A POSSIBLE ADAPTATION IN TIPULIDAE TO REDUCE PREDATION BY INHABITING *CHUSQUEA LONGIFOLIA* NODES

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Abstract: Cranefly larvae, (Diptera: Tipulidae) that typically reside in moist soils can be found in the accumulated litter within the nodes of a bamboo species (*Chusquea longifolia)* in the highland forest of Cerro de la Muerte. We hypothesized that cranefly oviposition in nodes is an adaption that reduces predation from arthropods and birds. We ran timed transects to observe potential avian predators of craneflies, and randomly sampled both *C. longifolia* nodes and 0.1 m^2 forest floor plots, counting cranefly larvae and potential arthropod predators. We found cranefly larvae exclusively in the nodes, and while we did not find a difference in the density of arthropod predators between nodes and forest floor, we infer that pressure from avian predators is reduced in the nodes due to a higher abundance of ground predators (Large-footed Finches) than node predators (Yellow-billed Caciques). The data suggest a selection differential between larvae on nodes and the forest floor, but we still lack knowledge of whether adults preferentially oviposit in nodes.

Key Words: adaptation, Chusquea longifolia, *cranefly larvae, predation,* Tipulidae

INTRODUCTION

Chusquea longifolia is a common understory bamboo of the oak-dominated forest of Cerro de la Muerte. It contains cup shaped nodes on its stem that collect detritus. Kemp et. al (2004) found that cranefly (Diptera: Tipulidae) larvae can inhabit these nodes. This is an unusual habitat for cranefly larvae because most are found in aquatic environments or in moist soil on the forest floor (Bland, 1978).

Cranefly larvae may face different predation risks on the forest floor and in nodes. Densities of generalist predators, such as spiders and beetles, may be greater on the ground, where a rich community of detritivores, scavengers, and predators inhabit the litter. It seems probable that predators foraging on the ground would acquire more prey per unit effort than those that attempted to forage in the isolated patches of detritus in the nodes.

This suggests the hypothesis that cranefly oviposition in *C. longifolia* nodes is an adaptation to reduce larval predation. We tested two predictions from this hypothesis: (1) a higher abundance of cranefly larvae per gram detritus in nodes than on the forest floor, and (2) reduced predation in the nodes.

METHODS

On 27-28 January, 2006, we performed stratified random sampling of cranefly larvae and their predators within the oak-bamboo forests, near the Cuerici Biological Station, in Cerro de la Muerte, Costa Rica. At each of 16 sites randomly chosen from along 250 m of trail, we overturned leaf litter and removed all arthropods found in the detritus of a 20 x 50 cm ground plot with forceps. We recorded the number of cranefly larvae and the number of potential predators found in

each sample. We collected the same data from two randomly selected *C. longifolia* nodes at each site. We bagged the detritus from two nodes and one ground plot, and measured dry weight to standardize arthropod abundances by grams of detritus. The average mass (± SE) of detritus per bamboo node was 10.6 ± 1.4 g, which compared to an average of 156.3 ± 15.0 g of litter searched per sample plot on the forest floor.

In addition to various arthropod predators, at least two avian species probably prey on cranefly larvae in this system. The Large-footed Finch (*Pezopetes capitalis)* forages for arthropods on the ground by using a stereotypical maneuver that involves kicking up detritus with their large feet (Stiles et al. 1989), while the Yellow-billed Cacique (*Amblycercus holocericeus)* is reported to sometimes forage for arthropods in bamboo nodes (C. Solano, pers. comm.). To observe potential avian predators of cranefly larvae, we walked 14 15-minute transects in the same area. We identified all ground birds and monitored their behavior, noting whether they were foraging on the forest floor or on *C. longifolia* nodes. We tested whether cranefly or bird and arthropod abundances were different between nodes and forest floor using Fisher Exact tests.

RESULTS

There were more cranefly larvae per gram of detritus in nodes than on the forest floor, with all 9 individuals found in nodes (Fisher Exact, P = 0.001). There were also more cranefly larvae in nodes than on the forest floor per minute spent searching (Fisher Exact, P = 0.03). All cranefly larvae appeared to be of the same species; at least three stadia were represented in our sample (including the last larval stadium).

Per gram of detritus, we found similar numbers of predatory spiders and beetles on the forest floor (n= 5 and 2 respectively) compared to in nodes (n= 2 and 1 respectively (Fisher Exact, P = 0.21). Our collections also included a snail, which appeared to be resident in the nodes, but was presumably non-predatory.

There were fewer avian predators that specialize in foraging within bamboo (0 Yellow-billed Caciques) vs. on the forest floor (6 Large-footed Finches; Fisher Exact, P = 0.09). Two of the Large-footed Finches were actively foraging in ground detritus. We observed two unidentified birds perched on *C. longifolia* shoots, but these birds did not forage in the nodes while we watched nor did they appear adapted for that foraging behavior.

DISCUSSION

Our results were consistent with the hypothesis that the tipulid we studied is a specialist of detritus clumps in bamboo nodes. We found nine larvae inhabiting nodes and none within 14.8x the biomass of similar soil litter. Although arthropod predator abundances did not differ between nodes and forest floor, predatory birds were absent in nodes. From our observations of Large-footed Finches foraging, we speculate that this species could efficiently find and consume large numbers of cranefly larvae on the forest floor, thereby exerting greater predation

pressure on cranefly larvae than predatory arthropods.

With the data collected, we cannot determine whether craneflies oviposit preferentially in nodes. It could be that craneflies oviposit indiscriminately but larvae inhabiting the forest floor are subject to strong predation. Nonetheless, our findings still suggest a selection differential that could, given the necessary genetic variation, lead to the hypothesized behavioral adaptation by adult craneflies to oviposit in *C. longifolia* nodes. Further studies could monitor adult cranefly ovipositing behavior to better address this question.

LITERATURE CITED

Bland, Roger G. *How to Know the Insects*. Wm. C. Brown Company: Dubuque, Iowa, 1978. p. 326-327.

Kemp, M.T. and R.Q. Thomas. 2004. Distribution and abundance of Tipulid larvae in bamboo litter clumps in a high elevation Costa Rican forest. Dartmouth Studies in Tropical Ecology, p. 69-71.

Stiles, G.F. and A.F. Skutch. *A Guide to the Birds of Costa Rica*. Cornell University Press: Ithaca, New York, 1989. p 407, 455.

SECONDARY METABOLITES IN PLANTS WITH KNOWN MEDICINAL USES IN SUN AND SHADE HABITATS

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Abstract: Herbivory pressure in the tropics has selected for high secondary metabolites. We investigated the effect of habitat (sun versus shade) on the production of secondary metabolites within species of plants. We hypothesized that plants with less access to light have higher cost of leaf replacement, resulting in a higher investment in chemical defenses. Alternatively, plants growing in sun habitats may shunt excess carbon (from high photosynthesis relative to nutrient acquisition) into chemical defenses. We tested these alternatives by comparing the secondary metabolites in leaves of the same four species between sun and shade habitats. Using a double blind smell test, pH measurements, and paper chromatography analyses, we detected significant differences in secondary metabolites between species. However, no difference was detected between light habitats for each species. Our results are consistent with relatively tight genetic regulation of secondary metabolites within these species.

Key Words: secondary metabolites, plant defense theory, phenotypic plasticity

INTRODUCTION

High levels of herbivory in the tropics have selected for increased levels of secondary metabolites, which can act as chemical defenses. (Coley et al. 2003). In Cerro de la Muerte, Costa Rica, local people use many different plants to remedy common ailments. The biologically active compounds within these plants, which confer their medicinal value, are generally thought to have evolved because of their function in plant defense systems.

Plant defense theory predicts that because replacing lost leaves entails a greater cost in low-resource environments, mature leaves of shade tolerant species should have higher levels of chemical defenses than mature leaves of species found in high-light conditions (Coley et al. 2003). Based on this theory, we hypothesized that varying light availability would produce the same pattern within a single species, but through phenotypic changes rather than genotypic changes. We therefore predicted that there would be higher levels of secondary compounds in individual plants growing in shade habitats for a given species.

Alternatively, high light conditions can lead to increased plant defense. If low nutrient (e.g. nitrogen or phosphorous) availability limits plant growth, surplus carbon fixed through photosynthesis in high light conditions may be shunted into the production of secondary metabolites (Bryant et al. 1983). Under this model, individual plants growing in sun habitats would be predicted to have higher levels of secondary metabolites than those growing in shade habitats.

Finally, it is possible that plant species may lack adaptive phenotypic plasticity in regulating secondary metabolite production. In this case, we would see no difference in the levels of

secondary metabolites across light habitats within a given species. To investigate the difference in the levels of secondary metabolites between sun and shade habitats, we selected four species of plants with known medicinal properties, distributed in both shade and sun habitats (Kehas 2003).

METHODS

On 27 January 2006 we sampled shaded understory habitat northeast of open pasture north of the Cuerici Biological Station in Cerro de la Muerte, Costa Rica. With the help of Sr. Carlos Solano we identified and collected samples in both open (sun) and understory (shade) environments. We selected one plant species each from the families *Urticaceae* (10 plants in sun, 10 plants in shade), *Winteraceae* (5, 5), *Verbenaceae* (6, 3), and *Clusiaceae* (1, 5). We took 1-4 mature leaves from each plant, sealed them in airtight bags, and kept them shaded until processing.

We conducted a double-blind smell test of each sample and rated scent intensity (1-3; 1 = weak, 3 = strong). We ran paper chromatography (PC) tests (modeled after thin layer chromatography) on 3 randomly selected replicates of each species in each habitat, using Whatman 4 filtration paper to create a PC plate. We placed the selected leaf over the bottom 1 cm segment of the filtration paper and rolled a quarter across the leaf to transfer a chemical extract onto the paper. We modified 5 oz transparent plastic cups, filled with 2 cc of 96% alcohol to support the PC plate and run the chromatography test, covering the samples during each run to prevent evaporation. The first orange band represented the presence of secondary metabolites. The second two bands, green and yellow, were identified as chlorophyll and disregarded. If the distance migrated by the orange band was consistent throughout all samples for a given species, we concluded that that band represented the same secondary metabolite. All orange bands were visually rated by intensity (0-3; 0 = not present, 3 = strong).

We then macerated a 6.25 cm^2 leaf sample of 3 randomly selected replicates of each species in each habitat, mixed it with 3 cc of water using a mortar and pestle, and measured the pH using Fisher Scientific short range alkacid no. 2 strips.

We ran three two-way ANOVAs to test how smell intensity, pH, and PC band intensity varied according to species, habitat, and the interaction between species and habitat (JMP 5.0.1).

RESULTS

We detected significant differences in smell, pH, and PC band intensity among species (Figure 1). However, we detected no overall difference between habitats, and no interaction between species and habitat (Table 1). We estimated that our analysis for habitat had a power of 0.82 to detect a difference in band intensity of 0.5, a power of 0.99 for a difference in pH of 0.2, and a power of 0.99 for a difference in smell intensity of 0.3.

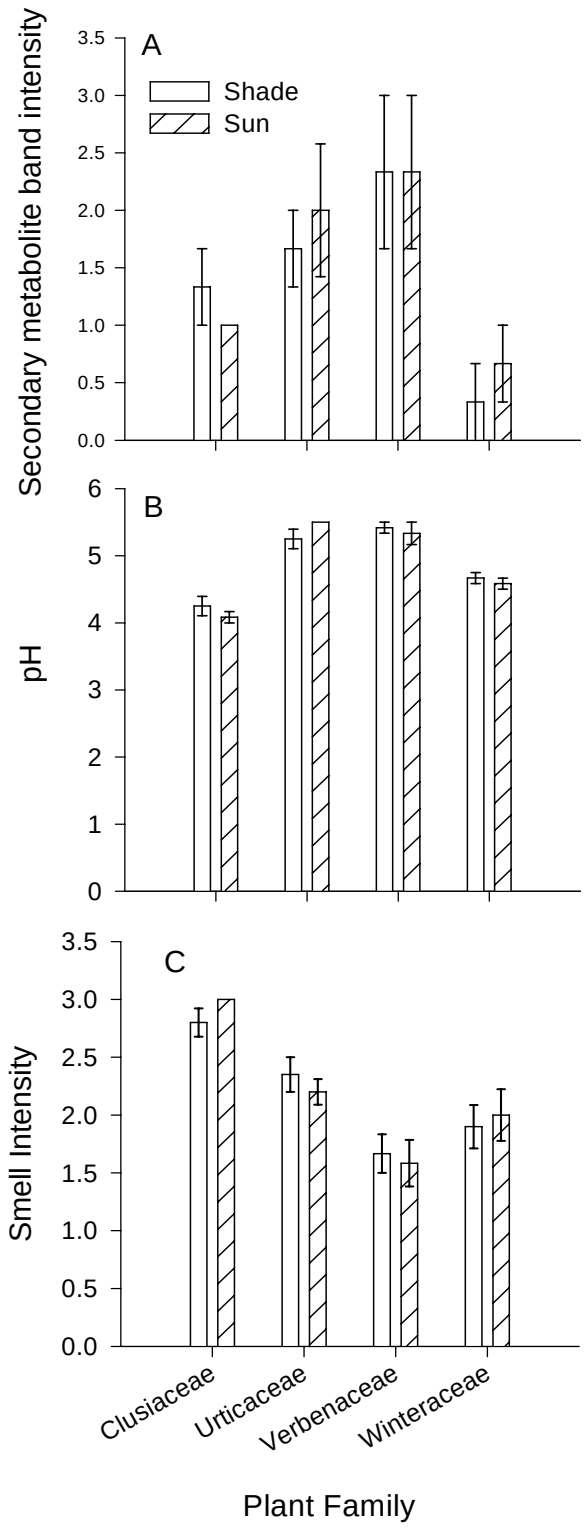

Figure 1. Variation in secondary metabolite concentration based on (A) paper chromatography band intensity, (B) pH, and (C) smell intensity (to the investigators) across four species of plants in both sun and shade habitats. Data were collected near the Cuerici Biological Station in Cerro de la Muerte, Costa Rica.

DISCUSSION

Although different plants showed clear differences in the amount and nature of their secondary metabolites, we found no evidence that light environment (sun vs shade) influenced intraspecific variation in plant chemistry. These results support the hypothesis that plants may lack adaptive phenotypic plasticity in regulating the production of secondary metabolites on the basis of light availability. These results do not match either: (1) the pattern predicted by extension to phenotypic variation of the resource availability hypothesis (Coley et al. 2003), or (2) the pattern of increased production of secondary metabolites in high light conditions, as predicted by the carbon shunting hypothesis (Bryant et al. 1983).

Even though we had power to detect differences in secondary metabolites between species, our methods could have masked variation in individual compounds which may have medicinal uses. Nevertheless, we found no evidence suggesting an individual seeking these species should discriminate between sun and shade habitats to find the most effective medicinal plant within a given species.

TABLE 1. Two-way ANOVA results for effects of pH, band intensity, and smell intensity on species and habitat (sun versus shade). Degrees of freedom for error = 16.

		pH		Band Intensity		Smell Intensity	
	df	F	P	F	P	F	P
Species	3	58.35	<.0001	6.11	0.0057	9.03	0.0001
Habitat	1	0.071	0.79	0.067	0.80	0.011	0.92
Species*Habitat	3	1.40	0.28	0.24	0.86	0.30	0.82

LITERATURE CITED

Bryant, J.P., F Chapin, D Klein. 1983. Carbon nutrient balance of boreal plants in relation to vertebrate history. Oikos 40(3): 357-368.

Coley, P.D., M.V. Heller, R. Aizprua, B. Araúz, N. Flores, M. Correa, M. Gupta, P.N. Solis, E. Ortega-Barría, L.I. Romero, B. Gómez, M. Ramos, L. Cubilla-Rios, T.L. Capson and T.A. Kursar. 2003. Using ecological criteria to design plant collection strategies for drug discovery. Frontiers in Ecology and the Environment 1(8): 421-428.

Kehas, A.J. 2003. A survey of medicinal and other useful plants at Cuerici Reserve, Cerro de la Muerte. Dartmouth Studies in Tropical Ecology. Dartmouth College, Hanover, NH.

NECTAR AVAILABILITY AND FLOWER PREFERENCES OF HIGH-ALTITUDE TROPICAL HUMMINGBIRDS

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Abstract: Hummingbirds are important pollinators for tropical flowers, especially at high elevations. We hypothesized that flower nectar production influences hummingbird flower preferences, and that these preferences vary between hummingbird species. We observed 5 species of hummingbirds at two flower patches near the Cuericí Biological Station, Cerro de la Muerte, Costa Rica, recording which flowers they visited as well as the flower composition of the sites. Hummingbirds preferred certain flower species over others, and flower preference differed between hummingbird species. Some hummingbird species preferred flowers with high but inconsistent nectar rewards while others sampled randomly from the environment.

Key Words: hummingbird foraging, nectar reward, flower density

INTRODUCTION

Many plant species exhibit a "bonanza" pattern of highly variable nectar production among their flowers (Feinsinger, 1978), with some flowers producing hardly any nectar while neighboring flowers produce copious amounts. As a result, hummingbird pollinators visit more flowers as they search for the nectar lodes (Feinsinger, 1978). Flowers in Costa Rica's high altitude environments depend heavily on hummingbird pollination and display a variety of strategies to attract pollinators. We hypothesized that some hummingbird species selectively visit plant species with these highly variable but potentially higher nectar rewards, while other hummingbird species prefer plant species that provide consistent but small nectar rewards.

We tested the following propositions: 1) hummingbirds preferentially forage on certain plant species, 2) hummingbird species differ in their preferences, and 3) some plant species produce highly variable, high-nectar reward flowers, while other species produce consistent but low-reward flowers.

METHODS

We conducted our study at two 20 x 20 m flower patches near the Cuericí Biological Station at Cerro de la Muerte, Costa Rica. We estimated the density composition of each flower species by having four people visually assess the percent coverage of each species in each patch and then averaging the estimates. The first patch contained primarily *Fuchsia paniculata* and *Sechium edule.* The second patch contained primarily *Wigandia urens*, *Hemichaeana fruticosa*, and *Razisea spicata.* To quantify nectar volume per flower, we bagged five random flower clusters of each species for 12 hours and then measured nectar volumes with capillary tubes. We

also assessed nectar robbing in *Razisea spicata* by counting the number of piercings at the base of 20 individual flower corollas.

We monitored both patches simultaneously between 11:00 and 12:00 and 14:00 and 18:00 on 27 January and 5:30 and 7:30 on 28 January, observing 105 individual hummingbird visits. We recorded for each hummingbird visit the time spent actively foraging, the species visited and the number of flowers visited per plant.

We performed a chi-squared test to determine if hummingbirds preferentially foraged on different flower species and if flower preference differed between hummingbird species. We evaluated species differences in nectar production by comparing the coefficients of variation (standard deviation /mean of nectar content).

RESULTS

At patch 1, we observed Magnificent Hummingbirds, Purple-Throated Mountain Gems, Gray-Tailed Mountain Gems, Fiery Throated Hummingbirds, and Volcano Hummingbirds. At patch 2, we observed Magnificent and Volcano Hummingbirds.

Hummingbird species differed in their relative visitation of different flower species within a patch (patch 1: $\chi^2 = 43.47$, $P < 0.0001$; patch 2: $\chi^2 = 5.04$, $P = 0.02$; Table 1). In patch 1, Gray-Tailed Mountain Gem Hummingbirds preferentially foraged on *Sechium edule* while Magnificent and Volcano Hummingbird foraging did not differ from the null model based on flower density. In patch 2, both Volcano and Magnificent Hummingbirds preferentially foraged on *Wigandia urens* (Table 1).

Flower species differed in both total volume of nectar available and in variance in nectar volume from flower to flower (Table 2). The Gray-Tailed Mountain Gem's preferential foraging behavior appears to be driven by nectar rewards in *Sechium edule*. In patch 2, flower preference in Volcano and Magnificent Hummingbirdwas not related to flower density, nectar availability, or nectar consistency. We noted that 9 *Razisea spicata* flowers out of 20 were nectar robbed.

DISCUSSION

We showed that (1) hummingbirds discriminate between flower species and (2) that different hummingbird species preferentially forage on different flower species. Results also supported our third proposition that some flower species produce highly variable, high-nectar reward flowers, while other species produce consistent, but low-reward flowers.

In patch 1, the Gray-Tailed Mountain Gem may employ the high-risk, high-reward foraging strategy. However, the Volcano and Magnificent Hummingbirds did not display flower preferences.

In patch 2, hummingbirds preferentially foraged on *Wigandia urens,* which was not the most abundant flower species, the highest in nectar volume, nor the most consistent nectar reward.

TABLE 1. Number of visits hummingbird species by patch at Cuericí Biological Station, Costa Rica, made to different flower species compared to expectations from two null models: hummingbird species have no flower preference and all hummingbirds have the same flower preference. These are represented in the table as: expected visits with no flower preference, expected visits with same flower preference, respectively.

Patch 1	*F. paniculata*		*S. edule*		flower preference	
	obs.	exp.	Obs.	exp.	χ^2	p
Gray-tailed	1	11.5, 9.9	12	1.2, 3.1	103.43	<0.0001
Magnificent	36	33.6, 28.9	2	3.6, 9.2	0.89	0.35
Volcano	21	20.4, 17.5	2	2.2, 5.5	0.04	0.85
Fiery	2	1.8, 1.5	0	0.2, 0.5	-	-
Purple throat	0	18.6, 2.3	3	0.3, 0.7	-	-

Patch 2	*H. fruticosa*		*R. spicata*		*W. urens*		flower preference	
	obs.	exp.	obs.	exp.	obs.	exp.	χ^2	p
Magnificent	1	3.9, 1.0	6	5.2, 3.5	6	2.6, 8.5	6.73	0.03
Volcano	1	3.9, 1.0	1	5.2, 3.5	11	2.6, 8.5	32.69	<0.0001

TABLE 2. Flower density (visual estimate of the percentage of all flower habitat covered by that species), nectar content (mean ± SE), and coefficient of variation (standard deviation / mean) for 5 flower species in two sites at Cuericí Biological Station, Costa Rica.

Flower species	Estimated flower density (% of habitat)	Mean nectar (μl) ±SE	Stdev/mean. nectar
Fuchsia paniculata	88.5	2.5 ± 0.18	0.314
Hemichaeana fruticosa	30	2.9 ± 1.4	1.079
Razisea spicata	40	6.0 ± 2.8	1.047
Sechium edule	11.5	138.4 ± 76.3	1.233
Wigandia urens	20	1.1 ± 0.35	1.110

Physical mismatches between hummingbird and flower morphology did not appear to drive flower preference as nectar appeared equally accessible to all bird species. Our findings suggest some other factors beside nectar availability and flower density may influence hummingbird foraging. In patch 2, relative floral prominence may increase the likelihood of visitation, explaining the high hummingbird visitation to the highly visible clumps of *Wigandia urens* which tended to protrude from the surrounding vegetation (although this speculation is not substantiated by experimental investigation into the direct role or flower prominence). Furthermore, the most dense and nectar rich flower species in patch 2, *Razisea spicata*, may have had low hummingbird visitation due to the high rate of nectar robbing.

LITERATURE CITED

Feinsinger, P. 1978. Ecological interactions between plants and hummingbirds in a successional community. Ecol. Monog. 48: 269-28.

SOCIAL STRUCTURE AND REPRODUCTIVE SUCCESS IN PASSALID BEETLE COLONIES

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Abstract: Aggregative behavior can evolve when individuals in aggregations of animals tend to have higher per capita fitness than solitary animals or smaller groups. Passalid beetles near Cuerici, Costa Rica, appear to be social, but it is not known what, if any, are the benefits to individuals within colonies. We hypothesized that passalid beetles have increased fitness from raising larvae in colonies (perhaps due to cooperation among adults). However, larvae-per-adult (a putative proxy for fitness) was unrelated to colony size. Analysis of the spatial configuration of larvae and adults revealed no spatial structure in colonies. However, one of the treatments appeared to evoke a coordinated escape response in which adults may have aided larvae. If so, this indicates some level of social integration in passalids.

Key Words: Passalidae, sociality, colony, reproductive success

INTRODUCTION

Aggregative behavior can be selected for if individual fitness is enhanced by joining a group or staying in a group. Individuals within groups might experience benefits in foraging efficiency, defense, and/or reproductive activities. The social structure within aggregations of animals can range from loose to highly complex. Many species of ants and bees provide examples of complex social structure with strict castes. Passalid beetles (Coleoptera: Passalidae) seem to exhibit a looser form of sociality in small colonies beneath rotting logs, where adults provide food for larvae (White, 1983). However, it is unclear what fitness benefits (if any) arise from living in passalid groups.

If passalids are aggregated because of the benefits for individuals, then, other things being equal, individuals within medium to large colonies should have higher fitness than individuals within small colonies. If individual fitness increases with colony size, and if the ratio of larvae to adults is a reasonable proxy for individual fitness, then the total number of larvae per colony should increase more than linearly with colony size (Fig. 1, Model I). However, if colony size is unrelated to per capita reproduction, total larvae per colony should increase linearly with colony size (Fig. 1, Model II). Finally, if larger colonies tend to experience intra-colony competition for resources, per capita reproductive success might decrease with increasing colony size, in which, case, total larvae as a function of total colony size could be a decelerating function (Fig. 1, Model III). We tested these alternatives using a survey of passalid colonies.

Sociality implies that there is some structure to the interactions of individuals within a group. We tested for nonrandom spatial configurations of larvae and adults within passalid colonies by comparing the actual configuration of larvae and adults in a colony with the random distribution predicted by a null model. Social structure

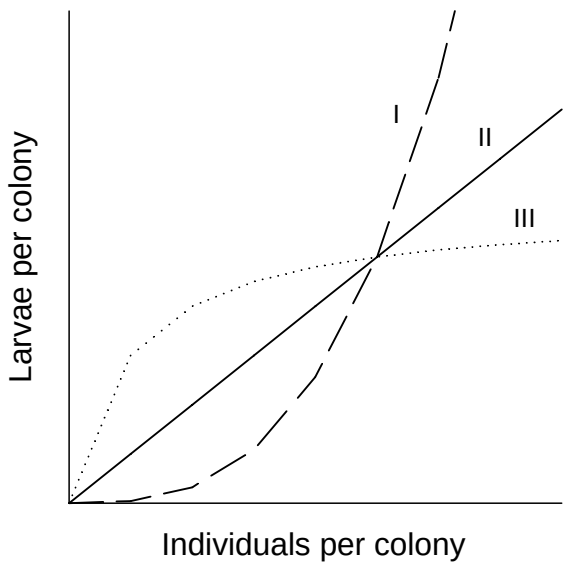

Figure 1. Three theoretical alternatives for the relationship between reproductive success and colony size. The number of larvae per total individuals in a colony might increase (I), remain the same (II), or decrease as colony size increases (III). The slope of these functions is a putative proxy for average fitness of adults within the colony.

could also be apparent temporally (individuals exhibiting a coherent schedule over time). We attempted to observe this by tracking the movements of individual passalids over time.

METHODS

We sampled logs located in the oak-dominated canopy areas along trails at Cuerici Biological Station, Costa Rica, and found 12 colonies of passalid beetles (the smaller of two species; 2.3 – 2.9 cm in length). In each colony, we counted the number of adults and larvae and sketched a map of the colony, determining the x-y coordinates of each individual. We gave each adult a unique mark using a colored oil marker. We repeated this process three times (morning and afternoon on 27 January 2006, and morning on 28 January), noting changes in spatial distribution on each occasion.

We estimated the ratio of number of larvae to total colony size with a linear regression, forced through the origin (using JMP 5.0.1). We evaluated lack of fit from this linear model to determine which of the three theoretical models in Figure 1 matched the data most closely.

For the five colonies containing at least two adults and two larvae, we used the x-y coordinates of each individual to quantify the spatial configuration. We calculated (1) mean larva-larva distance, (2) mean larva-nearest adult distance, and (3) mean adult-adult distance. We generated a null model of spatial configuration for each colony by randomly assigning stage identity to individuals 999 times (with the provision that adult and larvae number were constant and equal to that actually observed). For each simulated configuration of larvae and adults, we calculated the same three metrics (using the original distance matrix), and generated a frequency distribution of possible distances for each metric under the null hypothesis. For each log, for each of the three metrics, we calculated the distance between the observed distance and the median from the randomization results. Then we used a t-test (n = 5 logs) to test whether the observed distances tended to be larger or smaller than expected by chance.

RESULTS

Larvae constituted 75 ± 4% (mean ± SE) of each colony across colonies. A simple linear model of number of larvae vs. colony size provided good fit (r^2 = 0.80; Fig. 3). A

lack of fit test for this model was non-significant ($F_{4,7}$ = 2.29, P = 0.22), and a second order polynomial provided no improvement to fit (r^2 = 0.80). Thus, there was no evidence for any relationship between fitness and colony size.

We were unable to track marked adult beetles because most marked beetles could not be found. Between the first and second observations, 8 of the 12 beetle colonies decreased in apparent colony size, and 0 individuals were visible in 3 of those colonies (larvae disappeared from sight along with adults). Between the second and the third observations, 6 colonies decreased, and 0 individuals were visible in a total of 8 colonies. Only 2 colonies retained a constant visible population throughout all 3 observations. Therefore, we based the analyses of spatial structure on data from the first observation of each colony.

We found no evidence of spatial structure (Table 1). There was no aggregation in either larvae (t_4 = 0.38, P = 0.72) or adults (t_4 = 0.97, P = 0.39). The position of adults relative to larvae did not suggest care of larvae: the mean larva-nearest adult distance (3.58 cm) was 1.77 cm greater than the randomly predicted distribution (marginally significant, t_4 = 2.61, P = 0.06)

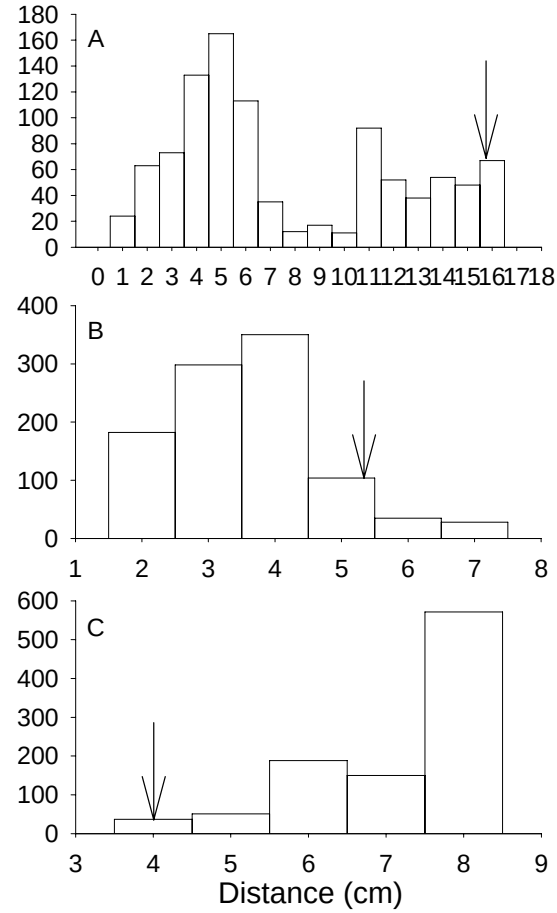

Figure 2.Random distributions of distances of (A) adult to adult, (B) larva to nearest adult, and (C) larva to larva, calculated for one passalid beetle colony (Colony 9) at Cuerici Biological Station, Costa Rica. Arrows indicate actual distances for the three distance categories. In Colony 9, the actual values for adult-adult and larva-larva distance were 96.2% and 99.9% more extreme than the randomized estimates (Panels A and C). However, these values were not typical of other logs and the overall tests for nonrandom aggregations of adults and larvae were not significant. The actual value for larva-nearest adult was 85.4% more extreme than randomized estimates in this colony, and among the five colonies, that value was significantly farther than the nonrandom estimates (Table 1).

Table 1. Actual mean adult-adult distance, larva-larva distance, and minimum adult-larva distance (average distance from a larva to the nearest adult) compared to the median value for the same metric from randomization tests. Studies involved five passalid colonies found under logs at Cuerici Biological Station, Costa Rica. All colonies that had at least 2 adults and 1 larva were analyzed. Units are cm.

			Adult-adult distance		Larva-larva distance		Larva-nearest adult distance	
Log #	Adults	Larvae	Actual	Random	Actual	Random	Actual	Random
2	3	11	16.20	7.95	4.50	7.77	5.80	4.13
6	2	3	4.00	2.48	2.00	2.33	1.30	1.63
9	3	12	12.30	6.57	3.40	6.60	4.80	3.03
10	4	4	3.60	11.21	17.40	11.00	10.00	6.06
11	2	3	12.30	6.57	3.40	6.60	4.80	3.03
Median	2.80	6.6	9.68	6.96	6.14	6.86	5.34	3.57

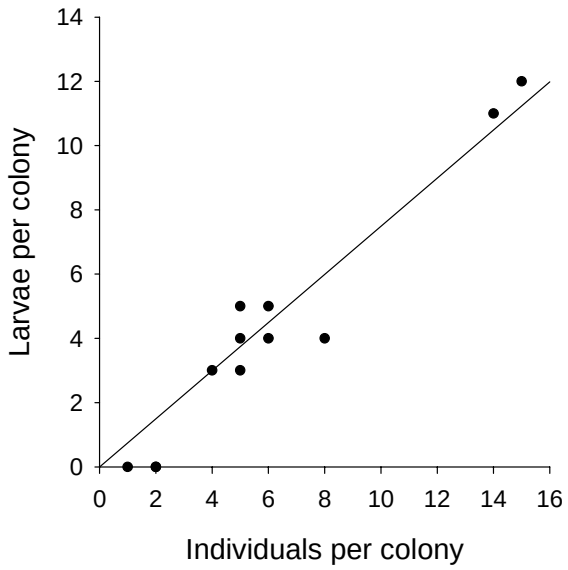

Figure 3. Relationship between reproductive success and colony size in 12 colonies of passalid beetles at Cuerici Biological Station, Costa Rica. Data match Model II in Fig. 1 (r^2 = 0.80), suggesting that colony size does not affect proportion of larvae in each colony.

DISCUSSION

We found no evidence that group size (a measure of sociality) influenced fitness (Figs. 1, 3) and no evidence for spatial structure of individuals within colonies (Fig. 2, Table 1). However, the benefits that colonies confer to individuals and the social mechanisms driving those benefits may be functioning in a different way. For example, although increased colony size does not seem to increase per capita larval abundance, it is possible that larval survival and/or the number of reproductive bouts per breeding season could increase with colony size. If colonies do confer such benefits to individuals, it is possible that the driving mechanism is something we were unable to observe, such as temporal social structure. Alternatively, because beetle larvae are known to make noise by stridulating (White 1983), it is possible that direct adult-larvae communication drives parental care in beetle colonies, rather than spatial or temporal structure.

We were surprised that apparent colony size decreased so much, and so fast, after our first visit to the logs. Some of the passalids were probably foraging inside the log, coincidentally out of view, but it appears that many colonies reacted to the handling disturbance by burrowing to hide themselves or abandoning the log collectively. Because we did not handle the larvae, and because larvae are not highly mobile, we did not expect them to move away from disturbance independently as an escape response. The disappearance of larvae following disturbance probably involved some form of assistance of larvae by adults. If so, this would represent a form of sociality.

LITERATURE CITED

White, R.E. 1983. Passalid Beetles. Pp. 137 in Peterson Field Guide to Beetles. Houghton Mifflin: New York.

LIVING ON THE EDGE: ADAPTATIONS BY EPIPHYTIC BROMELIADS TO LIGHT INTENSITY AND DESICCATION IN EXPOSED CANOPY HABITATS

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Abstract: Bromeliads in the tree canopy of high elevation forest in Costa Rica are subject to high variance in sun and wind exposure. However, adaptations such as red pigmentation to block UV-B and cupped leaves to hold more water may allow some species of bromeliad to occupy high exposure habitats. I compared two distinct but unidentifiable species of bromeliads in Cuericí, Costa Rica, with respect to exposure to sunlight, red pigmentation, and water holding capacity. Species 1 had more red pigmentation and held more mL water/ g plant than species 2. Also species 1 tended to be larger and more abundant in exposed habitats than species 2. These results are consistent with the hypothesis that increased red pigmentation and water storage help species 1 to better resist damage caused by light and water stress, allowing it to grow larger than species 2 in high exposure habitats.

Key Words: bromeliad, sun intensity, tree canopy

INTRODUCTION

Bromeliads living in the Costa Rican tree canopy in high elevation forest are exposed to large fluctuations in light intensity, wind, and water availability. Perhaps moderating the effects of light and water stress, some species of bromeliad have red pigmentation (which may protect against UV-B radiation) and a whorled leaf structure which forms tanks that store water. Two species of epiphytic bromeliads dominate the upper canopy of oak forests in Cuericí, Costa Rica: species 1 has distinctive, variable red pigmentation and large, concave leaves; species 2 is usually green colored and has narrower leaves. I tested three predictions derived from the hypothesis that red coloration and water holding capacity are adaptations for high light and low water conditions: (1) redness of species 1 increases with exposure and increases more dramatically than species 2; (2) leaf structure of species 1 allows greater water storage in mL water/g plant than that of species 2; and (3) species 1 is more abundant and grows larger than species 2 in more highly exposed areas.

METHODS

I studied bromeliads on 27 Jan 2006 at the Cerro de la Cuericí research center, sampling on the trail with northwestern aspect. Few bromeliads occurred under the darker, wetter southeastern aspect (≈ 3% the density under a trail with a NE aspect). For each randomly selected tree, I randomly sampled one bromeliad each of species 1 and 2 (yielding n = 30 and 32 bromeliads, respectively). For each bromeliad, I estimated the size, redness, and exposure on ordinal scales of 1 to 8, with 1 being the lowest size, redness, or exposure and 8 being the highest. I defined redness as the visually apparent intensity of the red pigmentation in bromeliad leaves, and I defined exposure as the level of

canopy openness around the bromeliad, taking into account shading around and above the bromeliad, as well as proximity to tree canopy edges. I also tested the water-holding capacity of both species, sampling eight bromeliads of each species (from recently fallen intact plants) with a similar range of sizes, first recording their dry weight and then measuring the volume of water each bromeliad retained after I had submerged it in water.

Taking the liberty of analyzing ordinal data as interval data, I tested for patterns in redness and size with a general linear model that included species, exposure, and the interaction between species and exposure using JMP 5.0.1. I also analyzed the difference in leaf water holding capacity between the two species.

RESULTS

I found both species across all levels of exposure, but I found species 1 more often than species 2 in high exposure habitats (t_{60} = 2.01, P = 0.050). The relationship between size and exposure differed between species (Table 1); while the size of species 1 did not vary with exposure, the size of species 2 decreased with exposure (Figure 1). Redness was positively related to exposure in both species (Table 1), but more so for species 1 than species 2 (Figure 2). Finally, species 1 tended to hold more mL water/g plant compared to species 2 (Fig. 3).

DISCUSSION

Results indicate that bromeliad species diver with respect to redness and water storage and that these trends are related to their distribution across habitats. Results also support the tentative conclusion that redness and water storage ability are adaptation of species 1 for high exposure environments.

The small size of species 2 at high exposures could potentially be explained by age structure if individuals of species 2 in high exposures tended to be younger. This seems unlikely to explain the patterns I recorded because (1) species 2 individuals in high exposures are probably not new colonizers because these exposed habitats must be about as old as less exposed habitats; and (2) if these individuals are young, this would imply that older plants in the same exposure all died at about the same time.

A better explanation for the difference in size between species 1 and species 2 in high exposure habitats is species differences in resistance to the damaging effects of canopy exposure.

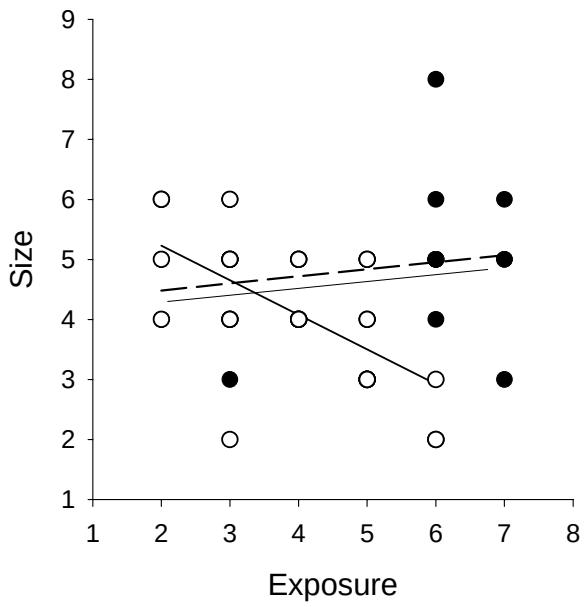

Figure 1. The effect of exposure on the size of bromeliad species 1 (closed dot) and species 2 (open dot) in Cuerici, Costa Rica. Species 1 plant size did not change with exposure (dotted line: P =0.32), but the species 2 plant size decreased with increasing exposure (solid line: r^2 =0.39, df =31, P>0.001). Exposure and size were visually estimated for each bromeliad on a scale of 1-8.

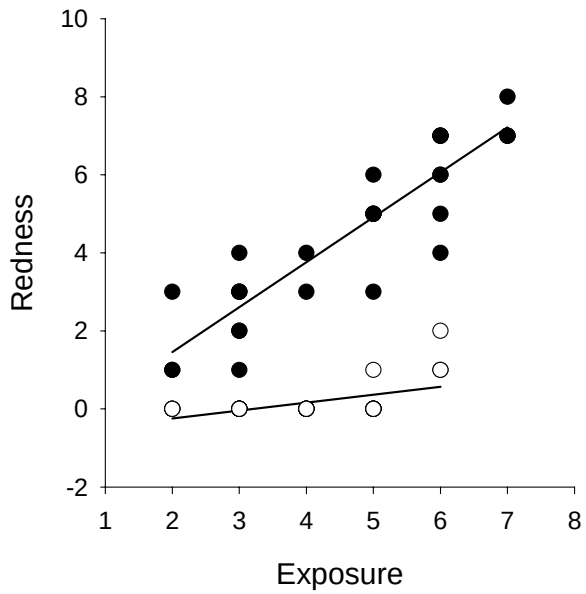

Figure 2. The effect of exposure on the intensity of red pigmentation of bromeliad species 1 (closed dot) and bromeliad species 2 (open dot) in Cuerici, Costa Rica. The redness of species 1 plants increased more with exposure (r^2 =0.84, df =29, P>0.001) than the redness of species 2 plants (solid line: r^2 =0.30, df =31, P=0.001). Exposure and redness were visually estimated for each bromeliad on a scale of 1-8.

Table 1. Tests of the relationships between exposure and red coloration, and exposure and size for two epiphytic bromeliad species at Cuerici, Costa Rica.

	Redness			Size		
	t	df	P	t	df	P
Exposure	21.35	1	<0.001	3.43	1	0.001
Species	10.41	1	<0.001	-2.55	1	0.013
Exposure*Species	7.28	1	<0.001	3.86	1	<0.001

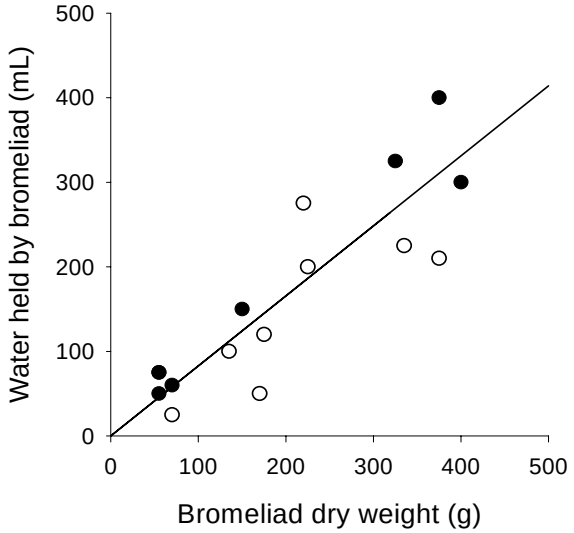

Fig. 3. The difference in water holding capacity of two species of bromeliad in Cuerici, Costa Rica. Closed circles are species 1, open circles are species 2, and the line shows the expected mL/g for all species. Species 2 holds more water in mL/g plant than species 1 (Matched Pairs, t = -2.24, df = 15, P = 0.04)

Species 2 displays extreme plasticity in red pigmentation, which may allow it to tolerate more extreme light intensities by dispersing or absorbing potentially damaging UV light. Species 2 can also store a larger reserve of water, which may allow it to cope with variable water availability and resist desiccation from wind and sun, all of which increase in exposed habitats. Red pigmentation and greater water storage may confer higher growth rate or greater survival (or both), that would explain the greater size of species 2 in open habitats. Larger size, in turn probably confers greater reproductive success.