estación Sirena, Corcovado National Park, Costa Rica. For each colony, we chose a primary trail (high ant activity, well-cleared, wide) and a secondary trail (low ant activity, less cleared, narrow) and recorded ant activity on each trail (ants per minute crossing an arbitrary line within 2 m of the nest). To test plant resource preference, we chose four different plant species—an unknown woody leaf species, a flower, a petal, and a heliconia leaf species—which all had evidence of leaf-cutter ant foraging. We calculated preference as the average time it took to pick up each plant resource, standardized by the trail's ant activity. For each test, we cut each plant species into five 1 x 0.5 cm square fragments and placed each resource at randomly selected points along the trail within 2 meters of the nest. We then recorded the time it took for the ants to pick up each fragment within a 10 minute trial, and whether the fragment was taken towards the colony or removed from the trail (dumped). We measured toughness, a putative criteria for plant preference, with a penetrometer.

To compare the difference in ant activity (number of ants per minute) on primary versus secondary trails, we performed an ANOVA. Next, to examine how time to pick up per ant-minute was affected by colony, trail type, plant type, and the interactions between colony and plant type and colony and trail type, we performed a three-way ANOVA. Finally, to compare how the rate of dumps per ant-minute was affected by colony, trail type, and plant type, we performed a two way ANOVA. We used JMP 5.0.1 for all analyses.

RESULTS

Primary trails had significantly higher ant activity than secondary trails ($F_{1,4}$ = 7.96, P = 0.03; Fig. 1). This was not surprising, as ant activity was part of the definition of trail type. *A. columbica* chose plant resources with a consistent preference: the woody leaf resource was always picked up first, followed by the petal and the flower, and last the heliconia ($F_{3,159}$ = 53.5, P = <0.0001; Fig. 2). All plant resources were picked up faster on primary trails than secondary trails ($F_{1,159}$ = 444, P = <0.0001; Fig. 3). The order of resource preference and the faster pick up time of resources on primary trails was the same across all colonies, but the pattern varied among colonies (colony x trail type: $F_{4,159}$ = 18.1, P = <0.0001; colony x plant type: $F_{12,159}$ = 6.93, P = <0.0001). There were no other significant effects in the general linear model (all P values > 0.2). The most preferred resource, the woody leaf species, was the most tough plant species whereas the least preferred species, the heliconia, was the least tough species ($F_{1,4}$ = 4.38, P = 0.06; Fig. 2).

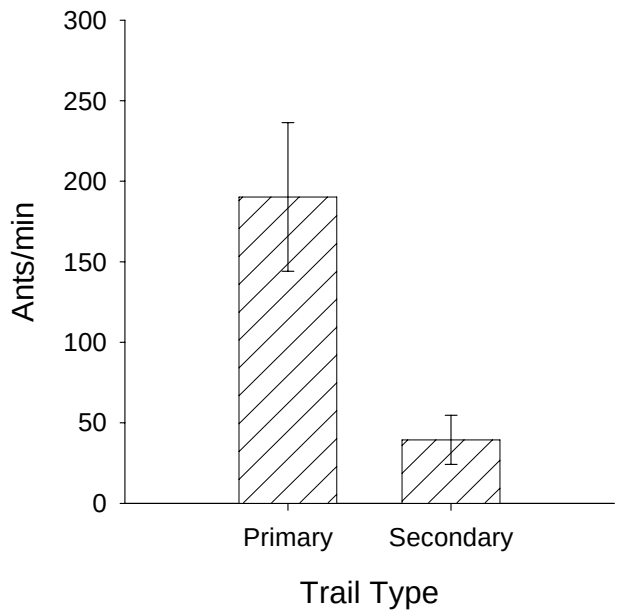

Figure 1. The number of ants/min on primary versus secondary foraging trails across five *A. columbica* colonies near Sirena Biological Station in Corcovado, Costa Rica.($F_{1,4}$ = 7.96, P = 0.03).

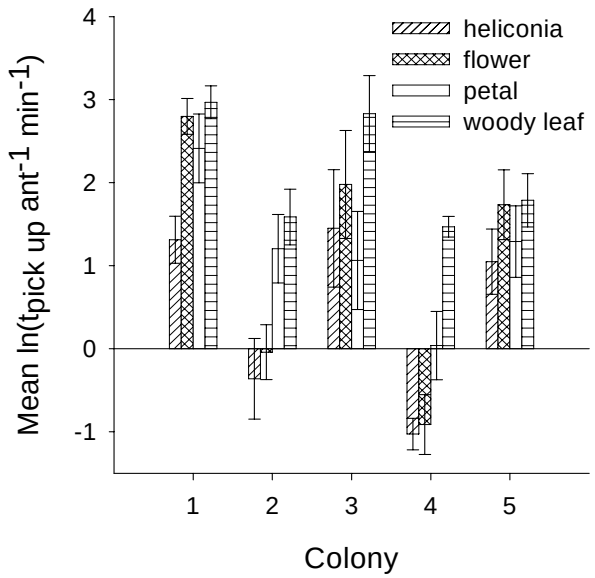

Figure 2. Preference ranking of five *A. columbica* colonies calculated as $\ln(t_{pickup} \cdot ant^{-1} \cdot min^{-1})$ for four species of non-target plant resources ranked in order of toughness (least tough to most tough) ($F_{12,198}$ = 6.81, P = <0.0001). Plant species that are more preferred have lower $\ln(t_{pickup} \cdot ant^{-1} \cdot min^{-1})$. Study was performed near Sirena Biological station in Corcovado, Costa Rica.

Finally, of the 200 total plant resource fragments, 31 of these were dumped. Heliconia, the least preferred species, was dumped substantially more than the other three resources, while the woody leaf resource was never dumped ($F_{3,39}$ = 5.09, P = 0.02; Fig. 4). However, there was no difference in dumping rate among colonies ($F_{4,39}$ = 1.31, P = 0.32) or trail types ($F_{1,39}$ = 1.51, P = 0.24; Fig. 4). There were also no significant interactions involving dumping rate, colony, trail type, and plant type (all P values were > 0.2).

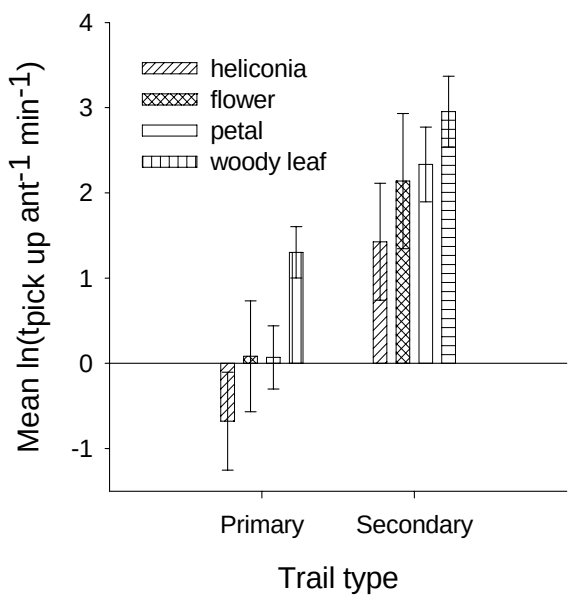

Figure 3. Preference ranking of *A. columbica* calculated as $\ln(t_{pickup} \cdot ant^{-1} \cdot min^{-1})$ for four species of non-target plant resources on primary versus secondary foraging trails. Primary trails have lower $\ln(t_{pickup} \cdot ant^{-1} \cdot min^{-1})$ for all plant resources ($F_{1,198}$ = 436.69, P = <0.0001).

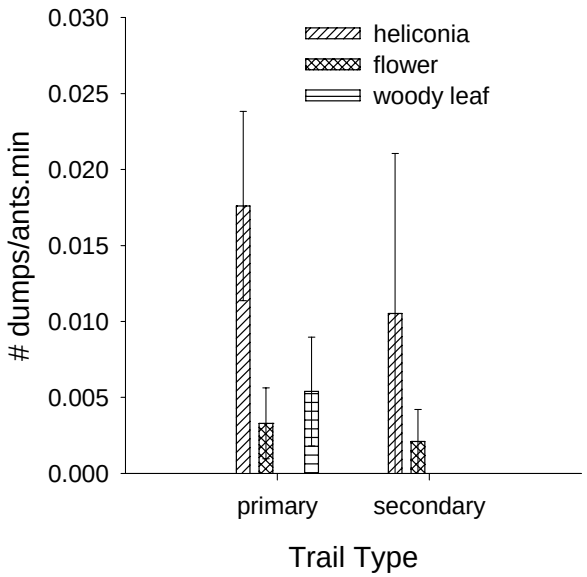

Figure 4. The mean number of dumps/ant/minute between primary and secondary foraging trails for four non-target plant resources. *Atta spp.* Number of dumps for petals across both trail types equals zero.

DISCUSSION

The consistent resource preference ranking across colonies indicates that certain plant resources are more valuable than others to *A. columbica.* The toughest leaves were the most preferred; they may have the highest nutrient availability.

The non-target plant resources were picked up faster by the ants on primary trails than secondary trails. Wider, well cleared primary trails may reduce the effort per ant-minute of bringing non-target resources back to the nest. Higher ant activity on primary trails may result in more pheromones, eliciting a faster behavioral response when the ant encounters a plant resource.

Our finding that rate of dumping of heliconia was higher than any other plant resource indicates that *A. columbica* actively removes the least preferred resources from foraging trails.

LITERATURE CITED

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

Stevens, G.C. 1983. *Atta columbica* Pp 689-691 in D.H. Janzen, ed. Costa Rican Natural History. University of Chicago Press: Chicago, IL.

EVALUATING THE EXPLOITATION ECOSYSTEMS HYPOTHESIS IN A MARINE-INFLUENCED RIVER COMMUNITY

ANDREW R. CARRERAS, BRIAN D. BATES, PAUL R. WRIGHT

Research advisors: Faculty and graduate students. Faculty editor: Matthew P. Ayres

Abstract: According to the Exploitation Ecosystems Hypothesis (EEH), the number of trophic levels in a system predicts the intensity of herbivory on the plant community. We applied this hypothesis to the Río Claro in Corcovado National Park, Costa Rica, where marine predators at high tide may represent an added trophic level. We also hypothesized that herbivorous fish would seek refuge upriver with consequences for trophic structure. We measured percent algal cover and herbivorous fish abundances and recorded substrate type in 1 km transects moving upriver from the mouth. Algal cover declined with increasing distance from the mouth within the tidal zone, and was higher above the tidal zone. Large herbivores were highest in abundance at the upriver edge of the tidal zone, while small herbivores were found exclusively above the tidal zone. The results support the existence of a shift in trophic interactions as predicted by the EEH, but also suggests that trophic structure may be so dynamic that equilibrium may not hold.

Key Words: Gobiidae, Exploitation Ecosystems Hypothesis, tide

INTRODUCTION

The Exploitation Ecosystems Hypothesis (EEH) predicts that herbivore pressure will be directly related to the number of trophic levels in an ecosystem. In ecosystems with an odd number of trophic levels, predators decrease herbivore abundance and green biomass will be high. In ecosystems with an even number of trophic levels, green biomass will be low because of intense herbivory (Oksanen et. al 1981). Many rivers contain two trophic levels: primary producers (algae), and herbivorous fish subject to little or no predation (Oksanen and Oksanen 2000). For example, the Río Claro, near Estación Biológica Sirena, Corcovado National Park, Costa Rica contains herbivorous gobies (Gobiidae) that feed on benthic algae. However, the Río Claro also empties into the Pacific Ocean, permitting large marine predators to enter the river at high tide.

Following the EEH, we hypothesized that the flux of large predators into the tidal zone of the river adds another trophic level and alters herbivore pressure. We predicted that there would be higher algal cover and lower herbivorous fish abundance in the tidal zone compared to the non-tidal zone. We also hypothesized that herbivorous fish move upriver during high tide to avoid marine predators. Thus, we expected that algal cover would be lowest and herbivorous fish abundance would be highest at an intermediate distance from the river mouth immediately beyond the tidal zone.

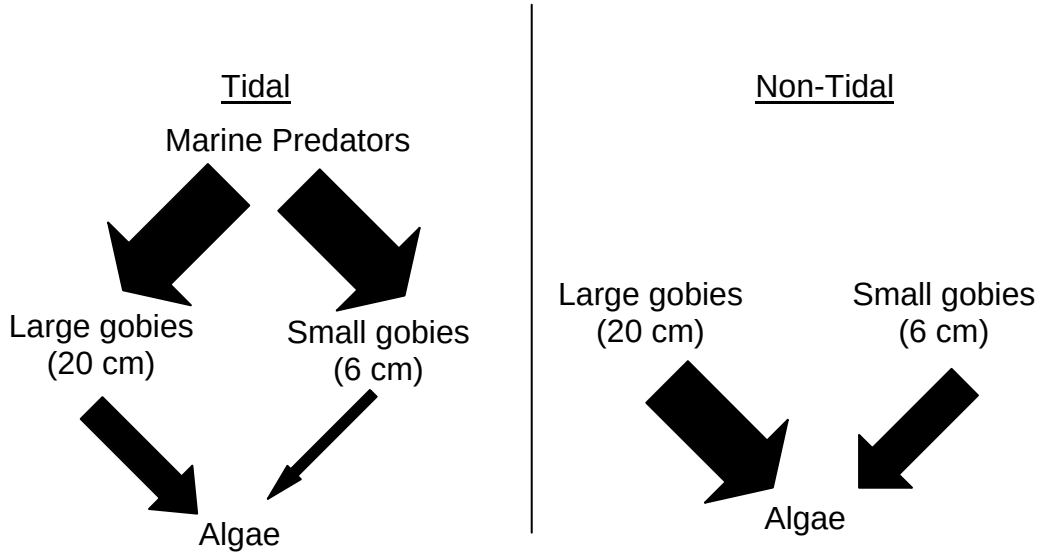

Fig. 1. Trophic structure of the tidal and non-tidal zones in the Río Claro, Corcovado National Park, Costa Rica, as predicted by the Exploitation Ecosystems Hypothesis. Arrow thicknesses represents relative intensities of speculative predation and herbivory.

METHODS

We performed our study on 2 February, 2006 in the Río Claro, Corcovado National Park, Costa Rica. We ran three transects at low tide from the mouth of the river to 1 km upriver. We selected 2 x 2 m plots located every 50 m along each transect, and visually estimated the percent algal cover of the substrate, identified the most prevalent substrate type (cobble, pebble, or sand) and measured water depth. We also recorded the abundance and morphotypes of gobies (Gobiidae), observed within a 5 meter radius during a 2 minutes period.

We employed a general linear model to test how percent algal cover and goby abundances varied with distance from river mouth and substrate. We used chi-square analysis to test for differences in goby abundances between tidal and non-tidal zones. We treated the first 650 m of our transect as the tidal zone based on (1) conductivity samples, and (2) the steepness in topography just after 650 m, which would make intrusion by either salt water or marine predators unlikely. We also looked for relationships between percent algal cover and goby abundances using linear regressions. We used JMP 5.0.1 for all analyses.

RESULTS

We observed changes in the river, both biotic and abiotic, with changes in tide. At high tide, the width of the mouth of the river increased by at least 20 m, and visibility changed from clear to murky. We noted evidence of large marine predators, such as smaller fish jumping and the presence of crocodiles. We conducted our study during a period of extreme variance in tidal levels (low: 21 cm, high: 302 cm).

Within the tidal zone, percent algal cover decreased with increasing distance from the river mouth ($F_{1,8} = 36.43$, $P < 0.001$).

Percent algal cover was again high immediately after the end of the tidal zone (Fig. 2). Substrate explained little or none of the changes in percent algal cover ($F_{2,8}$ = 2.44, P = 0.15).

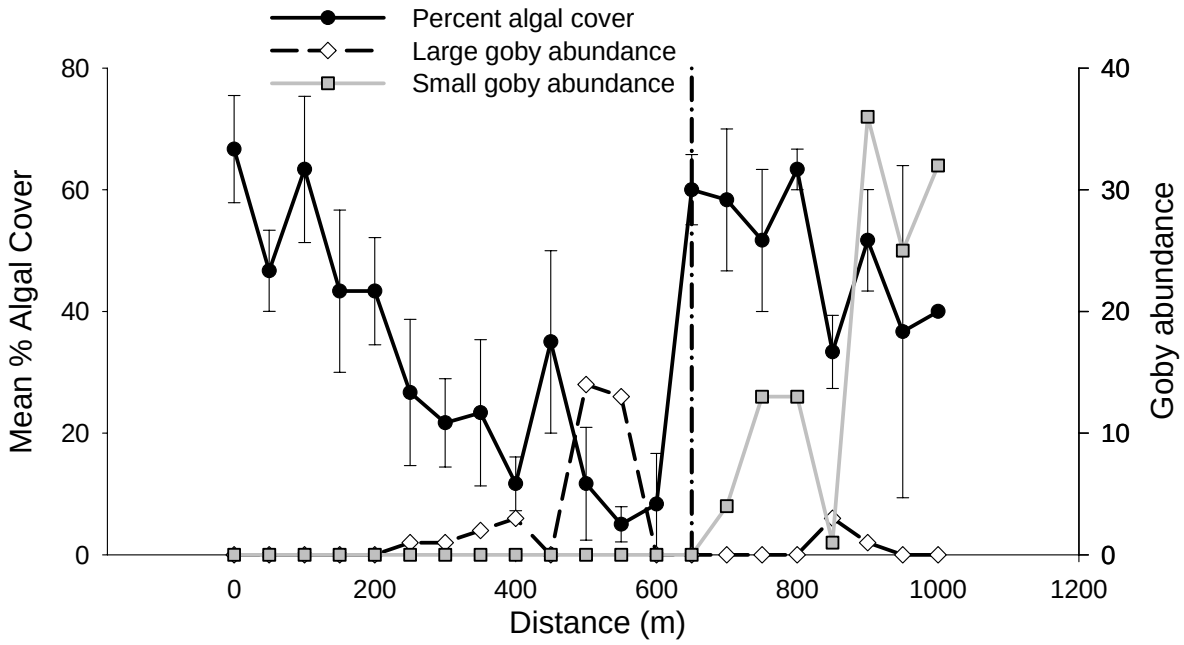

Fig. 2. Mean percent algal cover (± S.E.; black circles, solid black line), large goby abundance (white diamonds, dashed line), and small goby abundance (grey triangle, solid grey line) with increasing distance from the mouth of the Río Claro, Corcovado National Park, Costa Rica. Vertical dashed line at 650 meters represents the division between tidal (left) and above-tidal zones (right).

We observed at least two species of goby: a large species with an estimated length of 20 cm, and a smaller species (or multiple species), with an estimated length of 6 cm, both of which we observed feeding on algae. Large gobies were more abundant in the tidal zone (χ^2 = 201.5, P < 0.001), while small gobies were found exclusively in the non-tidal zone (χ^2 = 12.3, P < 0.001). Percent algal cover decreased with increasing large goby abundance (r^2 = 0.33, df = 19, P < 0.01; Fig. 3), and was still marginally significant after excluding extreme values of 13 and 14 large gobies (r^2 = 0.16, df = 17, P = 0.09; Fig. 3). We found no relationship between percent algal cover and small goby abundance (r^2 = 0.06, df = 19, P = 0.28).

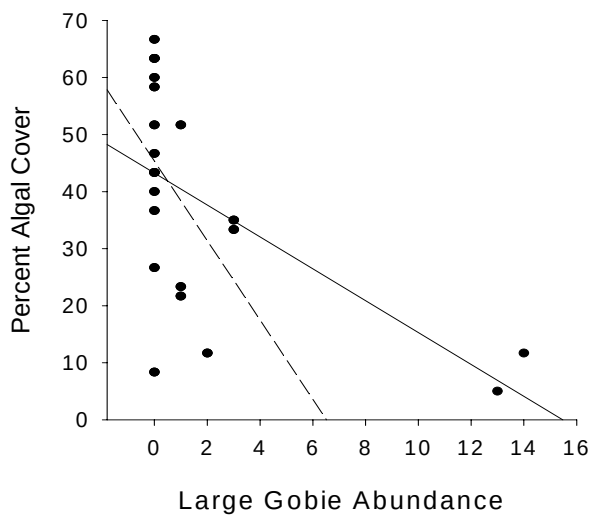

Fig. 3. Percent algal cover by abundance of large gobies in the Río Claro, Corcovado National Park, Costa Rica. Solid regression line (r^2 = 0.33, df = 19, P < 0.01) includes 2 extreme values (x = 13,14), while dashed regression line (r^2 = 0.16, df = 17, P = 0.09) excludes them.

Discussion

Goby and algal distributions and abundances in the Río Claro suggest that the addition of a trophic level has altered herbivory, as predicted by the Exploitation Ecosystems Hypothesis. The absence of gobies and the high percentage of algal cover closest to the river mouth were consistent with the prediction that marine predators drive down herbivorous fish abundances near the mouth. Greater large goby abundances and reduced percent algal cover at the upper end of the tidal zone support the second prediction that herbivorous fish find an upriver refuge from marine predators at an intermediate distance from the mouth. The distribution and abundance of large goby and algae may be a result of both factors: high predation at the mouth and migration to the upper tidal zone at high tide. However, we did not sample at high tide due to greatly reduced visibility and the presence of crocodiles, and we were unable to observe herbivorous fish moving upriver at high tide.

The absence of small gobies in the tidal zone suggests that large predators could have greatly depleted small gobies there. Alternatively, the small gobies may not be adapted to salinity and other conditions in the tidal zone. We acknowledge that our conclusions are speculative, and that many factors in addition to predation vary across the tidal gradient. Examining the salinity tolerance of herbivorous and predatory fish would help to determine the role of salinity in their distribution in the Río Claro.

Literature Cited

Oksanen, L. et al. 1981. Exploitation Ecosystems in Gradients of Primary Productivity. American Naturalist. 118(2): 240-261.

Oksanen, L. and T. Oksanen. 2000. The Logic and Realism of the Hypothesis of Exploitation Ecosystems. American Naturalist. 155(6): 703-723.

SIZE EFFECTS ON FORAGING PATTERNS IN *MACROBRACHIUM* SHRIMP

SCOTT W. SCHWARTZ

Research advisors: Faculty and graduate students. Faculty editor: Matthew P. Ayres

Abstract: A change in the size of an organism can select for changes in the behavior of an organism, and vice-versa. Small *Macrobrachium sp.* shrimp can be seen swimming in streams at all times around the Sirena Station in Corcovado National park, while larger shrimp are only visible at night. I compared large and small shrimp foraging behavior under light and dark conditions, and found that small shrimp are more likely to forage in the light. I evaluated two hypotheses to explain the behavior difference between large and small shrimp: (1) smaller shrimp's high metabolic rate requires that they forage during the day, and (2) a tradeoff between the predation risk while foraging and the protection afforded by reaching a greater size through increased foraging. In a 12 hour starvation period, I saw no evidence of differences between metabolic rates of shrimp. A mathematical model of the tradeoff hypothesis evaluated the effects of time spent foraging on probability of surviving to reproductive size under different scenarios of growth rate and predation risk. This exercise failed to identify any plausible scenarios in which small shrimp would maximize the probability of surviving to reproduce by sustaining more risks as a small shrimp to grow quickly through a vulnerable size class.

Key Words: crustacea, foraging behavior, Macrobrachium *shrimp, predation, stream invertebrates*

INTRODUCTION

A change in the size of an organism can select for changes in the behavior of an organism, and vice-versa. Shrimp of the genus *Macrobrachium* are common in streams around the Sirena Biological Station in Corcovado National Park, Costa Rica and can reach up to 15 cm in length. They are thought to be mainly detritivores, but may also function as predators (Brown et. al, 2000). Their foraging patterns probably have consequences for the stream community (Wilson et. al, 2004). Medium and large shrimp appear to be mainly nocturnal, but small individuals apparently forage at all times of the day. It seems paradoxical that the smaller, seemingly more vulnerable shrimp risk foraging more than the larger shrimp.

I propose two hypotheses to explain the difference in foraging behavior between small and large shrimp: (1) Smaller shrimp have greater metabolic requirements (need more grams of food per gram of mass) and needed to forage during the day to stay alive. I tested the prediction that during starvation periods, smaller shrimp will lose a larger proportion of body weight. (2) There is a tradeoff between the predation risk while foraging, and the protection afforded by reaching a greater size (which is contingent upon foraging). The probability of dying in any day has to be reduced by hiding more and foraging less, but the probability of dying before attaining reproductive size might be minimized by foraging more and increasing growth rate through the early vulnerable size classes (even if it means increasing the short term risk of mortality).

METHODS

I collected *Macrobrachium* from 5-meter sections of four small streams around the Sirena Station in Corcovado National Park in February, 2006. I sampled streams at the end of the airstrip, just inside the Pavo and Ollas trails, and one about 1 kilometer up Los Naranjos trail. I grouped the collected shrimp into small (0-3 cm), medium (3-7 cm) and large (7-15 cm) size classes.

I placed one large, one medium, and two small shrimp in a bucket with 50% of its bottom covered with sandy substrate from streams. I kept the bucket in darkness and recorded if shrimp were motionless (hiding) or moving around (foraging) every 15 minutes for 2 hours. I placed the bucket in a constant light source and repeated the process after a half-hour acclimation period.

I randomly chose 3 shrimp from each size class for a starvation trial to test metabolic rate. I measured the changed in body mass following a 12 hour trial, during which test subjects were isolated and activity kept to a minimum.

I developed a speculative model to explore whether decreasing predation risk with increasing size might explain the duration of daily foraging activity in small shrimp. The model simulated shrimp growth from a specified initial mass with growth as a function of time spent foraging:

$$RGR = RGR_{max} - (1/t^2) \qquad \textit{(Eq. 1)}$$

where RGR = the relative growth rate ($g * g^{-1} * d^{-1}$), RGR_{max} = maximum relative growth rate ($g * g^{-1} * d^{-1}$; set at 0.05) and t = the number of hours the shrimp spends foraging. I acknowledge that this functional form may not truly represent the trends in RGR with time spent foraging.

I modeled daily shrimp growth with the equation:

$$M_f = M_i * e^{RGR} \qquad \textit{(Eq. 2)}$$

where the M_f = final mass (g) and M_i = daily initial mass (g; M_i initially set at 0.2 g extrapolated from size of smallest shrimp caught in field).

I modeled daily shrimp mortality as a function of hours spent foraging, which increased mortality, and mass, which decreased mortality:

$$P(D) = k_{min} + (k * t_{forage}) - (k * y * M * t_{forage}) \qquad \textit{(Eq. 3)}$$

where P(D) = probability of shrimp mortality, k = predation rate (shrimp removed from the system per unit time; set at 0.01 for baseline predictions), k_i = initial value of predation rate (set at 0 for baselines predictions) and y = the effect body size has on decreasing predation rate (set at 1 for baseline predictions). I acknowledge that this functional form may not represent actual trends in P(D).

Using the mortality function (Eq. 3), the model calculated the percentage of shrimp that reached a mass necessary to reproduce (set at 0.75 grams based on onset of sexual dimorphism in captured shrimp). I ran the model with the baseline values, and testing the effect of varying y (to 2), RGR_{max} (to 0.1), and k (to 0.02) at three

different starting masses: 0.2 (size at birth based on visual estimation), 0.4, and 0.6 grams (smallest shrimp weighed).

RESULTS

All size classes of shrimp foraged for 81% of the time in the darkness, indicating no difference in foraging patterns. Large and medium shrimp foraged for 12.5% of the time in the light, while small shrimp foraged for 75% of the time in the light. There was no significant relationship between the percentage of mass lost and the initial mass of the shrimp over the 12 hour starvation period (Fig. 2). Within the modeling framework of equations 1-3, I could not find any plausible parameter combinations that predicted high daytime foraging by small shrimp but not large shrimp.

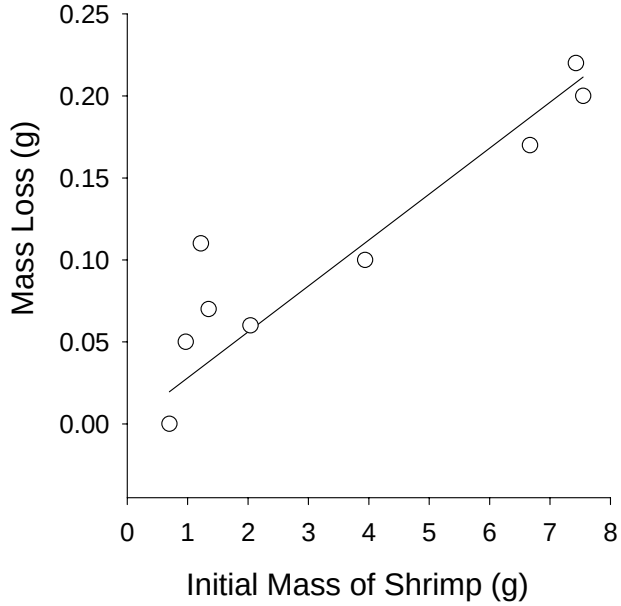

Figure 1. The relationship between the initial mass of Macrobrachium shrimp and mass loss during a 12 hour starvation period.

DISCUSSION

Experimental results confirmed the difference in diurnal foraging behavior between large and small shrimp. When kept in constant light, small shrimp continued to roam about and forage for detritus, while larger shrimp settled down into the substrate and remained motionless. All sizes of shrimp forage actively in the dark, with larger shrimp feeding on both detritus and small organisms, such as fish and tadpoles (Brown et. al, 2000). The behavior of the large shrimp suggests that they are avoiding a diurnal predator, such as large wading birds, while they are not threatened by stream predators that are always resident in the stream, such as fish.

Although it is generally true that small organisms have higher metabolic needs per gram, even the small shrimp that we studied did not die, lose appreciable mass, or show any ill effects from 12 hours of food deprivation. Possibly the smaller shrimp would have lost more mass if the starvation period was longer, and 12 hours of food deprivation might produce mortality if food had been scarce in the weeks before. I was unable to identify a combination of parameters in my speculative model in which small shrimp

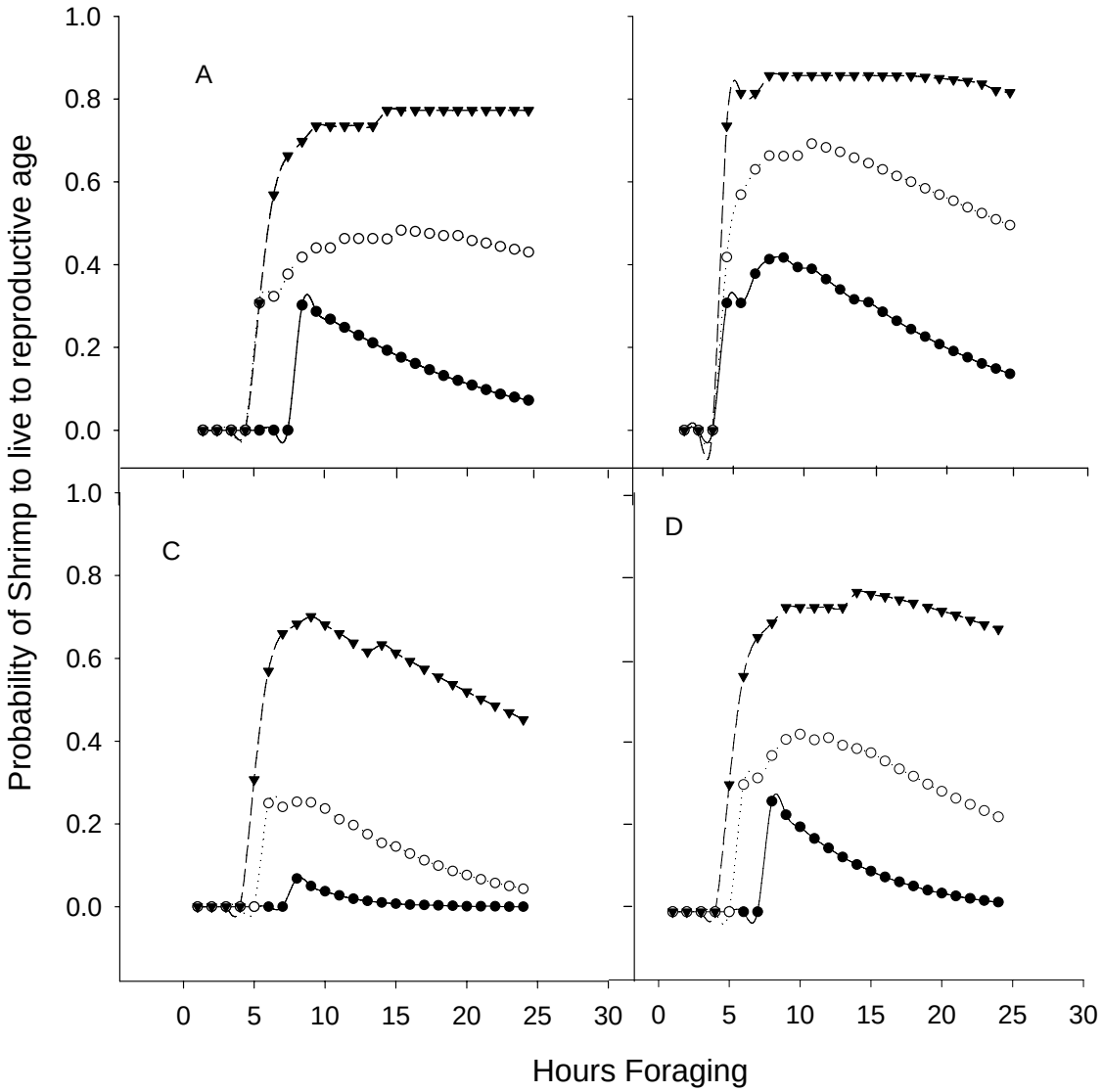

Figure 2. Visual representation of the cost benefit/analysis of the foraging behavior of small (•) medium (o) and large (▼) *Macrobrachium* shrimp. The zenith of each function correspond to the predicted optimum for hours spent foraging. (a)Estimation using baselines values for all parameters. (b) Estimation using increased effects of mass on predation. (c) Estimation using increased predation rates. (d) None of the scenarios within the model could explain the observed behavior of small *Macrobrachium* shrimp.

would benefit from day time foraging. Alternative formulations of the model might favor daytime foraging by small shrimp to reduce their duration of vulnerability.

More research must be performed to determine the mechanism behind the differences in foraging behavior between large and small *Macrobrachium* shrimp. I recommend focusing on community interactions in the stream, examining the different behaviors of predators that feed on large and small shrimp at different times of the day. It is possible that diurnal predators, such as birds, ignore the small shrimp while foraging for the large ones.

LITERATURE CITED

Brown, A.C., S.E. LaPlante, W.H. Lowe, and E.M. Mahar. 2000. Macrobrachium: Tiger of the night waters. Dartmouth Studies in Tropical Ecology. p. 108-111.

Wilson, E.V., R.Q. Thomas, and L.M. Evans. 2004. Macrobrachium as a possible determinant of astyanax fasciatus distribution in a neotropical lowland stream. Dartmouth Studies in Tropical Ecology. p. 99-102.

BAT SPECIES DISTRIBUTION IN PRIMARY AND SECONDARY FORESTS AT CORCOVADO NATIONAL PARK

NATHAN H. RAINES AND WILLIAM F.J. STORK

Research advisors: Faculty and graduate students. Faculty editor: Matthew P. Ayres

Abstract: As frugivores, nectarivores, and insectivores, bats will respond to differences in plant communities. Using an ultrasound detector and computer software to analyze bat calls as sonotypes (a proxy for bat species), we tested whether differences in the plant community between primary and secondary forests were associated with different bat communities. We calculated species-area curves and found greater alpha diversity of bats in secondary forest and greater beta diversity of bats in primary forest, with little species overlap between them.

Key Words: Chiroptera, *bats, species richness, species-area relationship, primary forest, secondary forest*

INTRODUCTION

Differences in plant composition can produce differences in higher trophic levels. Primary forest tends to have greater plant species richness, while secondary forest tends to have lower chemical defenses. The community structure in each type of forest may reflect these differences: herbivores in primary forests may be more scarce and specialized, while herbivores in secondary forests may be more abundant and omnivorous. Differences in the herbivore community could then influence the structure of the predator community.

As frugivores, nectarivores, and insectivores, bats are close to plants in the food chain. The species composition of bats in or near deforested areas could differ significantly from nearby, undisturbed areas.

We tested the predictions of three hypotheses regarding bat species distributions: (H_1) primary forest has higher bat species richness because greater vegetative diversity produces more diverse insect feeding clades spanning the prey preference of a greater number of bat species (Wainwright 2002); (H_2) secondary forest has higher bat species richness because lower levels of plant chemical defense result in more insects for bats to prey upon; this speculation rests on the assumption that insect abundance in primary forest is low enough to severely limit the number of bats in a given microhabitat; (H_3) primary and secondary forests have equal bat species richness, but bat species composition differs between the two forests, indicating that both habitats are suitable for bats but that different bat species prefer different habitats.

METHODS

We sampled bat calls at 16 sites (8 in primary forest, 8 in secondary) along the trail system surrounding Sirena Biological Station at Corcovado National Park, Costa Rica. We chose sites using a combination of scouting walks during the day and observations of high bat activity at night, and attempted to match pairs of microhabitats between the primary and

secondary forests. We recorded bat calls over a 15-minute interval at each site using a Petterson Ultrasonic Detector. We visited 4 sites (half in primary, half in secondary) from 21:00 – 24:00 on 2 February 2006, 4 more sites from 03:00 – 05:30 on 3 February, and 8 more sites from 01:00 – 05:30 on 4 February. We analyzed each bat call visually and audibly with Sonobat 2.0, and divided the bat calls into sonotypes (a putative proxy for species, see Krivak-Tetley et al. 2002).

For each forest, we calculated alpha diversity (mean number of species at one site) and then generated species-area curves by calculating the mean number of species found in permutations of 1, 2, 3, 4, 5, 6, 7, and 8 sites and then fitting a Michaelis-Menten saturation function to the data from our species-area curves:

$$y = \frac{K * x}{d + x}$$

[Eq. 1]

where K is the saturation value and d is the number of sites necessary to reach the half-saturation value. We then calculated beta diversity by linearizing the species-area curves using Gleason's (1922) logarithmic model:

$$\log(E[S_n]) = h\log(n) + k$$

[Eq. 2]

where k is the y-intercept and h is slope, where greater slope equals increased beta diversity.

RESULTS

We recorded 68 bat calls across all of the sites (47 in secondary forest, 21 in primary), and distinguished 19 sonotypes. Eight of these sonotypes occurred exclusively at sites in primary forest, 9 of the sonotypes occurred exclusively at sites in secondary forest, and 2 sonotypes were recorded at sites in both primary and secondary forest.

Alpha diversity in primary forest was lower than in secondary forest (mean species per site ± 1 SE; primary = 1.62 ± 0.42, secondary = 2.75 ± 0.36; $t_{1,13}$=2.02, p= 0.06). Beta diversity was higher in the primary forest than the secondary forest (primary: $\log(E[S_n]) = \mathbf{0.878}\log(n) + 0.521$, $r^2 = 0.998$; secondary: $\log(E[S_n]) = \mathbf{0.660}\log(n) + 1.067$, $r^2 = 0.994$; $t_{1,12}$= 7.97, p<0.001, Fig. 1). Based on the function's fit to the species-area curves, total species richness (K) was 35.9 ± 1.1 species in the primary forest and 19.5 ± 0.4 in the secondary forest($t_{1,12}$=1384.19, P<0.001).

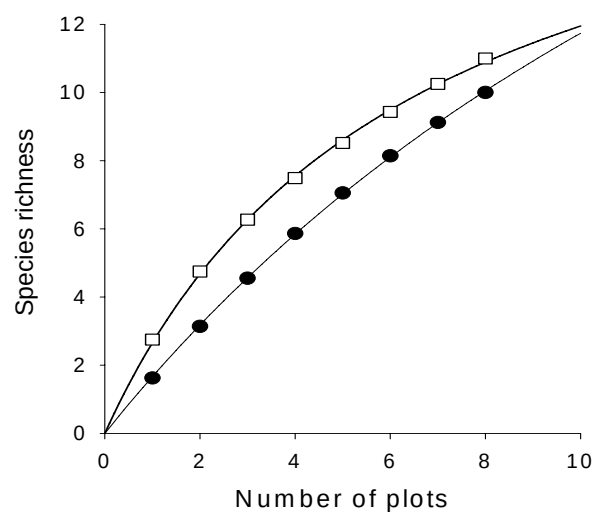

Figure 1. Species-area curves for bats in primary (●) and secondary (□) forests at Corcovado National Park, Costa Rica. Lines show Michaelis-Menten function fit to data; $y_{primary}$= (35.90 * x) / (20.58 + x), $y_{secondary}$=(19.53 * x) / (6.35 + x),

Discussion

We modeled higher total species richness in primary forest; this is consistent with greater vegetative species diversity driving greater bat species richness (H_1) on a forest-wide scale. However, we also found lower bat species richness at each site in primary forest; higher plant chemical defenses in these forests may result in less edible resources, leading to decreased insect prey abundance and thus reduced bat species richness (H_2) on a microhabitat scale. The small overlap in bat species composition between primary and secondary forests suggests that different bat species prefer, or are better able to utilize, different habitats (H_3).

Literature Cited

Gleason H.A. 1922. On the relation between species and area. Ecology 3: 158–162.

Krivak-Tetley, F.E., Brosnahan M.L., and Risk B.B. 2002. Temporal patterns in foraging activity of insectivorous bats on the Osa Peninsula. Dartmouth Studies in Tropical Ecology 2002. pp. 115-120.

Wainwright, M. 2002. *The natural history of Costa Rican mammals.* Miami: Zona Tropical, S.A.