COMPETITION IN TROPICAL BIRD FLOCKS: ARMY ANT FOLLOWERS VERSUS MIXED SPECIES FORAGING GROUPS

MATTHEW T. KEMP AND J. KHAI TRAN

Abstract: Multi-species flocks are a prominent feature of many Neotropical bird communities. Theoretical benefits and costs of flock membership for individual birds differ between two flock types: army ant followers and mixed species foraging flocks. We hypothesized that aggressive interactions and sensitivity to perceived predation risk would be greater in the ant following flocks. While our test of predation sensitivity yielded no change in response behavior in either flock type, we did record significantly more aggressive interactions among the ant followers than in the mixed flocks. The high number of aggressive interactions in the ant followers was largely a product of intraspecific interactions among gray-headed tanagers. Elucidating the mechanisms underlying these behaviors helps us to understand why birds choose to participate in multi-species flocks, which are a major theme in the structure of tropical bird communities.

Key words: aggressive interactions, Corcovado, Eciton burchelli*, intraspecific, interspecific, predation*

INTRODUCTION

Multi-species flocks are a prominent feature of many Neotropical bird communities. In lowland wet forest on Costa Rica's Osa Peninsula, two distinct types of flocks occur: aggregations of birds that follow army ant swarms and mixed species groups of insectivorous birds that forage together daily.

Theoretical benefits and costs of flock membership for individual birds differ between the two flock types. Ant followers profit from abundant arthropod prey flushed by the raiding ants, but they may be subject to competition with other birds attempting to exploit this same resource. In this view, the existence of the flock is an incidental byproduct of a localized resource, and benefits often associated with group foraging, such as increased vigilance against predators, might not apply. In fact, the active, noisy nature of these ant-following flocks could easily attract bird-eating predators, and ant-followers are indeed noted to be shy and wary of disturbance (Stiles and Skutch 1989).

In contrast, members of mixed species foraging flocks should enjoy benefits derived from the flock itself, including increased foraging efficiency and reduced predation risk. For foraging benefits of flock membership to be realized, resource competition among flock members should be minimized. Also, because some members of these flocks (e.g. shrike-tanagers, *Lanio* sp.) are known to act as sentinels (Munn 1986), birds enjoy greater perceived security and therefore should be relatively insensitive to predation risk. That is, they should resume normal foraging behavior more quickly than ant followers after perceived predation pressure.

To test these ideas, we observed the behavior of individual birds within both ant following flocks and mixed species foraging flocks. We hypothesized that there would be more aggressive interactions among ant following birds than among mixed species flock birds, and that ant followers would respond more strongly to a simulated predation risk than mixed species flock members.

METHODS

On 4 February 2004, from 0800 to 1100, we observed an army ant (*Eciton burchelli*) following flock approximately 3.5 km north of Sirena Biological Station along the Los Patos trail

in Corcovado National Park, Costa Rica. To maximize observation time, we selected focal individuals that were readily visible and followed them until they were out of sight. We recorded amount of time observed as well as the number of intraspecific and interspecific aggressive interactions. We defined aggressive interactions to include displacement of or by the focal bird as well as any other obvious confrontations between the focal bird and another bird.

On 4 February from 1430 to 1730 and 5 February from 0800 to 1100, we located and followed two mixed species flocks (one flock was observed on both days). We observed focal birds, recording aggressive interactions as with the ant-following flock. We compared the difference in total aggressive interactions between ant-following and mixed species flocks using a chi-square analysis. Expected values were calculated based on the observation time in each flock type (i.e., the total number of aggressive interactions multiplied by the proportion of total observation time for each flock type).

To test sensitivity to perceived predation risk, we played an audio recording of a collared forest-falcon (*Micrastur semitorquatus),* a bird eating raptor, and observed any changes in bird behavior, as well as the amount of time before the birds resumed normal foraging behavior. We only observed birds that were less than 10 m from the audio source. The recording was obtained from a commercial compilation of Costa Rican bird songs (Ross 1998).

Results

We obtained 80.5 min of focal individual data for one ant following flock and a total of 46.25 min for two mixed species flocks (Table 1). We recorded significantly more aggressive interactions among the ant followers than in the mixed flocks (observed vs. expected = 22 vs. 17 and 5 vs. 10, respectively; $\chi^2 = 3.76$, df = 1, P = 0.05; Table 2). We observed no change in behavior in response to the forest falcon call in either flock type; birds appeared not to notice the vocalizations at all.

Discussion

Our test of predator response was inconclusive because the birds were clearly not threatened by the recorded forest-falcon call. This lack of response may be due to poor quality or insufficient volume of the recording, or perhaps auditory cues do not trigger an alarm response in general. Because forest falcons and other raptors are probably silent when hunting, birds may only respond to visually perceived predation risks. However, our findings did support the hypothesis that there are more aggressive interactions among individuals in ant-following flocks than among those in mixed species foraging flocks.

Aggressive interactions in the ant-following flocks were dominated by gray-headed tanagers, which were the most numerous and active species present. Though chestnut-backed and bicolored antbird interactions both involved tanagers, all other gray-headed tanager interactions were intraspecific. Other ant-following species may show similarly elevated levels of competition, but more observation time is needed to test this.

Ideally, investigation of flock type on intensity of competition should be done at the species level; however, since no species occurs regularly in both ant-following and mixed species flocks, comparisons within phylogenetic groups or foraging guilds would be the most informative approach. For example, testing effects of flock type on woodcreepers would be more valuable than combining all species within each flock type, as was necessary with our study.

Obtaining a larger number of observa-

Table 1. Estimated numbers of each species in observed flocks. Mixed flock 2 was observed on two separate occasions.

Species	Scientific name	Number of individuals in flock.
Ant-following flock		
Barred Woodcreeper	*Dendrocolaptes certhia*	2
Tawny-winged Woodcreeper	*Dendrocincla anabatina*	2
Chestnut-backed Antbird	*Myrmeciza exsul*	2
Bicolored Antbird	*Gymnopithys leucaspis*	4
Russet Antshrike	*Thamnistes anabatinus*	1
Gray-headed Tanager	*Eucometis penicillata*	6
Total		17
Mixed flock 1		
Buff-throated Woodcreeper	*Xiphorhynchus guttatus*	2
Streaked-headed Woodcreeper	*Lepidocolaptes souleyetii*	1
White-shouldered Tanager	*Tachyphonus luctuosus*	3
Tawny-crowned Greenlet	*Hylophilus ochraceiceps*	1
Total		6
Mixed flock 2		
Buff-throated Woodcreeper	*Xiphorhynchus guttatus*	2
Streaked-headed Woodcreeper	*Lepidocolaptes souleyetii*	1
Black-striped Woodcreeper	*Xiphorhynchus lachrymosus*	1
Plain Xenops	*Xenops minutus*	2
Buff-throated Foliage-gleaner	*Automolus ochrolaemus*	2
Black-hooded Antshrike	*Thamnophilus bridgesi*	2
Dotted-winged Antwren	*Microrhopias quixensis*	2
White-throated Shrike-Tanager	*Lanio leucothorax*	1
Scarlet-rumped Cacique	*Cacicus uropygialis*	1
Total		13

tions for all flocking species would also allow an explicit test of the relative importance of intraspecific versus interspecific competition. Intraspecific competition should be minimized in mixed species flocks, where each species is represented by only one or two individuals. In ant-following flocks, however, many individuals of the same species can occur together, increasing

Table 2. Minutes of observation time and number of aggressive interactions for each species in each flock type. Woodcreepers in mixed flocks were grouped because not all individuals were positively identified during each observation period.

Species	Time observed (min.)	Intraspecific interactions	Interspecific interactions	Total interactions
Ant followers				
Barred Woodcreeper	25.5	2	0	2
Tawny-winged Woodcreeper	4	1	0	1
Chestnut-backed Antbird	9	0	1	1
Bicolored Antbird	7.5	0	1	1
Russet Antshrike	2.5	0	0	0
Grey-headed Tanager	32	17	0	17
Totals	80.5	20	2	22
Mixed flock				
Woodcreeper sp.	11.5	2	0	2
Plain Xenops	1	0	0	0
Buff-throated Foliage-gleaner	11	0	2	2
Black-hooded Antshrike	4	0	1	1
White-throated Shrike-Tanager	14.5	0	0	0
White-shouldered Tanager	3	0	0	0
Scarlet-rumped Cacique	1.25	0	0	0
Totals	46.25	2	3	5

the probability of intraspecific interactions (as evidenced by the gray-headed tanager in this study). The prevalence of interspecific interactions, then, would indicate the degree of niche partitioning among flocking species. Resource partitioning in mixed species flocks is expected, given the variety of foraging behaviors exhibited by its members (i.e., aerial insectivores, dead leaf searchers, leaf gleaners, bark probers; Powell 1979 and Munn and Terborgh 1979). Among ant-following species, spatial partitioning is well-documented (Swartz 1997 and Willis and Oniki 1978), though whether this is congruent with resource partitioning or simply the result of a dominance hierarchy is unclear.

Clearly, the nature of tropical bird flocks influences the behavioral ecology of individuals and species within those flocks. Elucidating the mechanisms underlying these behaviors helps us to understand why birds choose to participate in multi-species flocks, which are a major theme in the structure of tropical bird communities.

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WHERE IN THE WORLD IS *GECARCINUS QUADRATUS*? DISTRIBUTION OF AN ELUSIVE BUT INFLUENTIAL FOREST SPECIES

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Abstract: The land crab, *Gecarcinus quadratus,* influences sapling diversity in the 'crab zone', an area within 600 m of the beach bordering coastal neotropical rainforests. Despite their abundance and importance, little is known about the spatial population structure of this species because crabs are rarely seen. We suspected that intraspecific interactions would cause non-random crab distributions throughout the crab zone. We hypothesized that a sand-to-soil gradient would influence crab densities and hole structural characteristics. We tested these hypotheses by measuring crab spacing and density, as well as hole diameter and depth at varying distances from the beach. We found no evidence of intraspecific interactions affecting the spacing of crabs, but conclude that abiotic factors may affect the spacing of their holes. We also found that the density of holes decreases, the diameter of holes increases, and the depth of holes does not change with distance from the beach. We suggest that only larger crabs are able to dig through the non-sandy inland soil. The fact that *G. quadratus* is so abundant, yet so rarely seen, suggests that it experiences intense predation pressure.

Key words: crab zone, dispersion, hole structure, intraspecific interactions, land crab, substrate gradient

INTRODUCTION

The land crab, *Gecarcinus quadratus*, lives in holes dug in the coastal neotropical rainforest floor, in a zone extending 600 m inland from the beach. These crabs have been shown to affect plant community composition in this "crab zone" by selectively feeding on seedlings, thereby reducing the diversity and abundance of saplings (Sherman 2002). Despite the importance of this species in forest dynamics, little is known about the ecology of this crab. This is due, in part, to the shy nature of *G. quadratus*; it is rarely seen in the dry season despite the prevalence of its holes. In pilot studies we could not locate *G. quadratus*, and it seemed that some holes were occupied while others were empty. Because crab spatial distributions probably influence the surrounding plant community, we explored the spatial population structure of *Gecarcinus quadratus*.

We hypothesized that crab spatial population structure would be influenced by intraspecific interactions such as competition and territoriality. If crabs are territorial, the spatial distribution of crabs and their holes would be uniform. We also hypothesized that a gradient in soils from sand near the beach to fine mineral soil farther inland would affect crab distribution. It could be that only larger crabs can dig holes in the harder inland soil, in which case we would see decreased density of crabs and their holes, increased hole diameter, and decreased hole depth with increasing distance from the beach.

METHODS

We tested these predictions in a section of the crab zone at Corcovado National Park, Costa Rica, on 4 - 6 January 2004. We established eight 4 x 4 m plots haphazardly along the Sirena trail. The distance of each plot from the high water line (hereafter referred to as distance) ranged from 21 to 351 m. Each plot was divided into sixteen 1 x 1 m subplots, within which we counted the total number of crab holes. We determined whether holes were occupied by sprinkling beach sand around each hole in the afternoon and inspecting for tracks

Figure 1. Two holes dug by *Gecarcinus quadratus*, cleared of litter, sprinkled with beach sand and left overnight. We observed lizards, ants, spiders and hermit crabs crossing the sand, but these animals left no tracks. Therefore, holes with tracks coming from the entrance (left) were considered occupied by land crabs. Holes with no tracks (right) were considered unoccupied.

in the sand the following morning (Fig. 1). We haphazardly selected up to twelve crab holes in each 16 m^2 plot and measured depths and diameters. Depths were determined by inserting a vine as far as possible into each hole.

To test for nonrandom dispersion of crabs and crab holes, we calculated frequencies using a Poisson distribution calculated from the observed mean density of crabs (and crab holes) to compare to observed frequencies with a chi-square test. We also calculated crab and crab hole dispersion indices for each plot as variance/mean. A dispersion index of 1 indicated a random dispersion, while a value above or below 1 indicated a clumped or uniform dispersion, respectively.

We used correlation matrices to test the relationship between distance from the beach and crab hole characteristics. Crab abundance and number of crab holes were log transformed to correct for non-normality.

RESULTS

Since we were unable to find *G. quadratus* during daylight, we searched for crabs several times at night by walking through the crab zone and by waiting quietly by crab holes for 30 min. However, no crabs were ever sighted between 2100 - 2300 or 0230 - 0400.

Number of holes per m^2 and crabs per m^2 varied widely among the 128 subsample plots (holes: zero to nine, crabs: zero to eight), and 78% of all holes were occupied. Hole diameter ranged from 2.18 - 14 cm, and depth of holes ranged from 7.5 - 107 cm. Correlation matrices (Tables 1 and 2, Fig. 2) show that hole diameter increased and crab and hole density decreased with distance from the beach, but there was no trend in hole depth. Occupied holes had signifi-

Table 1. Correlation matrix for crab hole measurements (n = 80).

	Depth (cm)	Diameter (cm)	Distance (m)
Depth (cm)	1.00		
Diameter (cm)	0.49	1.00	
Distance (m)	0.50	0.68*	1.00

* $P < 0.08$

cantly larger hole diameters than unoccupied holes ($F_{1,79}$ = 4.47, P = 0.04). A contingency analysis showed that the distribution of holes was significantly different from random (χ^2= 20.07, df = 5, P = 0.001). Relative to the Poisson distribution, there was a surplus of plots with zero holes and a surplus of plots with five or more holes, but a lack of plots with three or four holes (Table 3). In contrast, the dispersion of crabs did not differ from random (χ^2= 4.67, df = 5, P = 0.46). Dispersion indices did not vary with distance from the beach for holes or crabs (r = 0.33 and 0.01, respectively, df = 7, P > 0.40; Fig. 3).

Table 2. Correlation matrix for plot measurements (n = 8).

	Log(# holes + 1)	Log(# crabs + 1)	Distance (m)
Log(# holes + 1)	1.00		
Log(# crabs + 1)	0.99**	1.00	
Distance (m)	-0.72**	-0.66*	1.00

* P < 0.08
** P < 0.05

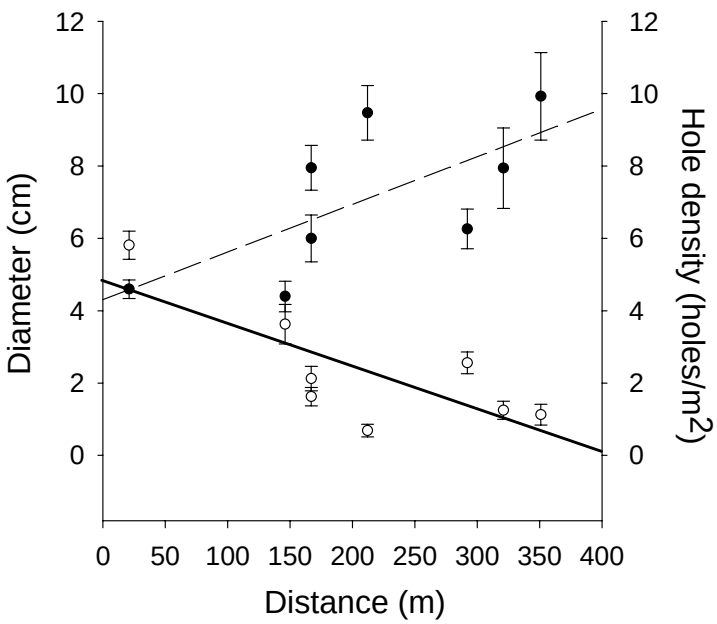

Figure 2. Hole diameter (filled circles) increased and hole density (open circles) decreased with distance from the high water mark. Means (± SE) are shown. The dashed line represents a regression of diameter with distance (r^2 = 0.59, df = 7, P = 0.03) and the solid line represents a regression of hole density with distance (r^2 = 0.47, df = 7, P = 0.06).

Discussion

The dispersion of *G. quadratus* did not show evidence of structuring from intraspecific interactions. Because the dispersion of holeswas non-random, but not clearly uniform or patchy, we posit that abiotic factors are influen-tial. For example, there may be coarse scale heterogeneity of substrate type in the crab zone. Patches of rocks or roots may cause clumping of crabs in soil where it is easier to dig. In areas where suitable substrate for digging is not limiting, intraspecific competition may still cause a more uniform spacing of crab holes. Future studies should look at larger scale plots to capture the effect of heterogeneous substrate on crab hole distribution and determine if and how intraspecific interactions are influential. Also, future studies should analyze substrate type in more detail to determine how it changes within

Table 3. Frequency of number of holes per m^2 as expected by the Poisson distribution and as observed, as well as the χ^2 value between them. The distribution of holes differs significantly from random.

# holes per m^2	# expected from Poisson	# observed	χ^2
0	12	21	6.37
1	29	29	0.00
2	34	33	0.01
3	26	18	2.68
4	16	7	4.68
> 4	11	20	6.31

the crab zone and whether it influences crab distribution.

A gradient of conditions from beach to forest may affect *G. quadratus* hole densities and hole diameters. Perhaps only large crabs have the strength to dig in a non-sandy dirt substrate, explaining the reduced abundance of holes and larger hole diameter when moving further and higher inland.

However, our prediction that hole depth would decrease with distance from the beach in harder soil was not supported. We suggest that hole depth may not depend on the sandiness of soil or the size of the crab digging the hole, but on other factors such as hole age. If crabs gradually dig deeper over time, the depth of holes would depend on how recently they were colonized, and not on the distance of holes from the beach. Future studies could test this by examining whether hole depths change through time.

We also found that occupied holes were larger than unoccupied holes, suggesting that large holes are more likely to be occupied than small ones. Assuming that hole diameter corresponds to crab size, perhaps the larger crabs in these holes are less susceptible to predation due to their size. In fact, we tended to see larger and more distinctive tracks coming from large holes. It would be informative to devise methods to capture crabs, and to examine the relationships between crab size, hole diameter, and hole occupancy. Perhaps crabs move further inland as they grow, to feed on preferred sapling types towards the edge of the crab zone, or perhaps they expand their holes as their own size increases.

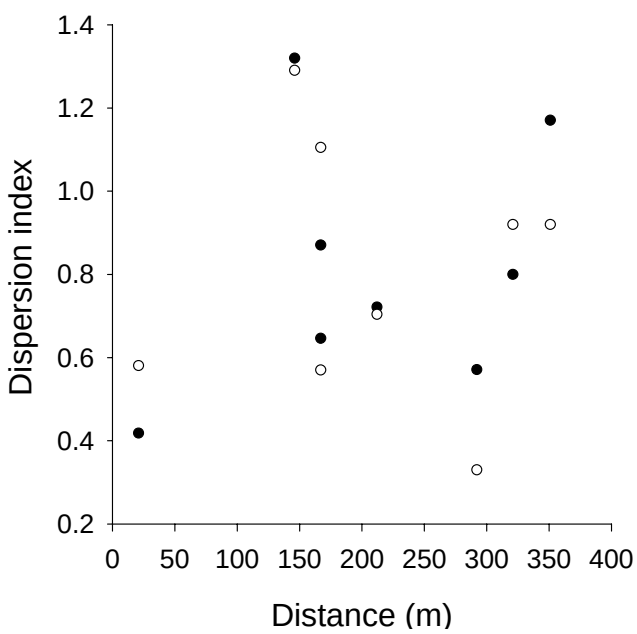

Figure 3. Dispersion indices for holes (filled circles) and crabs (open circles) displayed no relationship distance from the high water mark.

We were unable to find crabs either by watching holes throughout the day and night or by digging or flushing out holes. Given that *G. quadratus* is so difficult to locate, we speculate that there is strong predation pressure on this species, perhaps by animals such as large birds or raccoons. This pressure may limit the amount of time crabs spend above ground, and thus limit their impact on the plant community.

G. quadratus plays an important role in the dynamics of coastal sections of neotropical rainforests, yet the characteristics of their spatial population structure are poorly understood. Predation pressure and variation in substrate may explain patterns in crab abundance, hole structure, and diel activity patterns.

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MACROBRACHIUM AS A POSSIBLE DETERMINANT OF *ASTYANAX FASCIATUS* DISTRIBUTION IN A NEOTROPICAL LOWLAND STREAM

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Abstract: The giant shrimp *Macrobrachium*, sp. is a possible nocturnal predator on the tetra *Astyanax fasciatus* and therefore may affect their spatial distribution within a stream. We observed the natural distributions of tetras during the day and night in a stream, and performed controlled manipulations to test for effects of shrimp on fish behavior. The horizontal and vertical distribution of tetras varied between day and night, but not as predicted under the hypothesis of shrimp avoidance. In an aquarium, tetras moved away from shrimp, clumping together at night and spreading apart during the day. Shrimp predation may be a factor influencing the spatial distribution of tetras on the Osa Peninsula, but other predators and food availability are probably also important.

Key words: Corcovado, giant shrimp, predation pressure, predator-prey interactions, tetra

INTRODUCTION

The tetra, *Astyanax fasciatus* (Characidae), and the giant shrimp, *Macrobrachium* sp. (Palaemonidae), co-exist in streams near Sirena Biological Station, Corcovado National Park, Costa Rica. The giant shrimp can prey on tetras in experimental enclosures (Brown et al. 2000); if this predation also occurs in nature, it could affect the activity patterns and distribution of tetras. If so, night would pose increased predation pressure on tetras because shrimp are nocturnal. Thus, tetras might be expected to congregate higher in the water column and away from the edges of the stream (to separate themselves from the benthic shrimp). We tested these predictions with surveys of tetra location during the day and night. Also, tetras might be expected to perceive the presence of shrimp and adjust their position accordingly. We tested this by recording fish locations within an aquarium (with and without shrimp).

METHODS

On 5 February 2004 we observed the abundance and distribution of tetra fish in the low-order stream, Quebrada Cameronal, at Corcovado National Park, Costa Rica. We keyed fish to genus and consulted Winemiller (1983) to determine tetra species; *A. fasciatus* is the only species in this genus listed at Corcovado. At each of five pools we set up a 50 cm wide cross-section of the stream; this cross-section was then divided into grids of 40 cm long rectangles. Before each observation, we stood still in front of the cross-section for 2 min to acclimate fish to our presence. We then counted the number of tetras and giant shrimp in each grid area at the bottom, middle, and surface of the stream (each equal to one-third of the vertical profile). We also noted any feeding maneuvers by the tetras or the presence of other fish species within the sampling grid. This was repeated at each pool twice during the morning and twice again that night. For each sample grid, we also measured the depth, temperature, and percent area of the benthos covered by organic matter. At each pool, we measured the surface flow (as the velocity of a floating object). For our analyses, we classified each rectangle as edge or mid-stream and calculated the density of fish within each rectangle using estimates of volume based on depth at the center of each rectangle. Tetra abundances and tetra densities per m^3 were log transformed (x + 1) to improve normality. We

analyzed tetra abundance with an ANOVA model that included pool, depth, time of day, and depth x time of day. We analyzed tetra density with an equivalent model, except with horizontal location (edge or middle) substituted for depth.

On 6 February 2004 we performed an experiment to measure the effect of shrimp presence on tetra distribution during the day and night. We set up a 61 x 41 x 30 cm tank of stream water and added ten individually distinctive tetras. After 15 min, we observed the three-dimensional position of each fish within the tank from a corner defined as the origin (depth of each fish was estimated as 0 - 10, 11 - 20, or 21 - 30 cm). We then added a shrimp (~ 15 cm long) enclosed in a clear, breathable bag in one corner (the origin), waited 15 min, and observed the fish locations again. We repeated this procedure once during the day and once at night, both with and without shrimp. Nine of the ten tetras were used for all four trials (one individual died between day and night trials). The water in the tank was changed after shrimp trials.

We generated a null model of tetra distribution within the tank using randomly generated coordinates. The test statistic was average distance to the origin (in three-dimensional space) of ten fish. We calculated a frequency distribution of 999 averages (based upon the null hypothesis of random dispersion) against which to compare the actual average distance observed in each of our four trials. Actual fish locations were judged to be nonrandom if their average distance was greater that 95% of the randomly generated frequency distribution.

We also calculated inter-fish distances for each pair of ten tetras in each treatment and compared them with a two-way ANOVA (day versus night and shrimp versus no shrimp). This analysis assumes independence of observations, although our experimental design did not strictly satisfy this condition (only 10 individuals were observed but 45 inter-fish distances were calculated). Consequently, the associated P-values were treated as approximate.

RESULTS

In our field observations, tetra abundance (fish per 0.2 m^2) was greater during the day than at night ($F_{1,59} = 13.49$, $P = 0.0006$) and greatest at mid-depths in the water column ($F_{2,59} = 21.64$, $P < 0.0001$; Fig. 1). There was no significant interaction between time of day and depth ($F_{2,59} = 2.37$, $P = 0.10$). Tetras were also more abundant in edge areas than mid-stream ($F_{1,119} = 26.11$, $P < 0.0001$); there was no interaction between horizontal location and time of day ($F_{1,119} = 2.77$, $P = 0.10$; Fig. 2). There were also main effects of pool on tetra abundance ($F_{4,59} = 24.93$, $P < 0.0001$) and tetra density ($F_{4,119} = 4.93$, $P = 0.001$). Surface flow was negligible in all study pools and temperature was almost invariate across time, locations, and depth (range = 26.4 - 27.6 °C), so we eliminated abiotic factors from our analyses.

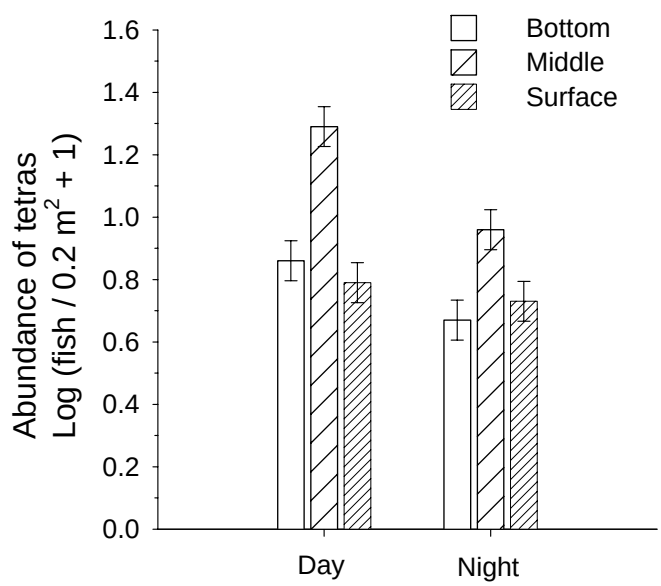

Figure 1. Abundance of *A. fasciatus* (means ± SE) during the day and night in the bottom, middle, and top of the water column of Quebrada Cameronal in Corcovado National Park, Costa Rica (n = 10 observations for each bar).

Fish density at day and night was also unrelated to percent organic matter in each rectangle (r = 0.17, P = 0.23 and r = 0.10, P = 0.55, respectively).

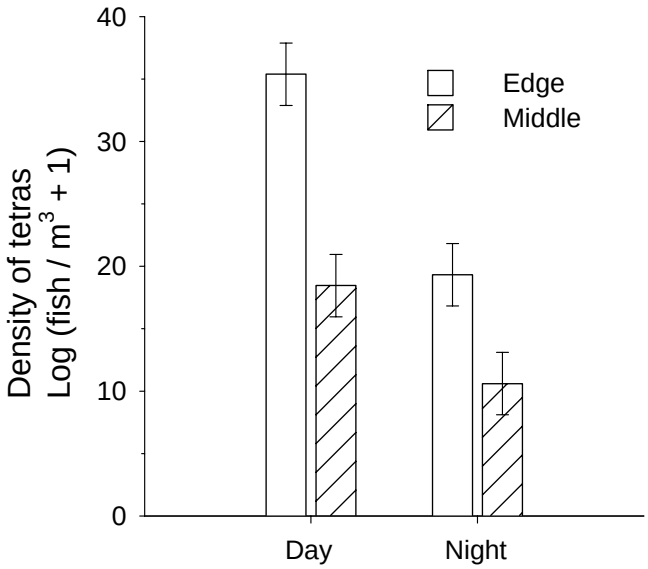

Figure 2. Density of *A. fasciatus* (means ± SE) during the day and night at the edge and mid-stream locations of Quebrada Cameronal in Corcovado National Park, Costa Rica (n = 30 observations for each bar).

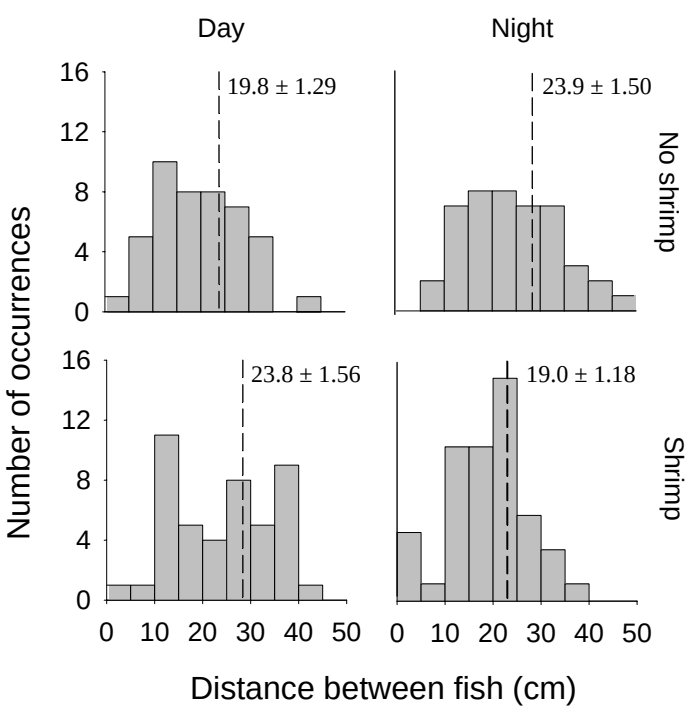

Figure 3. Frequency distribution of distances between fish in day trial (left) and night trials (right) with shrimp (bottom) and without shrimp (top). Means ± SE reported for each distribution. Vertical lines represent mean values.

We observed 15 events of tetra feeding maneuvers at the bottom of the stream and seven at the surface. Within our plots, we saw no shrimp during the day but 12 shrimp at night.

In our experimental manipulations, tetra in control treatments distributed themselves randomly with respect to the origin (mean distances for day and night = 47.6 and 46.2 cm versus expected distance under null model of 44.2 cm; P > 0.23 for both night and day). In the presence of shrimp, however, tetra tended to avoid predation by distributing themselves farther from the origin: 50.2 cm during the day (P = 0.11) and 55.3 cm at night (P = 0.01). The addition of a shrimp caused fish to shift farther apart from each other during the day and closer together at night. Main effects of shrimp and time of day were non-significant ($F_{1,179}$ = 0.076, P = 0.78); effect of shrimp x time of day was significant ($F_{1,179}$ = 10.31, P = 0.002; Fig. 3).

Discussion

There was a change in tetra abundance between day and night, but not in the directions that were predicted. Higher fish density in edge rather than midstream habitat suggests that there are greater benefits or fewer costs for tetras near the banks. Food availability may be higher or predation risk may be lower away from deep midstream areas. Tetras may be most abundant at intermediate depths because they are both surface and bottom feeders, and this position provides access to both food sources. However, we found no relationship between percent cover of organic matter and tetra position within a cross-section, so benthic food resources alone cannot fully explain distribution of tetras. Negligible variation in surface flow and temperature suggest that abiotic factors are not responsible for the observed distributions.

Our manipulative experiment demon-

strated that tetras respond to shrimp as though they are potential predators. Fish moved away from the shrimp during both day and night. At night, fish also became more clumped (smaller inter-fish distance) in the presence of shrimp, perhaps because being in a group reduces the chance that any one individual will be killed during a predation event. The fact that fish spread out in the presence of shrimp during the day may not be biologically relevant because shrimp seem to be inactive during the day, but it does demonstrate that reduced inter-fish distance was not a necessary consequence of avoiding the shrimp in the corner. It is also possible that during the day, grouping increases the risk from day-active predators which may be attracted to aggregations of tetras.

Our experimental manipulations show that in a controlled setting, shrimp do affect the spatial distribution of the fish. Our stream observations, however, indicate that shrimp predation is only one factor determining where fish are located in streams. The distribution of fish is likely a balance between foraging benefits and predator avoidance. Additionally, predation pressure in a stream may come from all directions (e.g. kingfishers and herons from above, caimans and piscivorous fish from below), further influencing the spatial distribution of tetras. Future studies should examine foraging behavior and food resource location as well as the effects of other predators as factors affecting *A. fasciatus* distribution.

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WHAT GOES IN MUST COME OUT: ASSIMILATION EFFICIENCIES OF *ATTA COLOMBICA* COLONIES IN PRIMARY AND SECONDARY FORESTS

HEATHER E. LAPIN, SARA M. HELLMUTH, JILL L. HARRIS AND BRENDA M. WHITED

Abstract: Leaf cutter ants are responsible for an estimated 42% of herbivory in Corcovado National Park, Costa Rica. Given this and their unique habit of cultivating fungi to digest plant matter, it would be valuable to understand the efficiency with which they process energy. Secondary forest leaves are preferred by ants for fungus cultivation compared to primary forest leaves. We attempted to estimate assimilation efficiencies of two *Atta colombica* colonies in both primary and secondary forests. Two colonies carried organic waste out of the colonies into waste piles, while two colonies transported mineral dirt from underground and had no apparent organic waste piles. Only one colony yielded an estimate of assimilation efficiency that was potentially valid, and that estimate was unrealistically high (89%). Apparently these colonies are not in steady state, so calculations of assimilation efficiencies taken over two days are unlikely to be accurate.

Key words: egestion, gut transit time, ingestion, leaf cutter ants

INTRODUCTION

As energy flows through trophic levels in an ecosystem, energy is lost during transfer (e.g., from producers to the consumers). The percent energy passed to the next level is related to the assimilation efficiency of the organisms that are consuming a lower trophic level. Assimilation efficiency is the percentage of food energy taken into the guts of the consumers which becomes available for incorporation into growth (Begon et al. 1986).

Mannan et al (1996) estimated that leaf cutter ants are responsible for 42% of the herbivory in Corcovado National Park. An estimation of the assimilation efficiency of these organisms would provide insight into how energy flows in this system. Secondary producers generally have low assimilation efficiencies (20 - 50%; Begon et al. 1986). Leaf cutter ants, however, have a unique method of digesting their diet. They harvest leaves and flowers for subterranean cultivation of fungus and then consume the hyphae and dispose of the waste material. *Atta colombica* dispose of this waste in piles outside their colonies (Stevens 1983). Because of this unique behavior, it may be possible to measure ingestion and egestion of individual colonies and therefore estimate their assimilation efficiency.

A. colombica occur in both primary and secondary forests. Nichol-Orians (1990, as cited in Bird et al. 1996) showed that because secondary forest leaves have fewer secondary metabolites, they are more suitable for fungus cultivation than primary forest leaves. Leaves from secondary forests may produce higher quality fungal food, which the ants will be able to assimilate at higher efficiencies. We therefore expected to see higher assimilation efficiencies in *A. colombica* colonies within the secondary forest.

METHODS

We studied four leaf cutter ant colonies, two in secondary forest and two in primary forest, at Corcovado National Park, Costa Rica. We located all exit and entrance holes around the central colony nest by searching for any ant activity within a 10 m radius from the furthest entrance or exit to ensure that no entrances or exits were missed. We collected ingestion and egestion data on 4 - 5 February 2004. To measure

ingestion and egestion rate we counted the number of ants carrying plant or waste material in and out of the nest during 3 min observation bouts at each entrance and exit point. We measured all four colonies during five different time blocks (0800 - 0900, 1000 - 1100, 1200 - 1300, 1500 - 1700 and 2100 - 2300) over the two different days. We combined the two days of data to model diel patterns in ant activity.

To convert the counts per minute to ingested and egested biomass per minute, we measured the total dry mass of 15 - 20 leaf fragments and 50 - 75 clumps of waste particle egesta carried by the ants, then divided by the number of units to estimate approximate biomass for average particles of leaf or waste.

To determine total daily ingestion of each colony, we used a Fourier transformation (Veysey et al. 2000) to fit multiple regression models corresponding to sinusoidal functions with a period of one day (Appendix 1). We then calculated the area under the function using a Taylor approximation to obtain the daily ingestion rate (grams dry mass entering the nest per day). Because egestion rates did not exhibit diel patterns, we simply calculated the daily egestion rate of grams dry mass exiting the nest for each colony based upon the average rate per minute.

RESULTS

We observed two different types of matter being carried out from the colonies. Ants in the primary forest (Colony P_1 and Colony P_2) carried material out of the colony from multiple holes in a large mound and deposited the material near the edge of the hole. Ants in the secondary forest (Colony S_1 and Colony S_2) carried material out of the colony from one hole and followed a trail away from the hole where they deposited the material onto a large mound. Microscopic examination revealed that the material from the secondary forest mounds was clearly organic (including leaf and stick remnants and mites), while the material from the primary forest mounds appeared to be entirely mineral soil, which was presumably the result of excavation activities rather than grooming fungus colonies.

The mass of leaf material from secondary and primary forest colonies did not differ greatly, while the mass of waste material did. The organic material from colonies S_1 and S_2 weighed less than the mineral soil from colonies P_1 and P_2 (Table 1). Colonies tended to have three to four active trails entering the nests, while there were six to nine active exits for the primary forest colonies and only one for each secondary forest colony (Tables 2 - 5).

The ingestion rates over one day followed a sinusoidal curve for Colony P_1 (r^2 = 0.89, $F_{2,4}$ = 8.45, P = 0.12), S_1 (r^2 = 0.95, $F_{2,4}$ = 18.57, P = 0.05) and S_2 (r^2= 0.96, $F_{2,4}$ = 29.43, P = 0.03), but not for Colony P_2 (r^2= 0.04, $F_{2,4}$ = 0.04, P = 0.96). Colonies differed in the timing of peak ant activity: Colony P_1 at 0130, P_2 had no peak, Colony S_1 at 1500 and Colony S_2 at 2130 (Fig 1). Average rates of material exiting the colony (± SE) were 1.26 ± 0.29, 10.51 ± 1.11, 1.39 ± 0.21 and 0.32 ± 0.06 g / min for Colonies P_1, P_2, S_1, and S_2 respectively (Fig 1). The colonies in primary forest did not have trails of ants carrying organic waste material, and the colonies in secondary forest showed no excavation.

Table 1. Approximate dry mass of individual leaf fragments and egesta for each colony, as used to calculate total biomass flux.

Colony	Individual leaf mass (g)	Individual exiting mass (g)
P_1	0.022	0.017
P_2	0.015	0.028
S_1	0.023	0.013
S_2	0.014	0.008

Table 2. Colony P_1 ingestion rate and excavation rate data recorded on 4 - 5 February 2004. Rates came from the sum of the rates from each trail. There was no evidence of organic waste exiting the nest.

Time of day	# active trails	Total ingestion / min	# active waste piles	Total excavation / min
0800	3	173.0	9	116.7
1045	3	30.0	9	123.0
1300	4	194.3	6	72.7
1600	4	250.7	6	95.0
2130	4	228.7	9	77.0

Table 3. Colony P_2 ingestion rate and excavation rate data recorded on 4 - 5 February 2004. Rates came from the sum of the rates from each trail. There was no evidence of organic waste exiting the nest.

Time of day	# active trails	Total ingestion / min	# active waste piles	Total excavation / min
0900	3	17.7	9	372.7
1120	3	51.7	9	306.7
1240	2	66.7	9	372.3
1645	3	36.7	8	405.3
2130	3	173.0	9	400.7

Table 4. Colony S_1 ingestion rate and egestion rate data recorded on 4 - 5 February 2004. Rates came from the sum of the rates from each trail. There was no evidence of excavation activity.

Time of day	# active trails	Total ingestion / min	# active waste piles	Total egestion / min
0900	4	17.7	1	99.3
1000	4	26.7	1	78.0
1230	4	50.7	1	84.0
1645	4	83.0	1	83.3
2200	3	48.7	1	65.0

Table 5. Colony S_2 ingestion rate and egestion rate data recorded on 4 - 5 February 2004. Rates came from the sum of the rates from each trail. There was no evidence of excavation activity.

Time of day	# active trails	Total ingestion / min	# active waste piles	Total egestion / min
0800	1	1.7	1	43.3
1100	2	69.7	1	38.3
1245	4	55.3	1	30.3
1600	3	86.7	1	38.3
2100	2	1.3	1	51.0

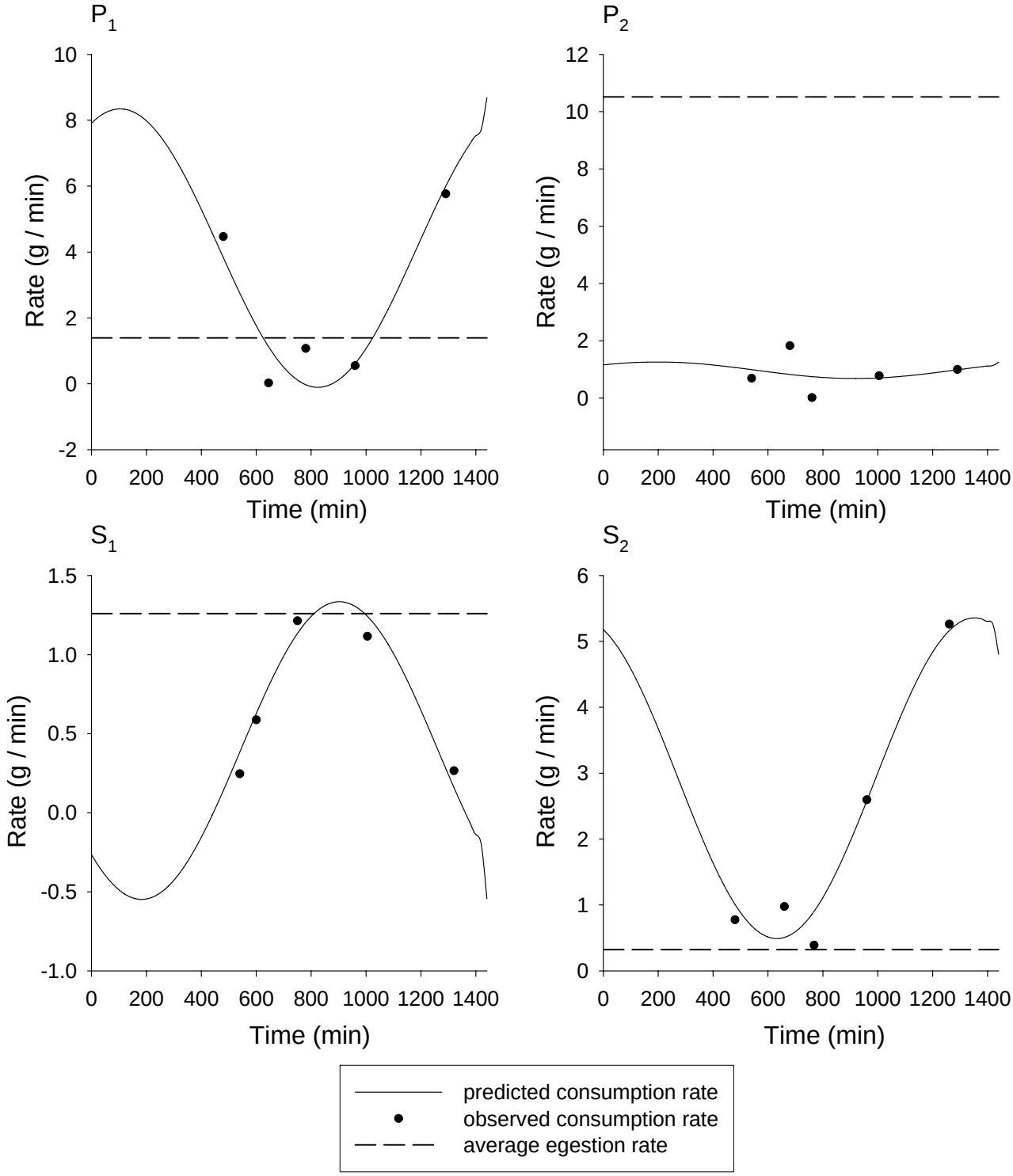

Fig. 1. Consumption rates (with best fit sinusoidal functions) and egestion rates over one day (1440 minutes) for colonies in primary forest (P_1 and P_2) and secondary forest (S_1 and S_2).

Assimilation rates could not be calculated for colonies P_1 and P_2 because we lacked estimates for egestion (Table 6). Calculated assimilation rate for S_1 was negative (and therefore impossible). For colony S_2, assimilation rate was estimated as 3.84 kg per day, and assimilation efficiency was estimated at 89%, which, if true, would be higher than for any other herbivore that has been studied.

Table 6. Calculated daily rates of ingestion, egestion, and excavation, along with corresponding estimates of assimilation rate (ingestion - egestion), and assimilation efficiency (assimilation / ingestion) for *A. colombica* in primary forest (Colony $P_1$and Colony P_2) and secondary forest (Colony $S_1$and Colony S_2).

Colony	Ingestion (kg/day)	Egestion (kg/day)	Excavation (kg/day)	Assimilation rate (kg/day)	Assimilation efficiency (%)
P_1	6.1	--	1.8	--	--
P_2	1.4	--	15.1	--	--
S_1	0.75	2.0	0	-1.25	--
S_2	4.3	0.46	0	3.84	89.2

DISCUSSION

Assimilation efficiencies were difficult to calculate over a two day time period. For one of the colonies, the calculated assimilation rate was negative, which is biologically impossible, and for another it was unrealistically high. One possible explanation is that it is not valid to assume that the system was in a steady state. *A. columbica* are selective foragers and may discover more preferred leaf types some days than others. A pulse in ingestion would presumably yield a subsequent pulse in egestion, so egestion could temporarily be greater than ingestion. Departures from steady state introduce particularly large errors in assimilation efficiency when the measurement period is brief compared to retention time in the system. We guess that the mean retention time for undigested material in an *A. colombica* colony is considerably more than two days.

Another difficulty in calculating assimilation for *A. colombica* colonies was that we could not locate egestion piles for two of the colonies. One possible explanation is that *A. colombica* stores some egested fecal matter underground. In fact, we were unable to find even inactive waste piles for the two colonies in primary forest.

Although we could not calculate assimilation efficiencies, we did observe some interesting behavioral patterns of the ants. Trails exposed to direct sunlight often have reduced ant activity during the hottest hours of the day, perhaps to reduce the risk of desiccation. Because sun exposure varied over the trails, this may explain the differences in timing of peak ant activity between colonies. Future studies should take into account trail exposure when making comparisons in ant activity.

Our study indicates that it is not easy to estimate assimilation efficiencies for *A. colombica* colonies. Nevertheless, an enormous volume of primary productivity passes into the underground chambers of leaf cutter ants throughout the Neotropics (4.8 tons / ha / year; Mannan et al. 1996). The efficiency with which biomass is processed has consequences for energy flux through the rest of the ecosystem. The habit of *A. colombica* of creating above-ground waste piles seems to create possibilities for further studies of how leaf cutter ants influence tropical ecosystems.

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Appendix 1. Fourier transformations to fit ingestion rates to a sinusoidal function.

Time was transformed twice with these equations:

SINE TIME = [1 + sin[π/2 + (time (min)) *2π/24]]/2

COSINE TIME = [1 + cos[π/2 + (time (min)) *2π/24]]/2

Multiple regressions were run with observed ingestion rate for each colony vs. sine time and cosine time to yield the three parameters b, m_1, m_2 , for the equation:

INGESTION RATE = b + m_1* [1 + SINE TIME] + m_2 * [1 + COSINE TIME]

This equation was used to interpolate ingestion rates for times in 20 minute intervals throughout the day, starting from 0000 to 2400.

Parameters for equation derived from a multiple regression of observed ingestion rate versus sine time and cosine time:

Colony	b	m_1	m_2
A	2.3581	7.2606	-3.7389
B	1.0244	0.3375	-0.4391
C	0.3166	-1.1985	1.351
D	-0.3261	4.6749	1.823

EFFECT OF SUBSTRATE TYPE ON FISH DISTRIBUTION IN THE RIO CLARO

R. SCOTT CUSHMAN, PAUL MARINO, AND STEPHEN WELLER

Abstract: Differences in fish communities among microhabitats in the Rio Claro of Parque Nacional Corcovado, Costa Rica, may be due to differences in abiotic factors. We examined fish communities and physical characteristics of three stream sections. One guild of Gobiidae was closely associated with cobble substrate. We manipulated substrates to test for changes in their local distribution. Where cobble substrate was added, these taxa generally increased, and where cobble substrate was replaced with sand, they decreased. High specialization of stream fish to abiotic factors appears to contribute to high local diversity.

Key words: Gobiidae, habitat selection, niche partitioning, substrate

INTRODUCTION

The distribution and abundance of tropical freshwater fish species can vary across different microhabitats (Weinmiller 1983). This could be a function of abiotic and/or biotic factors, as well as dispersal limitations. Preliminary observations suggested that fish species within one reach of the Rio Claro in Parque Nacional Corcovado, Costa Rica were separated among three distinct habitats - a shallow sandy area, a shallow cobbled area, and a deeper area with a mix of sand, rock, and cobble substrates.

We observed a high diversity of fish in a short (< 200 m) reach of the Rio Claro. In this small section of river, there were several distinct habitat types, and the species of fish appeared to group according to characteristics of the microhabitats. To determine the patterns of distribution and abundance of these species we created study plots to sample the community. In particular, taxa of the Gobiidae family, which have derived the ability to fix themselves to hard substrate and feed on algae via pectoral fin bones fused into a ventral suction cup (Bussing 1998), were found almost exclusively on cobble and rock substrate.

We hypothesized that differences in fish communities were linked to differences in abiotic factors, particularly substrate. We predicted that physical characteristics and fish communities tended to co-vary in unmanipulated systems and that members of the Gobiidae would shift their positions following substitution of sandy substrate with cobble and vice versa.

METHODS

We defined the boundaries of three adjacent sections of the Rio Claro with apparent physical differences. We measured the approximate area of each section, surface and mid-column velocity, depth, and temperature. To quantify substrate type, we drew two 0.25 m^2 plots, each 2 m to either side of the stream midline, at 10, 25, and 40 m in each section, and estimated percent cover of six substrate types: sand, pebble (1 - 5 cm diameter), cobble (5 - 10 cm), rock (10 - 20 cm), boulder (> 20 cm) and leaf cover. An index of velocity was calculated using the average velocity of four suspended objects over 15 m. For surface velocity, we used a floating bottle cap, and for mid-column velocity we used a neutrally buoyant plastic bottle.

We conducted pre-manipulation surveys of fish communities on the afternoons of 3 - 4 February 2004 by snorkeling four 25 m transects in each section. We moved slowly up transects and recorded the number of individuals of each taxon seen within 1 m of the transect.

We manipulated substrate in two 1 m^2

plots in each section during the morning of 5 February 2004. In sand and pebble dominated section 1, we created cobble and rock substrate plots. In cobble dominated section 2, we created sand substrate plots. In sandy regions of section 3, we created cobble and rock substrate plots. 1 m^2 control plots were located approximately 2 m from the manipulation plots in each section. We sampled taxa in manipulation plots and the control plots by snorkeling twice during the afternoon of 5 February 2004 and once on the morning of 6 February.

We used t-tests to look for differences in cobble and stone substrate cover among the three pools and for differences between manipulated plots and controls. We used a 2-way ANOVA to compare abundances of species among stream sections.

Results

The three stream sections had different mean depths, flow velocities, and substrates. Section 1 was intermediate in depth and lowest in velocity, section 2 was lowest in depth and greatest in velocity, and section 3 was greatest in depth and intermediate in velocity (Table 1). Section 2 had significantly higher mean combined cover of cobble and stone substrates (63%) than section 1 (20%) and section 3 (12%) ($F_{2,15}$ = 11.80, P = 0.0008; Table 2).

Species composition of fish communities differed significantly among the three stream sections ($F_{28,111}$ = 4.57, P < 0.0001 for species x section interaction). The fish in cobble dominated section 2 were predominantly cobble feeding Gobiidae and schools of open water fish moving through or feeding in the water column. Section 1 contained similar groups of open water fish and a taxon of Gobiidae seen only on sandy substrate. Section 3 was characterized by open water fish of the families Cichlidae, Gerreidae, Mugilidae, and Haemulidae, including some species that were never seen in sections 1 and 2 (Table 3). One taxon (Table 3: morphospecies 12) was almost exclusively found beneath a mat of detritus towards the lower end of section 3.

Cobble-associated species (CAS) generally increased on cobble addition manipulation plots and decreased on sand addition manipulation plots (Fig. 1). CAS appeared in the cobble addition manipulation plots in section 3 (t = 2.22, df = 10, P = 0.05), which otherwise had no CAS. CAS were completely absent from the sand addition manipulation plots in section 2 (t = 15.07, df = 10, P < 0.0001), strongly contrasting high CAS density in adjacent cobble control plots. The cobble addition plots in section 1, however, did not significantly attract more CAS than adjacent sand and pebble control plots (t = 0.21, df = 10, P = 0.84).

Discussion

Fish communities and physical stream characteristics co-varied among adjacent stream sections, as we predicted. This is consistent with the hypothesis that abiotic factors influence the fish taxa, but does not preclude alternatives. However, manipulations of substrate provided strong evidence that differences in fish communities were linked to physical differences in abiotic factors, particularly substrate type.

The linkage between CAS and cobble or rock substrate is likely related to a diet consisting largely of periphyton (Bussing 1998); periphyton algae grows only on solid substrate (e.g. cobble, not sand) and would likely be denser on rock or cobble which overturns less frequently than smaller substrate like pebble. In section 1, abundance of CAS did not differ between manipulations and control plots, which might be due to the close proximity of cobble habitat, or because periphyton was, in fact, available on pebble substrate due to low flow

Table 1. Abiotic characteristics (± SE) of stream sections in the Rio Claro. Measurements were taken in the dry season (February 2004); values are expected to change seasonally.

Stream section	Mean depth (m)	Length (m)	Width (m)	Temperature (C)	Mean surface velocity (m / s)	Mean bottom velocity (m / s)
1	0.40 ± 0.06	49	16	27.2 ± 0.05	0.14 ± 0.04	0.10 ± 0.03
2	0.23 ± 0.03	42	10	27.1 ± 0	0.58 ± 0.05	0.46 ± 0.03
3	0.96 ± 0.20	50	5-12	27.2 ± 0	0.30 ± 0.13	0.25 ± 0.07

Table 2. Mean percent cover of five different substrate types on plots in three sections of the Rio Claro.

Stream section	% sand	% pebble (< 2 cm)	% cobble (2 - 8 cm)	% stone (> 8 cm)	% detritus
1	56	7	13	7	17
2	16	24	30	29	0
3	70	15	7	4	2

Table 3. Fish morphotypes and their abundance in different sections of the Rio Claro.

	Family	Description	Individuals ± SE		
			Section 1	Section 2	Section 3
1	Cichlidae	red-orange caudal, eye-stripe	0	0	3.5 ± 1.8
2	Cichlidae	faint bars, reddish pectoral fins	0	0	2.3 ± 1.7
3	Cichlidae	no bars, red pectoral & anal fins	0	0	5.5 ± 3.2
4	Cichlidae	yellow anal fin	0	0.25 ± 0.25	0
5	Gobiidae	blue hue, extended dorsal fin	0	19.5 ± 4.2	0
6	Gobiidae	black stripe, grey bars	0	3.6 ± 10.7	0
7*	Gobiidae	red dorsal fin	0	8 ± 1.2	0
8	Gobiidae	red eye, sides speckled white	3 ± 1.5	0.5 ± 0.5	0
9	Gobiidae	very small, grey coloration	11.7 ± 11.7	5.8 ± 3.5	0
10*	Gerreidae	*Eucinostromus currani*	2.7 ± 0.3	0.25 ± 0.25	2.8 ± 0.5
11*	Mugilidae	silver with lighter stripe	0.7 ± 0.7	4 ± 3.3	2 ± 0.5
12*	Haemulidae	*Pomadasys bayanus*	0	1.5 ± 1.2	4.3 ± 4.3
13*	Syngnathidae	*Pseudophallus starski*	0	0.5 ± 0.3	0
14*	Characidae	*Astyanax fasciatus*	1 ± 1	0	0
15	Eleotridae	large red eye, black stripe	1.3 ± 0.7	0	0

*Reported by Beadell et al 1996. Others may also have been reported, but were not verifiable based on 1996 descriptions.

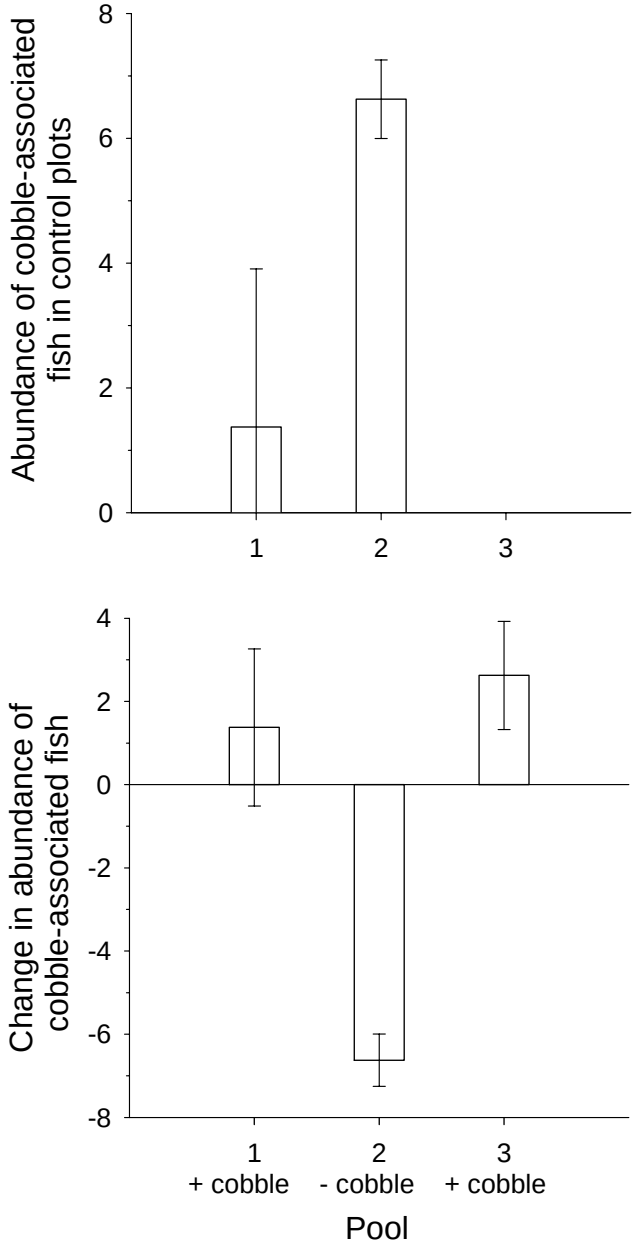

Figure 1. Effect of substrate manipulations on abundance (± SE) of three cobble-associated morphospecies (barred goby, blue goby, and tiny goby) in three sections of the Rio Claro. Manipulation plots in sections 1 and 3 were introduced cobble substrate from pool 2. Manipulation plots in section 2 were introduced sand substrate from section 1.

velocity and stable substrate conditions.

Variation in fish communities among physical environments at such a small scale (< 200 m of stream) is unique to tropical systems. Large variation in fish communities in different microhabitats of the Rio Claro could be evidence of a high degree of specialization by fish species on particular substrate types. Total fish biomass in this system was also remarkably high compared to northern temperate systems. The combination of high niche partitioning and high biomass suggests a very high resource base of primary production and detritus in the stream.

Within the Gobiidae alone we observed five morphotypes engaged in what seemed to be identical feeding behavior on the same substrate type. This apparent niche overlap has at least three possible explanations: (1) coexistence of multiple similar species is made possible by very fine partitioning of resources, (2) similar species are actually functionally identical and are competing unequally, but extinctions are compensated by a high speciation rate (Connell 1978), or (3) each species has a unique niche and distribution, but they are functionally identical within the study area. Future studies should further investigate niche partitioning among similar taxa, such as the cobble feeding Gobiidae.

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