AGGRESSIVE BEHAVIOR OF TWO ACACIA ANT SPECIES IN RESPONSE TO SIMULATED CATTLE BROWSING

MELISSA A. BARGER, GABRIEL H. CALVI, S. ALLIE HUNTER,
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Abstract: Near Palo Verde National Park, Costa Rica, *Acacia collinsii* trees occur in pastures where they are browsed by cattle. We focused on two ant species, *Pseudomyrmex spinicola* and *P. flavicornis,* which occur on *A. collinsii*. Protection of their host trees should influence the population dynamics of these obligate mutualists. We tested the null hypothesis that both *Pseudomyrmex* species would defend the tree equally by reacting similarly to simulated cattle browsing. Both ant species responded with similar aggression. The number of attacking *P. flavicornis* increased significantly during the course of morning experiment.

Key Words: Acacia collinsii, *defense, mutualism,* Pseudomyrmex flavicornis, Pseudomyrmex spinicola

INTRODUCTION

Acacia collinsii participates in a mutualism with several ant species in which the tree provides shelter and resources for the ant colony in exchange for protection from herbivory. Our study site, a pasture southeast of the field station in Palo Verde National Park in Costa Rica is dominated by *A. collinsii*, which are heavily browsed by cattle. Two common ants occupying *A. collinsii* are *Pseudomyrmex spinicola* and *Pseudomyrmex flavicornis*. As obligate mutualists, their population dynamics should be influenced by differences in their defense of their host. We compared the defense behavior of the two ant species in response to simulated cattle browsing. We tested the hypothesis that the two *Pseudomyrmex* species would defend the tree equally and therefore react similarly to simulated cattle browsing.

METHODS

We used a matched-pair design to compare the response of *P. flavicornis* and *P. spinicola* to cattle browsing. We chose ten *A. collinsii* trees occupied by *P. flavicornis* and paired each with a nearby *A. collinsii* occupied by *P. spinicola.* Pairs were chosen based on proximity (within 10 m), height (within 1 m), number of branches, and foliar condition (by visual assessment). We did this to control for potential differences in ant aggression due to these variables. Trees in very poor foliar condition were not used.

On 10 January 2005 we gathered data at a pasture 6 km SE of the Palo Verde research station, beginning at ca. 0930. We spent ca. 10 minutes at each tree pair and finished at ca. 1130. We observed that temperature increased during this time, while cloud cover decreased.

We mimicked cattle browsing on

each tree and recorded the ants' response. Cows browse by wrapping their tongues around foliage, closing their mouths over the leaf, and pulling (Lyons 2000). To simulate the inside of a cow's mouth we used a leather glove, conditioned with human saliva upon arrival at each tree. We browsed the leaves that appeared most healthy, just as a cow might. Our simulated cow browsed each tree for three minutes, pulling off a leaf every fifteen seconds. At every one-minute interval during browsing we counted the number of ants stinging the cow (the sleeve of the person removing leaves), and the number of ants on the cow that were not stinging. We also recorded the number of ants removed from our simulated cow during each one minute interval. (To protect the researcher, ants were removed when they reached the shoulder.)

Using JMP 5.0.1, we compared mean number of attacking ants and total number of ants between ant species, using a paired t-test. We also evaluated time trends in the number of attacking ants for both species.

RESULTS

We found no significant difference between the number of attacking *P. flavicornis* and *P. spinicola* after 1, 2, or 3 minutes of simulated herbivory (Table 1). We also found no significant difference between the total numbers of *P. flavicornis* and *P. spinicola* on the simulated cow after 1, 2, or 3 minutes (Table 1). Our results were not affected by the inclusion or exclusion of removed ants in our data. We conclude that *P. spinicola* and *P. flavicornis* have similar aggressive responses to cattle browsing.

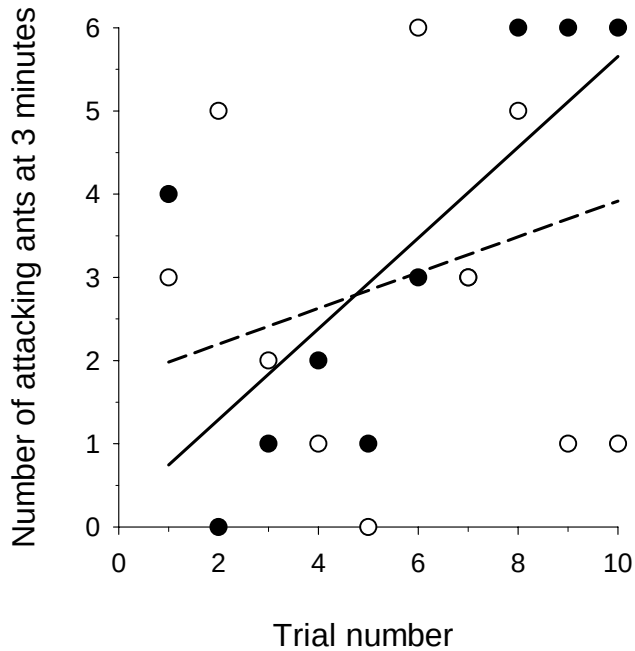

Figure 1. Number of attacking *P. flavicornis* [black dot, solid line] and *P. spinicola* [open dot, dashed line] after 3 minutes of simulated cattle herbivory as a function of trial number. Trial number corresponds to time of day, (between 0930 and 1130). The number of attacking *P. flavicornis* increased with time ($r^2 = 0.54$, df = 8, $P < 0.02$). *P. spinicola* response did not change over time ($r^2 = 0.029$, df = 8, $P < 0.64$). Trends were similar after 1 and 2 minutes.

We noticed an increase in temperature over our sampling period. Trials were consecutive, so we used trial number to represent time. The number of attacking *P. spinicola* showed no significant trend with time. In contrast, the number of attacking *P. flavicornis* increased over the course of the morning (Fig. 1).

DISCUSSION

The similar number of attacks by *P. flavicornis* and *P. spinicola* in response to cattle browsing suggests that exposure to

cattle browsing should not favor either ant species in their population dynamics in pasture habitats. However, it is possible that *P. flavicornis* trees could be better defended. Cattle browsing peaks in the early to mid-morning, and again in the early afternoon (Lyons 2000). If *P. flavicornis* continue to increase in aggression throughout the afternoon and cattle tend to browse when *P. flavicornis* aggression is relatively high, *P. flavicornis* would provide more effective defense than *P. spinicola* over the course of the day. If so, this may offset the better defense by *P. spinicola* against arthropod intruders and competing vegetation (Cook 1993, Janzen 1984).

To elucidate mechanisms that may influence population trends of *P. flavicornis* and *P. spinicola* in pasture habitats in Guanacaste, we suggest two priorities for future research. First, trends in *P. flavicornis* and *P. spinicola* defense over a 24h cycle could be investigated more thoroughly. Second, the species could be compared in their abilities to colonize young *A. collinsii* hosts. Finally, because several other obligate and facultative ant mutualists occur on *A. collinsii* in pastures, research on defense and colonization could be usefully extended to this wider suite of ant species.

LITERATURE CITED

Cook, S., S. Dyhrman, D. Kornet, E. O'Hara, and M. Seandel. 1993. Differences in response of two species of acacia ants to disturbances of their host trees. Dartmouth Studies in Tropical Ecology, p. 5-7.

Janzen, D. H. 1984. Swollen-Thorn Acacias of Central America. Smithsonian Contributions to Botany, 13: 4.

Lyons, Robert K. and Richard V. Machen. 2000. Interpreting Grazing Behavior. Texas Agricultural Extension Service. Texas A+M University.

Table 1. Comparison of the responses of *P. flavicornis* and *P. spinicola* to simulated cattle herbivory.

	Minute	Difference between mean number of ants (*P. flavicornis- P. spinicola*)	Paired t-test results
Attacking ants	1	-0.4	t = 0.37, df = 9, P = 0.72
	2	0.8	t = -0.94, df = 9, P = 0.37
	3	0.5	t = -0.51, df = 9, P = 0.62
Total ants	1	-1.1	t = 0.66, df = 9, P = 0.53
	2	-0.3	t = 0.21, df = 9, P = 0.84
	3	-1.1	t = 0.66, df = 9, P = 0.52
Total ants + removed ants	1	-1.1	t = 0.66, df = 9, P = 0.53
	2	-0.2	t = 0.13, df = 9, P = 0.90
	3	-1.2	t = 0.63, df = 9, P = 0.54

FRUIT AND LEAF VISITATION BY *PSEUDOMYRMEX SPINICOLA* IN RESPONSE TO DISTURBANCE OF *ACACIA COLLINSII*

CAYELAN C. CAREY, ELVINA C. CHOW, JENNY E. JUN,
DANIEL J. MADIGAN AND EMILY L. SHARP

Abstract: Acacia collinsii exists in an obligate mutualism with *Pseudomyrmex spinicola*, creating the potential for a conflict between ant protective response and seed dispersal. We hypothesized that when an *A. collinsii* branch is disturbed, *P. spinicola* would avoid fruits in their defensive response. We created a disturbance on *A. collinsii* and then recorded ant visits to fruits and leaves. There was no significant *P. spinicola* avoidance of fruits after disturbance.

Key Words: mutualism, seed dispersal

INTRODUCTION

The ant *Pseudomyrmex spinicola* is an obligate mutualist with the tree *Acacia collinsii*, in which the ant receives habitat and nutrients and defends the tree from herbivores and competitors. *P. spinicola* display aggressive host protection behavior in response to a disturbance on *A. collinsii*. This creates the potential for a conflict in which *P. spinicola* deter the visitation of their mutualists, such as pollinators and seed dispersers.

P. spinicola decrease visitation on mature flowers, which may prevent a conflict between ants and pollinators (Ghazoul 2001, Raine et al. 2002). A similar conflict may exist between ants and seed dispersers, because *A. collinsii* seeds are thought to be animal-dispersed (Hunter and Trierweiler 2005).

We hypothesized that *P. spinicola* would avoid fruits after disturbance on *A. collinsii*.

METHODS

Data were collected on 9 January 2005 from ten *P. spinicola*-inhabited *A. collinsii* trees 500 m east of the Palo Verde air strip and on El Pizote Trail, in Palo Verde National Park, Costa Rica. We selected branches with a green fruit opposite from a leaf (Fig. 1). Disturbances were created by tapping the branch for the first 30 s of every minute, for five minutes. Ant visits to the leaf and pod were recorded each minute by two recorders.

The difference between leaf and pod ant visitation was analyzed using a paired t-test. We analyzed the change of ant visitation on pods and leaves per minute with a one-way ANOVA.

RESULTS

There was no difference between the number of ant visits on leaves (22.7 ± 14.5) and visitation frequency on pods (20.9 ±

18.8); (t = 0.45, df = 7, P = 0.66). Mean difference between leaf and pod visits was 2.0 (SE = 4.40). There was no difference in ant visits with respect to time on leaves (F = 0.38, df = 4, 35, P = 0.82) or on pods (F = 1.53, df = 4, 30, P = 0.22; Fig. 2).

DISCUSSION

Our results refuted the hypothesis that *P. spinicola* would avoid fruits after disturbance on *A. collinsii*. We suggest two possible explanations for this behavior. First, *A. collinsii* fruits dehisce, potentially allowing seeds to fall to the ground. In this case, ants would never come into contact with dispersers, eliminating potential for a conflict. Second, we studied immature fruits; therefore, we cannot determine if ants alter their visitation on mature fruits.

We had to compromise our samples in two ways. Ideally, we wanted the ants to choose between defending a single healthy fruit or a leaf, as shown in Fig. 1. However, this specific condition was not always available. Also, two trees were excluded from our analysis because ants did not visit the focal leaf or fruit, despite ant presence on other parts of the tree.

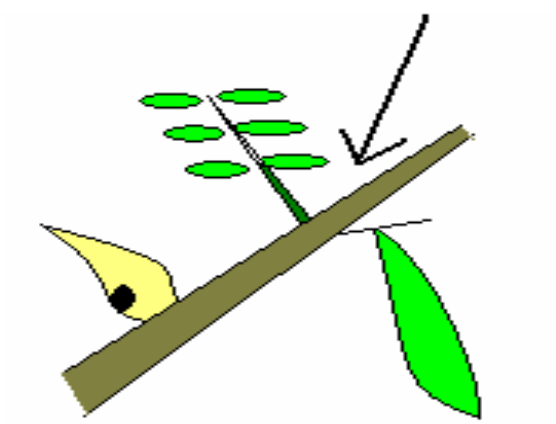

Figure 1. Idealized diagram of the configuration of leaf and fruit sampled for ant activity. The arrow refers to the junction of fruit and leaf. The structure at the stem's base represents a thorn that houses *P. spinicola*.

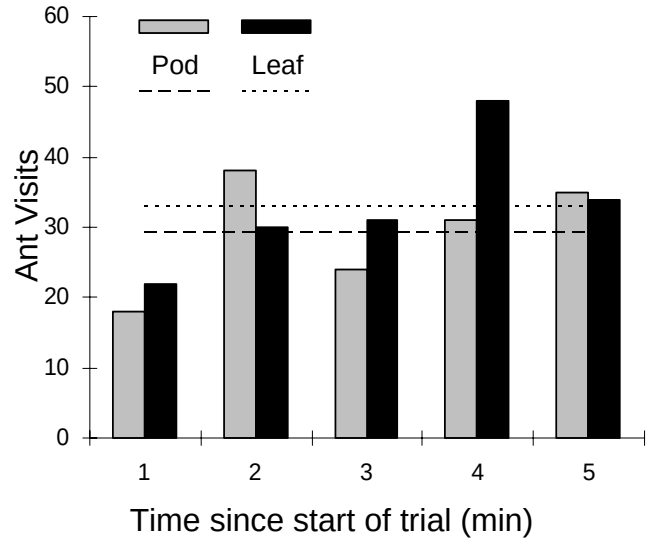

Figure 2. Ant visits per minute on fruits (n = 8) and leaves (n = 8) following disturbance of *Acacia collinsii* at Palo Verde National Park, Costa Rica.

LITERATURE CITED

Ghazoul, J. 2001. Can floral repellents pre-empt potential ant-plant conflicts? Ecology Letters, 4: 295-299.

Hunter, S. and Trierweiler, R. 2005. Fate of *Acacia colinsii* Seeds. Dartmouth Studies in Tropical Ecology.

Raine, N. E., Willmer, P. and G. N. Stone. 2002. Spatial structuring and floralavoidance behavior prevent ant-pollinator conflict in Mexican ant-acacia. Ecology, 83 (11): 3086-3096.

NECTAR PRODUCTION AND PLANT SIZE IN *ACACIA COLLINSII*

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RICHARD W. TRIERWEILER AND CHELSEA L. WOOD

Abstract: Plants have limited resources for growth, reproduction and defense. Resource allocation varies among and within species, and may depend on age and environmental conditions. We hypothesized that allocation to the nectar resource, for maintenance of its mutualist ant defenders, would be less in small *A. collinsii,* because allocation to growth may be more critical in small plants. We found a significant positive relationship between size and defense (measured by nectaries per leaf). Other measures of defense investment (i.e. nectaries per cm branch, nectary volume, and nectar sugar content) were unrelated to size. Overall, our findings provide moderate support for our hypothesis.

Key Words: extra-floral nectaries, plant defenses, Pseudomyrmex spinicola, *resource allocation*

INTRODUCTION

Resource limitation in plants usually results in a tradeoff between allocation to growth and defense. In *Acacia collinsii,* a mutualism with ants of several species provides defense against herbivory. Defense occurs through an intermediary step: the plant invests in extra-floral nectaries, and ants protect their food source by deterring herbivory, as well as removing competing vegetation in the vicinity of their host. The ant mutualists are maintained only if adequate resources are invested (Janzen 1989).

Small plants generally invest more in growth than larger ones. Fast growth may help a small plant compete for limiting resources (e.g. light), or minimize the time for which the plant is highly vulnerable to herbivory.

Abram (1994) documented a positive relationship between individual growth rate and the number of ant defenders for *A. collinsii*. We propose that small trees invest less in nectar rewards than larger conspecifics, because resources available to small trees are preferentially allocated to growth. Thus, we predicted that larger trees would produce more nectaries per cm of branch, more nectaries per leaf, nectaries of greater volume, and nectar of higher sugar content, than small trees.

METHODS

We sampled 12 *A. collinsii* trees with populations of *Psuedomyrmex spinicola* within 2 m of the Metia trail in Palo Verde National Park, Costa Rica. Equal numbers of small (≤ 120 cm tall) and large (≥ 250 cm) trees were selected.

We attached non-absorbent gauze to two petioles per tree on the day prior to sampling. This prevented ant feeding at those petioles which could have biased our results. We wrapped petioles only on

branches with new growth and thorns, as well as active ants. After removing the gauze, we measured the length, width, and height of nectaries on the petiole to the nearest 0.1 mm, to calculate the total volume of nectaries per petiole. We obtained an index of sugar concentration by crushing the nectaries in 40 μL of tap water and measuring the sugar concentration of the solution, using a Sugar/Brix Refractrometer (Model 300010).

We clipped two branches from each sample tree and recorded length, number of leaves, and number of nectaries for each. As before, clipped branches had new growth, new thorns, and active ants.

We performed simple linear regressions using tree height as a continuous variable in JMP 5.0.1. Data met the assumptions of the tests performed.

RESULTS

We found no relationship between tree height and nectary volume ($r^2 = 0.01$, df = 22, P = 0.67), nectaries per cm of branch ($r^2 = 0.00$, df = 22, P = 0.84), or nectar sugar concentration ($r^2 = 0.03$, df = 21, P = 0.39). There was a significant increase in the number of nectaries per leaf with increasing tree height (Fig. 1).

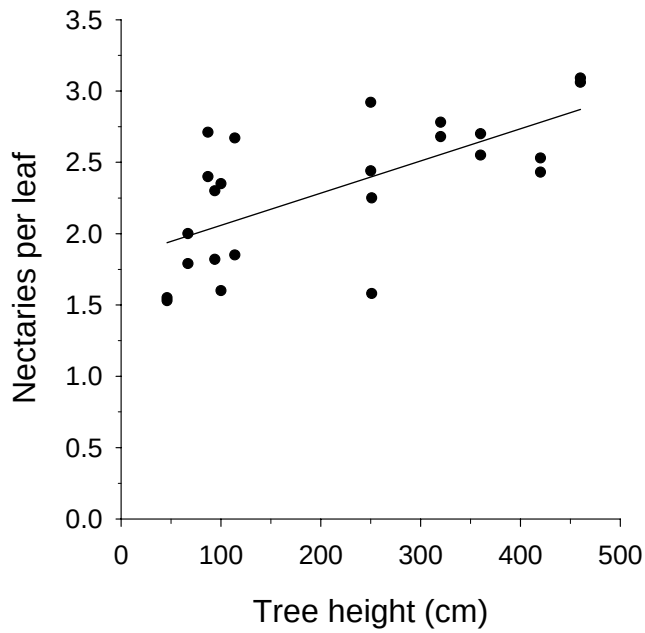

Figure 1. A. collinsii trees sampled along Metia trail in Palo Verde (n = 24; linear regression, $r^2 = 0.44$, df = 22, P < 0.001; lack of fit, F = 1.96, df = 10, P = 0.134).

DISCUSSION

Larger trees produced more nectaries per leaf. Because each nectary is a feeding point for ant mutualists, increasing the number of nectaries increases the reward for defenders, as well as the investment in defense. We found no evidence that the nectaries of larger trees contain more sugar than those of smaller trees (although we suspect that our methods for detecting sugar concentration in the nectary suspension were unreliable).

We suggest that the lower ant abundance on smaller *A. collinsii* (Abram et al. 1994) results from a trade-off between growth and defense. Investigation of plant investment in Beltian bodies, a nitrogen-based ant resource, may reveal similar patterns.

LITERATURE CITED

Abram, E. H., M. P. Ayres, H. M. Fouts, P. L. Kunz, A. E. Liebert and J. J. Ruel. 1994. Resource allocation in *Acacia collinsii*: Plant growth and ant colony maintenance. Dartmouth Studies in Tropical Ecology.

Janzen, D. H. 1989. Costa Rican Natural History. University of Chicago Press: Chicago, Illinois.

WEAK SELECTION ON FLORAL CHARACTERS IN *JUSTICIA COMATA*

EMILY L. SHARP, DANIEL J. MADIGAN, JENNY E. JUN,
ELVINA C. CHOW AND CAYELAN C. CAREY

Abstract: Spatial variation in selection pressures on floral traits has not been explored in many plant-pollinator systems. We observed two populations of *Justicia comata* that were visited by different potential pollinators. We predicted that the population visited by predominantly larger butterflies would exhibit different patterns of selection on floral traits than the population visited by smaller flying insects. We measured six floral characteristics and two fitness estimates on 24 plants at each site. A multiple regression showed only one significant trend; petal width was positively associated with one fitness estimate, at one site. We infer that petal width is under selection by pollinators at one site and that patterns of selection on petal width vary between the two sites.

Key Words: directional selection, pollination

INTRODUCTION

*Justicia comata (*Acanthaceae*)* flowers are common at the Palo Verde National Park in Costa Rica. *J. comata* have several floral visitors, including butterflies, hummingbirds, small bees and other insects. Observation of two distinct populations at Palo Verde showed that floral visitors at one site were dominated by larger butterflies and hummingbirds, while smaller flying insects were dominant at the other site. Because these visitors may be attracted by different flower traits, we hypothesized that *J. comata* may be experiencing different patterns of selection at the two sites. Our goal was to compare patterns of phenotypic selection on floral traits through estimates of seed production at the two sites.

Many floral traits affect pollinator attraction. We predicted that six traits would alter pollination success in this system: petal size, which affects the pollinator's ability to locate the flower; corolla width and length, which affect a pollinator's ability to gain access to nectar or pollen rewards; and the distance between the stigma and anthers, which may affect the morphological fit between the flower and visitor. Plant height and number of flowers per plant may both affect pollinator attraction. To estimate plant fitness, we chose the percentage of fruits developed (not aborted), and the mean number of viable seeds in successful fruits.

We predicted that smaller pollinators would select for narrower and shorter corollas, smaller stigma-anther distances,

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Key Words: directional selection, pollination

INTRODUCTION

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We predicted that smaller pollinators would select for narrower and shorter corollas, smaller stigma-anther distances,

shorter plants and smaller petals. Larger pollinators would select for larger flower traits.

METHODS

We sampled two *J. comata* populations in dry secondary forest at Palo Verde, one on El Pizote Trail and one between the airstrip and road, which were separated by approximately 2.5 km. We sampled 24 plants at each site and measured plant height, corolla length, corolla width, distance between stigma and anther, and petal width (diameter of flower face to the nearest cm) of 2 flowers per plant. For each plant we counted total flowers and haphazardly sampled 10 calyxes where the flower had fallen off; we identified ovary condition as an expanded or aborted fruit, and recorded expanded fruit per 10 calyxes as a fruit set ratio for the first fitness estimate. We haphazardly sampled 3 expanding fruits from each plant, counted seeds in each fruit, and averaged them to obtain an estimate of mean seeds per fruit per plant for the second fitness measurement. In all selection analyses, we estimated relative fitness for each plant by dividing each fitness estimate by the mean value per site. We made observations of floral visitors for 15 min at each site, recording the identity and activity of flower visitors.

We analyzed floral characteristics by site using a one-way MANOVA. A significant MANOVA was followed by univariate ANOVAs for each floral character, and correlation analysis among floral characteristics at each site. Finally, we assessed selection on floral characters through relative fitness estimates using a multiple regression at each site. Parameter estimates in the multiple regression represent direct selection on traits after accounting for selection on other traits in the analysis. We tested only for directional selection in the analyses; we could not test for non-linear patterns (e.g. disruptive selection) due to low sample size.

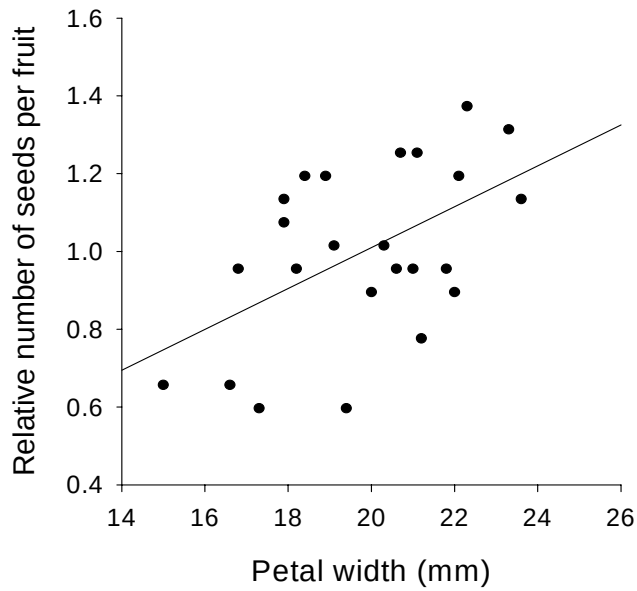

Figure 1. Regression of relative number of seeds per fruit on *J. comata* petal width at Site 1 (open habitat at Palo Verde National Park, Costa Rica, n = 24). Relative number of seeds per fruit is standardized to the mean for the population.

RESULTS

Plant characters were marginally different between the two sites (MANOVA, F = 2.18, df = 8, 36, P = 0.053). Plant height was 7.94% greater at Site 1 than at Site 2 (F = 13.31, df = 1, 44, P = 0.0007). No other floral characteristics were significantly different between sites

(in all cases, $F < 3.02$, df = 1, 44, $P > 0.09$).

Within Site 1, only corolla length and corolla width ($r = 0.52$, df = 23, $P = 0.0095$) and petal width and stigma-anther difference were correlated ($r = 0.71$, df = 23, $P = 0.0001$). There were no significant correlations between floral characteristics at Site 2 (in all cases, $r < 0.39$, $P > 0.06$). The only character to experience significant selection was petal width at Site 1, (regression between longer petals and number of seeds per fruit as the fitness estimate, $r^2 = 0.14$, df = 1, $P = 0.02$; Fig.1).

DISCUSSION

Our hypothesis that different pollinators drive selection was refuted, as floral traits did not differ between the two sites. Though we did not detect differences in selection between populations, pollinators may have driven weak directional selection toward larger petal width at Site 1. Increased petal width may attract more pollinators.

In contrast, petal width was not under significant selection at Site 2, which could be explained by at least three factors. First, smaller pollinators may not find larger petals more attractive. Second, Site 2 had been recently mowed, which may have introduced artifacts. Third, pollen supply may not limit seed production at Site 2, so that greater attractiveness of larger petals would not influence relative fitness.

This study did not fully assess the effects of petal width on fitness, so it would be useful to examine the heritability of petal width and assess experimentally how changes in petal width affect individual fitness.

FOREST STRUCTURE ON OPPOSITE SIDES OF CERRO CALIZOS RIDGE AT PALO VERDE, COSTA RICA

CHAD M. VALDERRAMA, ANNA R. NOWOGRODZKI , S. ALLIE HUNTER, GABRIEL H. CALVI AND MELISSA A. BARGER

Abstract: The Cerro Calizos limestone ridge at Palo Verde, Costa Rica divides a deciduous, tropical dry forest into north- and south-facing slopes. The north side has gentle slopes, while the south side is steep; the slopes also differ in microclimate. We hypothesized forest structure would differ on the two slopes, and predicted that the north side would have greater number and size of trees, total basal area, canopy cover, ground cover, and sapling density. We found more ground cover and canopy cover on the north side, and greater DBH on the south side, but no differences in basal area, number of trees, or sapling density. The lack of significant difference in most of these measures of forest structure was surprising given that the differences in slope are likely to cause differences in soil depth and moisture-holding capacity in this seasonally dry tropical forest.

Key Words: slope, topography, tropical dry forest

INTRODUCTION

Even on a very small scale, topographical features can cause differences in productivity and plant distributions, especially in mountainous regions (Ricklefs 1990). The Cerro Calizos limestone ridge in Palo Verde National Park, Costa Rica divides the local deciduous, tropical dry forest into north- and south-facing slopes. These slopes differ in aspect, with the south slope receiving more solar radiation and perhaps more wind. Therefore, microclimate probably differs between the two slopes. On the north side, slopes are gentle and the saddle-shaped topography may result in less erosion and thus deeper soils, than on the steeper south side. We hypothesized that forest structure would differ on the two sides of this ridge. We expected the north side to have larger and more numerous trees, and higher total basal area, canopy cover, ground cover, and sapling density.

METHODS

We set up parallel transects 30 m off the Guayacan trail on the north side of the ridge and 30-45 m below the cliff face on the south. There were seven circular plots, 25 m in diameter, approximately 100 m apart along each transect. Transects were set up running N/S and E/W through the center of each plot. To measure forest structure, we quantified sapling density, canopy cover, ground cover, number of trees, diameter at breast height (DBH) of trees, and basal area for each plot. Within 0.5 m on each side of the transects, we measured sapling density, defined as the number of woody plants above breast height < 6 cm in diameter. To measure percent canopy cover, we took the average of

five spherical densiometer readings, one in the center of each plot and one in each of the four quadrants. We included the cliff on the south side as measured canopy cover (because it prevented sunlight from reaching the understory). Percent ground cover of the whole plot was visually estimated. We counted the number of trees > 6 cm DBH per plot and measured the diameter of each. Basal area was measured from the center of each plot using a 10x English prism.

We recorded the elevation in meters of the center of the plot with an altimeter, calibrated to 0 m at the Palo Verde marsh. Because the slope on the south side was estimated to be 30° steeper, plot sizes were slightly different. To account for this, we corrected sapling density and number of trees for plot size after data collection, using the formula: corrected plot size = cos 30 * measured plot size. We analyzed these data using JMP 5.0.1 and verified the assumption of normality and homogeneity of variance. ANOVAs were used on each measure to determine differences between the two sides of the ridge, and a non-parametric Spearman's Rho correlation matrix was used to assess whether our measures of forest structure were correlated.

RESULTS

Percent ground cover and elevation were greater on the north side than the south side of Cerro Calizos (Table 1). DBH differed slightly, being higher on the south side. There were no differences in basal area, or in sapling or tree density (Table 1).

We calculated a correlation matrix, using Spearman's Rho, for all measures of forest structure, combining data from both slopes. The only significant correlations were between number of trees and basal area ($\rho = 0.63$, $P = 0.01$), DBH and elevation ($\rho = -0.60$, $P = 0.02$), and percent canopy cover and ground cover ($\rho = 0.70$, $P = 0.005$).

DISCUSSION

We found significantly higher canopy cover and ground cover on the north side of the ridge. This may be because soils on the north side are probably deeper and retain moisture longer into the dry season.

Table 1. Differences in forest structure metrics between north and south sides of the Cerro Calizos ridge, Palo Verde. Values are means ± 1 SE; n = 7 circular plots, 25 m in diameter, per slope.

Metric	North	South	P
Basal area	8.0 ± 2.4	7.9 ± 1.7	0.9008
Ground cover (%)	21.57 ± 13.25	7.14 ± 10.17	0.0143
Sapling density	7.1 ± 3.5	8.4 ± 5.9	0.6172
DBH	15.99 ± 2.74	19.50 ± 3.93	0.0764
Tree density	34.1 ± 5.0	30.1 ± 6.6	0.2159
Canopy cover (%)	62.40 ± 4.49	44.78 ± 26.89	0.1130
Elevation	139.9 ± 10.1	105.0 ± 16.6	0.0005

Also because of these characteristics, leaf-fall may be later on the north side than the south side of the ridge. When we collected data, we noted that many of the trees on the south side had already lost their leaves, resulting in a more open canopy. Additionally, we included the cliff on the south side as measured canopy cover, so the true difference in forest canopy cover between the north and south sides was probably greater than our results indicated.

The finding that canopy cover and ground cover were positively correlated was unexpected, since increased canopy cover often prevents light from reaching the understory. However, in this dry deciduous forest, canopy cover may not be dense enough on either side of the ridge to affect growth and development of understory plants. Also, if the north side has richer soil, this could result in both greater canopy cover and ground cover. The higher average DBH on the south side, however, is difficult to explain if the soil is poorer there. Although there was a difference in mean elevations between our two transects, this difference (35 m) seems unlikely to be biologically significant.

Overall, these results indicate that there are relatively few differences in forest structure between these two habitats. This was surprising, given the probable differences in soil depth, moisture-holding capacity, and microclimate associated with these north- and south-facing slopes.

LITERATURE CITED

Bailey, R. 1996. Ecosystem geography. Springer-Verlag New York, Inc.: Fort Collins, CO.

Begon, M., J. L. Harper, and C. R. Townsend. 1990. Ecology: Individuals, populations and communities. Blackwell Scientific Publications: Boston.

Ricklefs, R. E. 1990. Ecology. W. H. Freeman and Company: New York.

DIFFERENTIAL RESPONSE TO DISTURBANCE BETWEEN OBLIGATE AND FACULTATIVE ANT MUTUALISTS OF *ACACIA COLLINSII*

CHELSEA L WOOD, RICHARD W. TRIERWEILER, JONATHON C. RAFFENSPERGER, LAKSHMI NARAYAN AND TIMOTHY R. MATSUURA

Abstract: Due to their dependence on the host plant, obligate ant mutualists of the tree *Acacia collinsii* should defend their host more vigorously than facultative mutualists. We hypothesized that the activity level of the obligate mutualist *Pseudomyrmex spinicola* would respond more strongly to disturbance than that of the facultative mutualist *Crematogaster brevispinosa*. We also expected that ant response would depend on local resources provided by extra-floral nectaries. We found that *P. spinicola* did respond more vigorously to disturbance than *C. brevispinosa.* However, the response was unrelated to local resources. This indicates that, even though *P. spinicola* responds more strongly to disturbance of the host tree, the realized level of host defense may be similar for trees colonized by either ant mutualist.

Key Words: Crematogaster brevispinosa, *mutualism,* Pseudomyrmex spinicola

INTRODUCTION

Ant mutualists defend their host plant, which provides both habitat and energy resources (i.e. extra-floral nectaries; Janzen 1989). The activity level of obligate mutualists like the ant *Psuedomyrmex spinicola,* which can live only on *Acacia collinsii,* should respond strongly to disturbance. Increased activity level is likely to be associated with better defense of the host. In contrast, facultative mutualists, like the ant *Crematogaster brevispinosa,* may not exhibit the same strong response in activity levels. Ant response to disturbance may also depend upon the availability of resources provided by the host tree. Arnold et al. (2000) found that branches with experimentally reduced numbers of extra-floral nectaries had lower *P. spinicola* abundances, both before and after artificial disturbance. We predicted that the activity level of an obligate mutualist would exhibit a stronger response to disturbance than that of a facultative mutualist, and that local resource availability would be positively related to ant response for both types of mutualists.

METHODS

We haphazardly sampled 14 *A. collinsii* trees of approximately equal height (to control for effects of tree size) at a site near the main road, 2 km east of the OTS biological station at Palo Verde National Park, Costa Rica. We chose seven trees colonized by *P. spinicola* and seven colonized by *C. brevispinosa*. To control for effects of tree size, we chose trees of approximately equal height.

We quantified the number of leaves, nectaries, total thorns, occupied thorns, and length of woody tissue on one branch

per tree. We selected branches with varying numbers of leaves and thorns, so that we could evaluate ant responses across a range of resource abundances.

We chose a point on each selected branch and counted the number of ant crossings ("ant activity") at that point over five-minute periods, prior to and following the disturbance. The disturbance consisted of vigorous tapping for 10 s at the beginning of each minute interval.

Data were analyzed with one-way ANOVA and linear regression tests using JMP version 5.0.1.

RESULTS

Pre- and post-disturbance number of ant crossings were normalized by logarithmic transformation. Pre-disturbance ant activity was positively related to post-disturbance ant activity in *C. brevispinosa* ($r^2 = 0.97$, df = 1, 5, $P < 0.0001$), but not in *P. spinicola* ($r^2 = 0.02$, df = 1, 5, $P = 0.74$; Fig. 1).

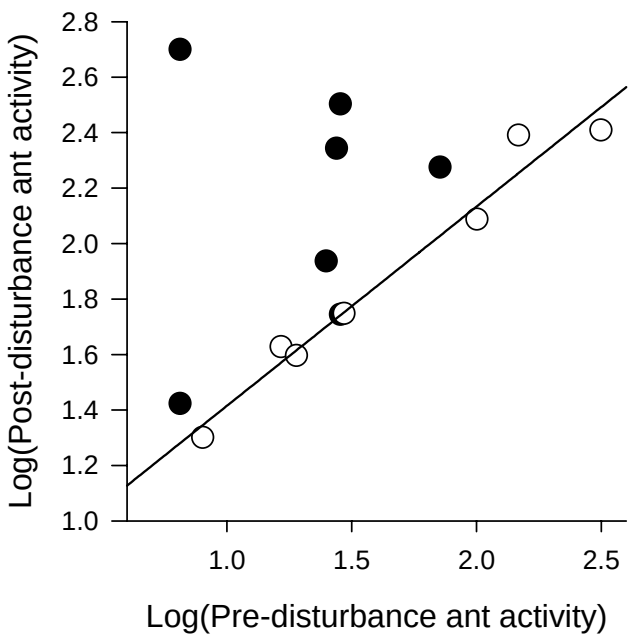

Figure 1. *Pseudomyrmex spinicola* and *Crematogaster brevispinosa* activity before and after disturbance. Filled circles represent *P. spinicola* and open circles *C. brevispinosa*. Line is a least-squares linear regression.

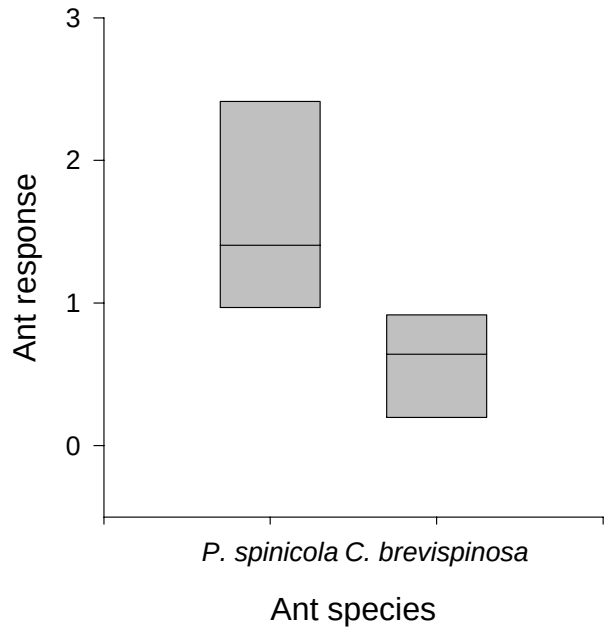

Figure 2. Response to disturbance of *Acacia collinsii* by the obligate ant mutualist *Pseudomyrmex spinicola* (n = 7) and facultative mutualist *Crematogaster brevispinosa* (n = 7). To calculate ant response, we divided the number of ants crossing a line on a branch for five minutes prior to artificial disturbance, by the number of ants crossing that line for five minutes following the artificial disturbance. The disturbance consisted of vigorous tapping.

We divided post- by pre-disturbance numbers of ant crossings, to obtain an index of change in ant activity, which will hereafter be referred to as ant response to disturbance. *P. spinicola* responded more strongly to disturbance than *C. brevispinosa* ($t = -2.70$, df = 12, $P = 0.02$; Fig. 2).

We found no relationship between ant response to disturbance and number of nectaries per unit branch length, for either *P. spinicola* or *C. brevispinosa*. Neither was there any relationship between ant re-

Table 1. Results of linear regressions of *Pseudomyrmex spinicola* and *Crematogaster brevispinosa* response on several measures of resource availability on *Acacia collinsii* branches. To calculate ant response, we divided the number of ants crossing a line on a branch for five minutes prior to artificial disturbance, by the number of ants crossing that line for five minutes following the artificial disturbance. The disturbance consisted of vigorous tapping.

Source	r^2	df	F	P
Number of nectaries / cm branch				
P. spinicola	0.05	1, 5	0.27	0.10
C. brevispinosa	0.03	1, 5	0.18	0.69
Length of branch	0.00	1, 12	0.04	0.84
Number of occupied thorns	0.16	1, 12	2.22	0.16
Number of leaves	0.02	1, 12	0.22	0.64

sponse and length of branches, number of occupied thorns, or number of leaves (Table 1).

We also compared post-disturbance ant activity of the two ant species, to determine the relative intensity of defense each provides to the host tree; we found no difference between the two species (F = 1.16, df = 1, 12, P = 0.30).

DISCUSSION

The obligate mutualist *P. spinicola* responded more vigourously to artificial disturbances than the facultative *C. brevispinosa*. *Pseudomyrmex spinicola* maintained a relatively low baseline level of activity, but exhibited a high post-disturbance activity level relative to that baseline. In contrast, the facultative *C. brevispinosa* did not respond to disturbance. Its pre- and post-disturbance activity were similar to *P. spinicola's* post-disturbance activity. These results are supported by Wickre et al. (2003), who observed a higher patrol rate in *C. brevispinosa* than in *P. spinicola*. This indicates that the two species may provide equivalent levels of defense to their host plants, even though *P. spinicola* responds more vigorously to disturbance.

The absence of positive relationships between resources (i.e. nectaries, thorns and leaves), and ant response to disturbance is consistent with the observations of Arnold et al. (2000), who found no relation between the presence of nectaries and ant abundance. For mutualist ants, the fate of the colony may be tied to the survival of the entire tree, rather than depending on the defense of resource-rich branches. Even though *P. spinicola* responds more strongly to disturbance of the host tree, the realized level of host defense may be similar for trees colonized by either ant mutualist. This interpretation rests upon the assumption that individuals of each species are equivalent in their ability to deter herbivores (i.e., severity or rate of bites from each species are equivalent). Future studies could test the validity of this assumption by examining the attack rate or efficacy of herbivore deterrence for each ant species.

LITERATURE CITED

Arnold, B. R., A. C. Brown, M. S. Calvi, M. N. Conte and S. E. LaPlante. 2000. An experimental study of *Pseudomyrmex spinicola* abundances on branches of *Acacia collinsii* with and without extra-floral nectaries. Dartmouth Studies in Tropical Ecology, p. 7-9.

Balser, T. C., J. L. Dudycha, A. L. Guerrerio, C. N. O'Neill and S. L. Soucy. 1992. The aggressiveness of three species of acacia ant. Dartmouth Studies in Tropical Ecology, p. 1-3.

Coleman, M. L., T. D. Dempsey, M. E Harrison, E. L. Kinney and F. E. Krivak-Tetley. 2002. Relationship between herbivory damage and resident ant species in *Acacia Collinsii*. Dartmouth Studies in Tropical Ecology, p. 1-3.

Wickre, J. B., C. R. Chamberlin, A. J. Kehas, K. E. Simon, and K. A. Theoharides. 2003. Do facultative and obligate mutualist ants provide equal protection for their acacia host? Dartmouth Studies in Tropical Ecology, p. 9-12.

EFFECT OF COLOR AND SIZE ON AGGRESSIVE BEHAVIOR AND FEMALE ACCESS IN THE LIZARD *CTENOSAURA SIMILIS*

LAKSHMI NARAYAN AND JONATHON C. RAFFENSPERGER

Abstract: Male *Ctenosaura similis* are highly territorial lizards that vary greatly in their physical attributes. We studied the effects of mature male size and color on territorial head-bobbing displays and access to females in Palo Verde National Park, Costa Rica. We hypothesized that large orange males would show more frequent head-bobbing behavior, and have more females in their territories, than smaller or blue-colored individuals. Orange males did have more females in their territories, but we were unable to separate the effects of male color and size on number of females. Neither size nor color influenced head-bobbing behavior.

Key Words: head-bobbing, male coloration, sexual selection, territoriality

INTRODUCTION

Ctenosaura similis, a large Central American iguanid lizard, exhibits both color-change and head-bobbing behavior. Coloration and body size vary among mature individuals. Within individuals color may vary both seasonally and daily, and also with developmental stage (Fitch and Hackforth-Jones 1983). During the breeding season, some adults, which normally range from tan to gray-blue in color, may develop spots of dull red or orange coloration, although little is known about the function of this coloration (Fitch and Hackforth-Jones 1983).

Ctenosaura similis uses head-bobbing displays to communicate with conspecifics (Fitch and Hackforth-Jones 1983). Vanderbuilt et al. (1990) described two distinct bobbing behaviors of males, one for territorial displays and another for courtship of

LITERATURE CITED

Arnold, B. R., A. C. Brown, M. S. Calvi, M. N. Conte and S. E. LaPlante. 2000. An experimental study of *Pseudomyrmex spinicola* abundances on branches of *Acacia collinsii* with and without extra-floral nectaries. Dartmouth Studies in Tropical Ecology, p. 7-9.

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Coleman, M. L., T. D. Dempsey, M. E Harrison, E. L. Kinney and F. E. Krivak-Tetley. 2002. Relationship between herbivory damage and resident ant species in *Acacia Collinsii*. Dartmouth Studies in Tropical Ecology, p. 1-3.

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Ctenosaura similis uses head-bobbing displays to communicate with conspecifics (Fitch and Hackforth-Jones 1983). Vanderbuilt et al. (1990) described two distinct bobbing behaviors of males, one for territorial displays and another for courtship of

females. Males typically defend territories which provide them reproductive access to the females within their territory, although females sometimes move between the territories of different males (Blanchard 1992). During the breeding season, large adult males defend their territories by driving off medium-sized males, while they may tolerate the presence of small, juvenile males that resemble females in size and coloration (Savage 2002).

Here, we examine the effects of size and coloration on the head-bobbing behavior and reproductive access of adult males. We hypothesized that large males with more orange coloration would have greater access to females, and that size and coloration are associated with the aggressive bobbing behavior that allows males to maintain their territories. Therefore, we predicted that large orange males would perform territorial head bobs at a higher rate and have a greater number of females in their territories, compared to smaller or blue-colored males.

METHODS

On 13 and 14 January 2005, we observed territory-holding male ctenosaurs at the OTS Field Station and at the "hacienda", 0.5 km to the west along the main road in Palo Verde National Park, Costa Rica. We selected seven focal males differing in size and color at each location and attempted to observe each for 45 min. Adult males were defined as those of relatively large size and distinctive head crest morphology, which were exhibiting aggressive or dominance behavior. All observations were completed between 0800 and 1630. We excluded data for males that retreated from sight after < 20 minutes of observation and those that did not demonstrate territorial behavior.

At the start of each observation period, we recorded time, air temperature, and predominant color (blue or orange) of the focal individual. Over each period, we noted every instance of territorial head-bobbing by the focal male. We distinguished undirected bobs from those delivered in the presence of other males, and stationary bobs from those following any change of position. For each focal male we also recorded the number of females within 20 m (a typical radius for the normal ctenosaur activities--Fitch and Hackforth-Jones 1983). At the end of each observational period, we estimated focal male body size (snout-vent-length or SVL) by sighting points on the ground aligned with snout and vent, approaching the focal male until it retreated, and measuring the distance between the two points.

For each focal individual, we calculated bobs/min, bobs/min in the presence of another male, undirected bobs/min, post-movement bobs/min, and stationary bobs/min. We used regression to analyze relationships between bobbing rates and physical and environmental factors, and between male body size and number of females in a territory. We used residuals from these analyses in an attempt to separate the effects of size and color (see Results). Our data met the normality assumptions of the tests performed, and data were analyzed using JMP 5.0.1.

RESULTS

We observed 13 males in all, seven from the OTS field station and six from the hacienda. Focal male size ranged from 37 to 53 cm SVL, and number of females in the territories of these males ranged from 0 to 11. Because there were no significant effects of site on color, snout-vent-length, or number of females (Table 1), we combined data from the two sites for all further tests.

Orange males had a significantly greater number of females within their territories than did blue males (F = 4.90, df = 1, 11, P = 0.05, Fig. 1). Snout-vent length (SVL) was also positively related to the number of females (r^2 = 0.26, df = 1, 11, P = 0.08, Fig. 2), and greater male SVL was related to orange coloration in males (F = 3.61, df = 1, 11, P = 0.08, Fig. 3).

To determine the effect of male color alone on number of females in a territory, we first removed the effect of SVL on number of females by taking the residuals of a linear regression between SVL and number of females (r^2 = 0.26, df = 12, P = 0.08). Using these residuals, we then performed a one-way ANOVA between male color and number of females which showed that male color alone had no effect on number of females in a territory (F = 1.60, df = 1, 11, P = 0.23). Similarly, to determine the effect of male SVL alone on number of females, we removed the effect of color by subtracting the mean number females for each male color group (orange vs. blue) from each observation, and analyzed the residuals with a one-way ANOVA. The relationship between SVL alone and number of females was not significant (F = 0.90, df = 1, 11, P = 0.36).

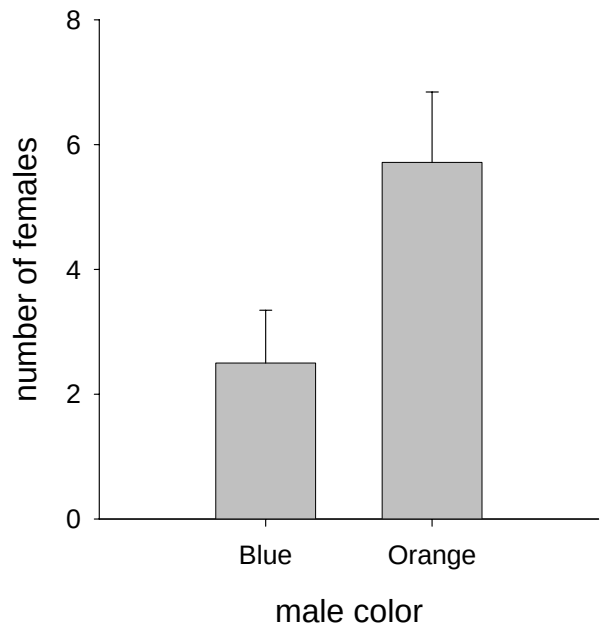

Figure 1. Mean number of females present in territories of ctenosaur males of predominately orange or blue coloration. Error bars show mean ± 1 SE (n = 7 blue males, 6 orange males).

Finally, we tested for correlations between head-bobs per minute and each of the following variables: number of females, color, SVL, and ambient temperature. None of these relationships was significant (Table 2).

Table 1. Relationship between number of females, snout-vent length, and color of male *Ctenosaura similis* at the OTS station and hacienda sites Palo Verde

Variable	Test	F or X^2	df	P
Number of females	One-way ANOVA	2.96	1, 11	0.11
SVL	One-way ANOVA	0.82	1, 11	0.39
Color	Contingency analysis	0.07	1, 11	0.80

Figure 2. Relationship between male ctenosaur snout-vent length and the number females in their territories (n = 13).

DISCUSSION

Our results indicate that both color and size are important determinants of the number of females in a male's territory, but because these two characteristics were related we were unable to determine which of these factors was more important in predicting the number of females per territory. Instead, our results suggest that while neither color nor size alone significantly influences number of females, the combination of these characteristics allows large orange males to have greater reproductive access than small blue individuals. Clarification of the independent relationships between size and color and number of females in a male's territory will require larger sample sizes and a sampling design focused on separating the effects of color and size.

Neither male size nor color was related to head-bobbing in male ctenosaurs. We observed that most head-bobs were performed without another male present and were done directly following movement, but we did not statistically analyze these patterns. We suggest that head-bobbing may be more of an advertisement of territorial boundaries to conspecifics of either sex than a direct interaction between males.

If large males do have territories with more females than small males, this would be consistent with previous findings (Tran and Harris 2004). Larger males can secure higher quality territories, which may attract more females than those of smaller individuals (Vanderbuilt 1990). Orange coloration of mature male ctenosaurs may be an advertisement of both individual and territory quality, since this conspicuous coloration appears only dur-

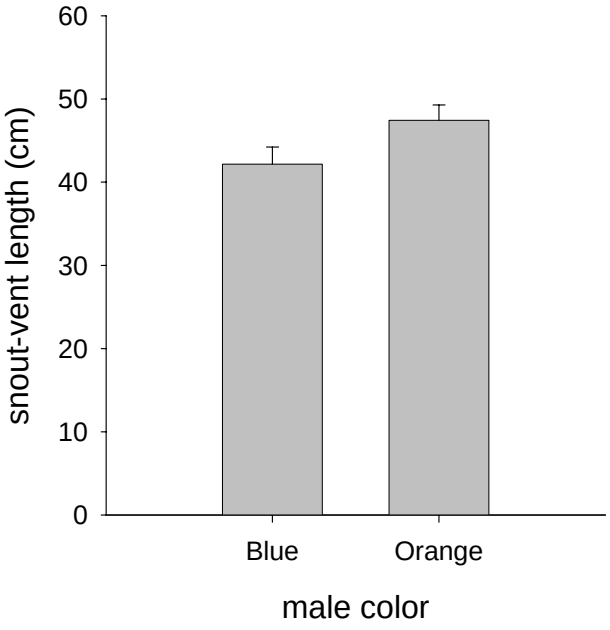

Figure 3. Mean snout-vent length of ctenosaur males with predominately orange vs blue coloration. Error bars show mean ± 1 SE (n = 7 blue males, 6 orange males).

Table 2. Relationships between number of male head-bobs/min and attributes of the male *Ctenosaura similis* and their territories at Palo Verde

Variable	Test	F	r^2	df	P
Number of females	Linear regression	-	0.00	12	0.88
SVL	Linear regression	-	0.04	12	0.50
Color	One-way ANOVA	3.21	-	1, 11	0.10
Temperature	Quadratic regression	-	0.12	12	0.53

ing the breeding season (Fitch and Hackforth-Jones 1983) and may be costly if orange lizards are more visible to predators, or it is energetically expensive to produce orange color.

LITERATURE CITED

Fitch, H. S. and J. Hackforth-Jones. 1983. *Ctenosaurus similis* in Costa Rican Natural History. Ed. D. H. Janzen. University of Chicago Press: Chicago, IL, p. 394-396.

Savage, J. M. 2002. The Amphibians and Reptiles of Costa Rica. University of Chicago Press: Chicago, IL.

Tran, J. Khai and Jill L. Harris. 2004. Factors influencing the outcome of behavioral encounters in *Ctenosaura similis*. Dartmouth Studies in Tropical Ecology, p. 24-26.

Vanderbuilt, C. , J. R. Nuttle, G. Mora, J. Heinen, K. Stoner and D. Wijesinghe. 1990. Territorial and courtship behaviors in Ctenosaura. OTS Tropical Ecology, 90: 136-139.

AGGRESSIVE BEHAVIOR IN THE BUTTERFLY *ANARTIA JATROPHAE*

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TIMOTHY R. MATSUURA AND CHAD M. VALDERRAMA

Abstract: Territoriality has been observed in many butterfly species, but the resources being defended are often unclear. We observed aggressive interactions of the nymphalid butterfly, *Anartia jatrophae,* to assess its territorial behavior. We marked individuals, released them into a well-defined patch of flowers, and recorded interactions in the patch. *A. jatrophae* individuals interacted aggressively with conspecifics and other organisms. Each individual's aggressive interactions were concentrated within specific areas of the habitat. Apparent mating behavior and lack of foraging point to reproductive resources (females) as the basis for *A. jatrophae* aggressive behavior and territoriality.

Key Words: resource defense, territoriality

INTRODUCTION

Male defense of territories is common in butterflies (Cordero 1996). Territoriality has been studied extensively in temperate species, especially those in the family Nymphalidae (Cordero 1996), and in various tropical taxa (Freitas et al. 1995). The reasons for territoriality in butterflies are not well understood because defensive behavior may occur in regions without apparent nutritional resources. Instead, enhanced mating success has been proposed as the most common benefit of butterfly territoriality (Freitas et al. 1995, Cordero 1996).

We observed and recorded aggressive behavior of individually-marked *Anartia jatrophae* (Lepidoptera: Nymphalidae) individuals within a patch of *Justicia comata* (Acanthaceae) flowers near the OTS field station at Palo Verde National Park, Costa Rica. We hypothesized that aggressive interactions of *A. jatrophae* individuals would be localized spatially, defining recognizable territories. We also investigated whether interactions were associated with foraging, mating behavior, or both.

METHODS

On 13 January 2005, we netted all *A. jatrophae* in a 10 m x 15 m area with abundant *J. comata* plants in secondary forest bordering the marsh, ca. 1 km east of the field station. The area, bounded naturally on three sides by trees, shrubs, and a dirt trail, was divided into four equal triangular quadrants of 37.5 m^2 each, using string. The 27 butterflies captured within the patch were given unique color markings using permanent markers, and released back into the patch at 1030. We were unable to distinguish between the sexes. We observed butterflies within the patch from 1030 - 1130 and 1445 - 1515 for a total of 2.5 h. For each butterfly interaction, we recorded the type of interaction (aggressive

a.

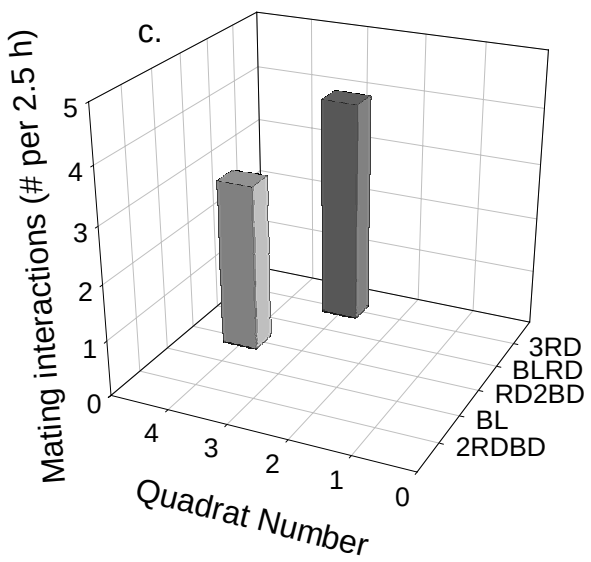

Figure 1. Number of a) aggressive interactions with conspecifics, b) aggressive interactions with other butterfly species, and c) mating interactions by marked *A. jatrophae* by quadrat number within a patch of *J. comata* flowers in Palo Verde National Park, Costa Rica. Individuals were given unique color marks, e.g. 3RD refers to 3 red dots, BLRD refers to blue line and red dot, etc. Data shown are for the five individuals that consistently remained within the patch and which had the most interactions.

or apparent mating behavior), the aggressor butterfly, the aggressed butterfly, the perceived victor, and quadrant number in which the interaction occurred.

We used a contingency analysis to compare the frequencies of aggressive interactions between quadrants for *A. jatrophae* individuals.

RESULTS

Most marked individuals immediately left the plot or were only seen infrequently. Five marked individuals remained consistently, however, and we quantified aggressive behavior in these individuals. These *A. jatrophae* interacted aggressively with conspecifics, as well as with other species of butterflies, moths, bees, and hummingbirds. Each individual's aggressive interactions were concentrated in certain quadrants ($X^2 = 84.95$, df = 12, $P < 0.0001$; Fig. 1a, b), and only the two individuals with the most intraspecific aggressions engaged in mating interactions

(Fig. 1c). Quadrants 2 and 3 were each dominated by one individual throughout our observations. Quadrant 4 was dominated by individual RD2BD (marking of red dot, 2 blue dots) until this individual was killed by an arachnid; after that, BL (marking of blue line) dominated this quadrant. Quadrant 1 was not dominated by any one individual.

DISCUSSION

Each *A. jatrophae's* aggressive interactions were concentrated in specific quadrants, suggesting territoriality in these butterflies. We did not observe any *A. jatrophae* feeding on *J. comata* during our study, though *J. comata* is a known food resource (DeVries 1987). Thus, flower resources did not appear to be the basis for the territoriality that we observed in this study.

We observed two types of interactions between *A. jatrophae*. Butterflies either rapidly circled in the air, violently batting their wings, or one butterfly slowly approached the other from behind, with both fluttering together, sometimes landing together. These two types of interactions were very distinct. We assume that they represent aggression and mating behavior, respectively (Freitas et al. 1995, Cordero 1996). The seven mating-type interactions observed always involved one of our marked individuals and an unmarked one. Thus, we assume the territorial individuals were all male. Since we witnessed several mating-type interactions but no foraging, we suggest that *A. jatrophae* defended areas primarily for mating purposes.

The capture and marking may have caused confusion and stress to the butterflies resulting in most of the marked individuals leaving the plots. Each released individual that stayed in the plot established dominance and defended one primary quadrant during our 2.5 h observational period. It is unknown for how long *A. jatrophae* defend territories. We suggest that it would be useful to follow individuals for longer time periods to measure the ephemeral nature of territories as well as to determine where and when they forage.

LITERATURE CITED

Cordero, C. The number of copulations of territorial males of the butterfly *Callophrys xami* (Lycaenidae). Journal of Research on the Lepidoptera, 35: 78-89.

DeVries, Philip. J. 1987. The butterflies of Costa Rica and their natural history. Princeton University Press: Princeton, New Jersey.

Freitas, André V. L., W. W. Benson, O. J. Marino-Filho, and R. M. De Carvalho. 1995. Territoriality by the dawn's early light: The Neotropical owl butterfly *Caligo idomenaeus* (Nymphalidae; Brassolinae). Journal of Research on the Lepidoptera, 34: 14-20.

Kemp, D. J. and R. L. Rutowski. Spatial and temporal patterns of territorial mate locating behavior in *Hypolimnas bolina* (Lepidoptera: Nymphalidae). Journal of Natural History, 35: 1399-1411.

DO RARE SPECIES OF FLOWER RECEIVE MORE POLLINATOR VISITS IN THE PRESENCE OF A COMMON FLOWER SPECIES?

GABRIEL H. CALVI

Abstract: Pollination facilitation occurs if pollination success of one plant increases as number of neighboring flowers, regardless of species, increases. In eight flower patches at Palo Verde National Park, I recorded the number of visits to flowers before and after removal of the dominant species, *Justicia comata*. I hypothesized that *J. comata* facilitates the pollination of locally rare flower species. I found the rare flowers did experience more visits in the presence of *J. comata.* The percent of insects that stopped at a patch increased with flower density and with increased percentage of *J. comata*. Flower visits to *J. comata* increased proportionately with the percentage of *J. comata* in study plots.

Key Words: Justicia comata, *pollination, pollinator facilitation*

INTRODUCTION

Facilitation occurs when one species of flower benefits from the presence of other species. Increasing densities of flowers, regardless of species, may help attract pollinators, which may benefit all flowers in a patch (Feinsinger 1991). I therefore hypothesized that rare flowers would be visited by more pollinators when they are surrounded by more abundant flowers of another species.

I studied this in the open habitats along the air strip and road of Palo Verde National Park, Costa Rica. *Justicia comata* (a low-growing shrub, with a small, purple, insect pollinated flower) is the dominant flower species in this area. Flower patches varied in size, species composition, and flower density but most patches contained relatively high abundance of *J. comata*.

METHODS

On 13 January 2005, I chose eight plots in the fields along the roadside and air strip within 1 km of the OTS field station at Palo Verde National Park. The 4 m^2 plots contained various densities of flowers, but *J. comata* was the dominant flowering species in each. Species composition and abundances were recorded for each plot. During a 10-min observation period, I counted the number of flowers of each species visited by pollinators. I also recorded the number of insects that flew over the patch so I could calculate the percent of insects that stopped at flowers in the patch. I then removed the *J. comata* blossoms and conducted another similar 10-min observation within 20 min of the flower removal.

I used a matched pair analysis to compare the number of visits to flowers before and after removal of *J. comata.* I conducted a regression analysis comparing the percent of insects stopping at a patch num-

ber of insects stopping/number of insects flying over x 100) to both the total number of flowers in the patch and the percent of the *J. comata* flowers in the patch.

To remove any effect of total number of flowers on pollinator visits, I calculated the residuals from the regression of percent visits to *J. comata* on total number of flowers in the patch. I regressed the residuals on the percent *J. comata* in the patch. All statistics were calculated using JMP 5.0.1.

RESULTS

The mean number of non- *J. comata* flowers visited by pollinators dropped from 8.0 ± 8.6 visits before the removal of *J. comata* to 1.43 ± 2.3 visits after removal. This change was marginally significant (t = -2.07, df = 7, P = 0.08). As flower density increased, the percent of insects that stopped at a patch also increased (r^2 = 0.18, df = 15, P = 0.09; Fig. 1). As the percent of *J. comata* in the patch increased, the percent of insects that stopped significantly increased (r^2 = 0.53, df = 15, P = 0.0009; Fig. 2). Individual pollinators often visited more than one flower species in the plot. The percent of pollinator visits to *J. comata* increased directly with the percent of *J. comata* in the patch (r^2 = 0.62, m = 0.78, P = 0.002; Fig. 3). The slope of this line was not significantly different from the theoretical slope of one (95% confidence interval for slope = -0.004 to 1.56).

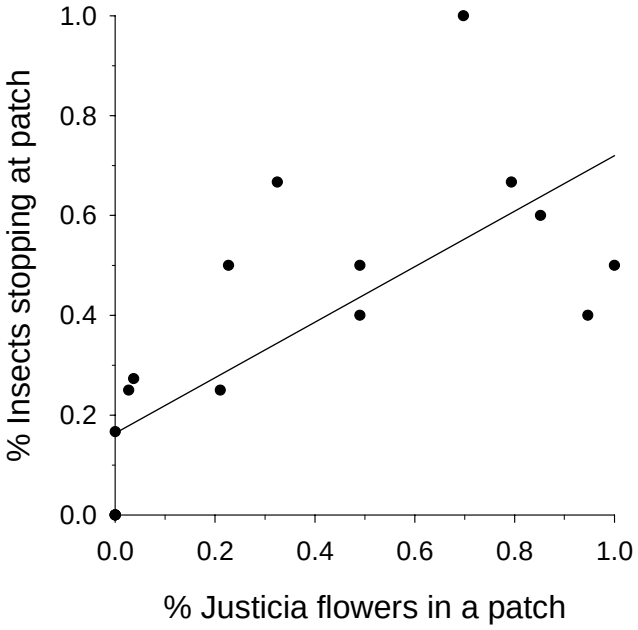

Figure 2. Percent of insects flying over a patch that stopped vs percent *Justicia comata* flowers in the patch. As flower density increased the percent of insects that stopped at a patch also increased.

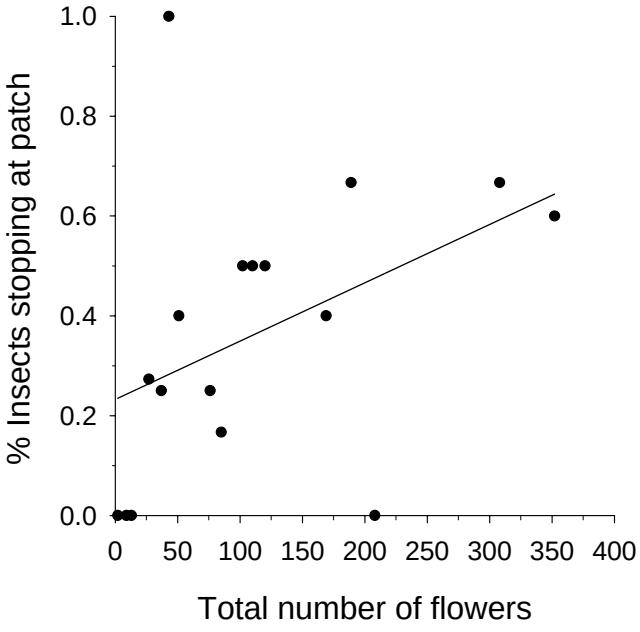

Figure 1. Percent of insects flying over a patch of flowers dominated by *Justicia comata*, that stopped vs total number of flowers in a patch. Patches were observed in open habitats at Palo Verde, Costa Rica.

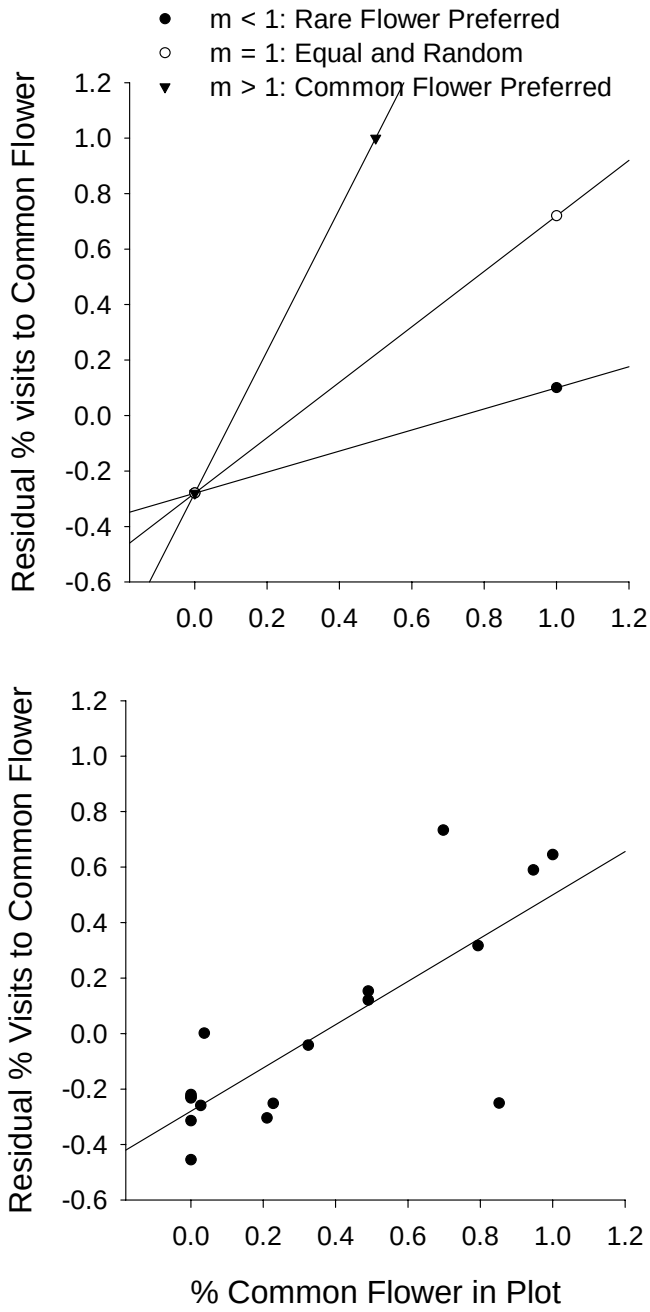

Figure 3. Percent of total visits by *Justicia comata* with the effect of number of flowers removed. Top panel presents three theoretical results. A slope of 1 indicates a random selection of flowers by pollinator. Slope > 1 would indicate disproportionate selection of *J. comata*. Slope < 1 would indicate unequal selection of a rare flower species. Bottom panel shows the experimental slope of 0.78 derived from field data in this study. This slope was not significantly different from 1 (see text).

DISCUSSION

A patch with many flowers, regardless of species, attracted more pollinators than a patch with few flowers. Additionally, the percentage of insects that stopped at a patch greatly increased as the percentage of *J. comata* flowers increased. It seemed that pollinators cued in on high *J. comata* densities and visited patches with the most *J. comata* flowers. Once a pollinator decided to stop at a particular patch it would not visit just one flower species, but would visit many different flower species. Locally rare flowers might then receive more pollination visits in a patch of one dominant species than it would in a patch with similar density but with greater species diversity. These findings suggest that *J. comata* could facilitate the pollination success of other less common species by increasing the number of pollinator visits received by these less common flowers.

LITERATURE CITED

Feinsinger, P. and H. M. Tiebout III. 1991. Do tropical bird-pollinated plants exhibit density-dependent interactions? Field experiments. Ecology, 72: 1953-1963.

EXPERIMENTAL ASSESSMENT OF THE BENEFITS TO THE ALGA *ANABAENA AZOLLAE* IN ITS SYMBIOSIS WITH THE FERN *AZOLLA MICROPHYLLA*

CAYELAN C. CAREY AND EMILY L. SHARP

Abstract : The alga *Anabaena azollae* and the fern *Azolla microphylla* are symbionts, with *A. azollae* receiving nutritional benefits. To identify additional benefits to the alga, we compared algal abundance under three experimentally-altered conditions: herbivore density, water temperature and prolonged *A. microphylla* submersion. *A. azollae* in the submerged treatment declined in abundance, indicating that *A. azollae* may receive a benefit from the *A. azollae- A. microphylla* symbiosis that is compromised by *A. microphylla* submersion.

Key Words: environmental stressors

INTRODUCTION

Anabaena azollae, a nitrogen-fixing cyanobacterium, is symbiotic with the water fern *Azolla microphylla*. *A. azollae* lives on the top surface of floating *A. microphylla* leaves. *A. azollae* is not motile, but can, by expending energy, control its buoyancy in the water column. In the symbiosis, *A. microphylla* receives nitrogen and *A. azollae* receives photosynthetic assimilates (Dawar and Singh 2003). Little else is known about benefits to the alga.

A. microphylla and *A. azollae* are capable of existing independently, but are usually found in symbiosis. High phosphorus addition causes *A. azollae* to leave *A. microphylla* (Dawar and Singh 2003).

To determine if environmental stressors other than nutrient limitation could disrupt the *A. azollae-A. microphylla* symbiosis, we designed three treatments simulating commonly-occurring variations in the environment of symbiotic *A. azollae*: increased herbivore density, increased water temperature, and prolonged *A. microphylla* submersion in the water column. We predicted that these treatments would disrupt the symbiosis and cause *A. azollae* to separate from *A. microphylla*, suggesting that *A. azollae* receives other benefits from *A. microphylla* that were compromised by the changed environmental conditions.

METHODS

Our experiments were conducted in the Rio Tempisque marshland at Palo Verde National Park, Costa Rica on 13 and 14 January 2005. The marsh floods annually during May - October and dries up when the Rio Tempisque recedes in February - April. We constructed opaque water columns 30 cm tall that contained 1 L of marsh water collected under patches of *A. microphylla*. Our columns were held in a large plastic container placed in the marsh, to prevent any disturbance from wind or waves. Each column contained ten *A. microphylla* plants from the same patch. Col-

umns were placed at 0800 and removed at 1400, when *A. azollae* abundance on *A. microphylla* was measured.

In our first experiment, we examined the effects of herbivory by creating two levels of herbivore densities with four replicates of each. The low density treatment had no herbivores, while the high density treatment had 5x the average natural herbivore density per volume of marsh water.

In our second experiment, we examined the effect of increased water temperature, as may occur late in the dry season as the water level drops. As a control, four 30 cm water columns were placed in a large plastic container in the marsh. By placing the columns in a large container of water in the marsh, the column temperatures were maintained at the marsh temperature of 28.9 °C at 1200. Four smaller 10 cm columns were placed in open air for the high temperature treatment. They reached 34.5 °C at 1200.

For our third experiment, we simulated prolonged submersion of *A. microphylla*, which commonly occurs due to wind and waves. We used four 30 cm water columns with a 0.4 cm mesh exclusion that restricted *A. microphylla* to the bottom third of the water column, but allowed uninhibited *A. azollae* vertical migration. For a control, we used four 30 cm water columns, without a mesh exclusion, that allowed *A. microphylla* to remain at the surface.

We quantified *A. azollae* abundance on *A. microphylla* by haphazardly removing five plants from each column and scraping *A. azollae* off two haphazardly-chosen leaves from each plant. We counted the number of *A. azollae* colonies on each leaf using 50x light microscopy. We used a one-way ANOVA on JMP 5.0.1 to analyze the differences between treatments in the herbivore density, water temperature and submersion experiments. A two-way nested crossed ANOVA examined the effects of time, treatment and interactions in the submersion experiment.

RESULTS

There was no significant difference in algal colonial abundance between reduced and increased herbivory treatments ($F = 0.08$, $df = 1, 78$, $P = 0.78$) nor between 29.7 °C and 33.3 °C water patches at 1400 ($F = 0.13$, $df = 1, 78$, $P = 0.72$). In the sub-

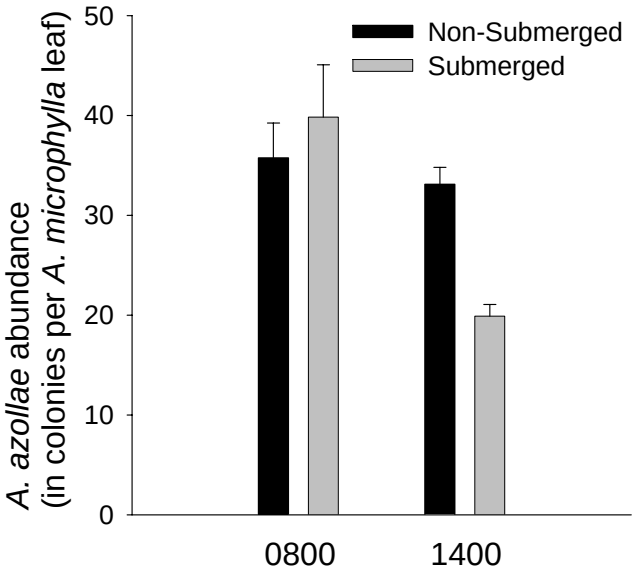

Figure 1. Decline of *Anabaena azollae* colony abundance on *Azolla microphylla* after *A. microphylla* submersion in the Rio Tempisque marsh, Palo Verde. *A. microphylla* was submerged for 6 hours in four 30 cm columns.

mersion experiment, we found a significant interaction in a model of time, treatment, and time x treatment interaction, with plant as a non-random effect ($F = 13.26$, $df = 1$, $P = 0.002$; Fig. 1). *A. azollae* colony abundance decreased with time ($F = 22.64$, $df = 1$, $P = 0.0003$), while treatment, and plant as a non-random effect, were both insignificant ($F < 1.99$, $df = 1$, $P > 0.11$). In the submerged treatment, mean algal abundance decreased from 40 to 20 colonies per leaf between 0800 and 1400 ($F = 22.10$, $df = 1, 14$, $P = 0.0003$). Algal abundance in the non-submerged treatment did not significantly change from 0800 to 1400 ($F = 0.60$, $df = 1, 12$, $P = 0.45$).

DISCUSSION

Our hypothesis that altering environmental conditions could cause *A. azollae* to leave its *A. microphylla* host was confirmed. Cyanobacteria are not preferred food particles for copepods, the primary herbivores found in the marsh, thus it is not surprising that changing herbivore density had little effect on *A. azollae*. The minimal temperature interval (3.6 °C) between treatments at 1400 may explain the lack of a significant temperature effect. It remains possible that *A. azollae* could leave *A. microphylla* if temperature rises higher than 34.5 °C.

The lower algal abundance on submerged *A. microphylla* may be due to reduced *A. azollae* photosynthesis at depth, due to light attenuation. This would imply a benefit to *A. azollae* using *A. microphylla* as a substrate. Submerged *A. azollae* could face a tradeoff between the nutritional benefits from *A. microphylla* symbiosis and the necessity for photosynthesis.

We assume that decreased *A. azollae* abundance on *A. microphylla* was due to *A. azollae* actively separating from *A. microphylla*. It was possibly due to the death of *A. azollae*; however, we do not think this is likely and were unable to examine the water columns for dead algal cells. If *A. azollae* died, they would probably remain on top of the *A. microphylla* leaves while submerged, because they are negatively buoyant (Karlsson-Elfgren and Brunberg 2004).

LITERATURE CITED

Dawar, S. and P. K. Singh. 2003. Disappearance of the symbiont *Anabaena azollae* in *Azolla* subjected to high phosphorus. International Rice Research Notes, 28 (1): 53-54.

Karlsson-Elfgren, I. and A. Brunberg. 2004. The importance of shallow sediments in the recruitment of Anabaena and Aphanizomenon (Cyanophyceae). Journal of Phycology, 40: 831-836.

FATE OF *ACACIA COLLINSII* SEEDS

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Abstract: The fate of *Acacia collinsii* (Fabaceae) seeds, in terms of dispersal and predation, is not well known. We hypothesized that many seeds would be dispersed from the ground because vertebrate dispersers might be deterred by mutualistic ants defending fruits on the tree. Our observations and measurements at a pasture site near Palo Verde suggested that 10-20% of the ripe fruit fell to the ground per day. We found *A. collinsii* seeds in feces of deer and observed consumption by ants (in the field) and two species of captured mice (in the lab). Some entire seeds were also removed by army ants.

Key Words: dispersers, seed predation

INTRODUCTION

Acacia collinsii is a small tree with yellow brush flowers and legume fruits that open on the plant to reveal seeds surrounded by a sweet yellow pulp. *A. collinsii* is a mutualist with several species of ants. The tree provides the ants with shelter and nutrition in exchange for protection from herbivores and competing vegetation (Brown 1960, Janzen 1966). Acacia ants reduce aggressive behavior around flowers, which may enhance pollination (Baptista 1998). However, because the ants do not reduce aggressive behavior near fruits, dispersal may be diminished (Carey et al. 2005).

Our goal was to determine the fate of *A. collinsii* seeds. We hypothesized that many of the seeds would fall to the ground and be dispersed from there because vertebrate dispersers would be deterred from the trees by the defensive behavior of the mutualistic ants.

METHODS

We spent > 13 h at a pasture study area containing abundant *A. collinsii* trees, ca. 6 km SE of the OTS Palo Verde field station (within 100 m of the Dartmouth long-term *A. collinsii* study plot) on 13 and 14 January 2005. On the first day, we selected 11 *A. collinsii* trees and counted the numbers of yellow fruits on the ground, and those remaining in the tree. Ten fruits from each tree were randomly taken to determine the average number of seeds per fruit. We removed all fruits from under four of the trees so we could know on the second day how many had fallen during the night. Sheets were set up under one of the trees to catch fruits that fell and keep them off the ground away from animals. However during the night, the sheets were ripped off at the corners and carried away by an unknown animal.

On the second day we counted fruits under all of the trees again, to determine the change in fruits under each tree. We observed animal activity, including

birds and bats, between 0500 and 1130 noted animal signs.

At the field station, during the nights of 13 and 14 January, we baited Sherman traps with the fruits and peanut butter. We placed the captured rodents in containers with *A. collinsii* fruits. We also left ~30 fruits under *A. collinsii* surrounded by fluorescent tracking powder.

RESULTS

Fruits contained an average of 8.8 seeds (SD = 1.8). For the four trees for which we removed all the fruit underneath, 10-20% of the ripe fruit on the trees fell to the ground in a 12 h period (Table 1). From this we infer that a large portion of the overall seed production reaches the ground.

There was evidence of ground foraging on *A. collinsii* fruits under at least two trees (Table 1). We also observed 15 *A. collinsii* seeds carried intact by army ants for at least 5 m (although some army ants struggling under a load of two connected seeds dropped one or both). Other (smaller) ant species divided the seeds into small pieces. Ants ate most of the fruits and seeds we left in rodent traps or surrounded by UV powder, in some cases consuming a pile of over 30 fruits overnight. There was one trail of UV tracking powder, presumably by a rodent, based on size and nocturnal activity. Both mice we caught (a spiny forest pocket mouse and a house mouse) ate the fruits we provided within minutes, including seeds. We found two piles of deer excrement near the *A. collinsii* trees, containing an estimated 50-100 *A. collinsii* seeds each.

DISCUSSION

A. collinsii is a light-demanding tree (Janzen 1966) which presumably requires seed dispersal to reach colonizable sites. Based on our observations, we propose that most seed dispersal occurs after seed fall, because then dispersers do not have to contend with mutualistic ant defenders. Deer, and possibly other large mammals, may disperse the seeds long distances in their feces. Deer tend to feed in open areas which are suitable for *A. collinsii* colonization. A local guide claimed to have witnessed white-faced capuchin and howler monkeys taking fruits directly from the tree. Small and numerous seeds, like those of *A. collinsii*, may escape mastication and

Table 1. Number of ripe fruits under and on trees. Changes from first to second day. Fruits left under tree is the number left after we removed some to count seeds and removed all fruits from under trees 8-11.

Day	Tree number	1	2	3	4	5	6	7	8	9	10	11
1	Fruits on tree	43	180	55	109	56	41	108	81	72	30	46
1	Fruits under tree	39	25	17	40	24	8	30	28	30	14	19
1	Fruits left under tree	39	20	12	35	19	3	25	0	0	0	0
2	Fruits under tree on 2nd day	91	42	12	98	32	0	14	9	16	4	7
1 - 2	Net change under tree	52	22	0	63	13	-3	-11	9	16	4	7

pass through vertebrate guts unharmed (Janzen 1983).

We observed no bird or bat seed dispersal during our short observation periods to support the contention that birds and bats are the main seed dispersers (Janzen 1983).

Seed-fall makes seeds available not only to dispersers, but also to predators, including ants and mice. Both of which are capable of eating a large quantity of the seeds that fell to the ground. Army ants might be dispersers as well as predators since they remove seeds and may not always consume them.

Literature Cited

Baptista, A. I., et al. 1998. Avoiding ant-pollinator conflict on *Acacia collinsii.* Dartmouth Studies in Tropical Ecology, p. 1-3.

Brown, W. L. 1960. Ants, acacias and browsing mammals. Ecology, 41: 587-592.

Carey, C. C., E. C. Chow, J. E. Jun, D. J. Madigan and E. L. Sharp. 2005. Fruit and leaf patrolling by *Pseudomyrmex spinicola* in response to disturbance of *Acacia collinsii*. Dartmouth Studies in Tropical Ecology.

Janzen, D. H. 1966. Coevolution of mutualism between ants and acacias in Central America. Evolution, 20: 249-275.

Janzen, D. H. 1983. *Jacquinia pungens* in Costa Rican Natural History. University of Chicago Press: Chicago. p. 265.

Janzen, D. H. 1983. *Pseudomyrmex ferruginea* in Costa Rican Natural History. University of Chicago Press: Chicago. p. 764.

Addendum

We planted eight of the Acacia seeds found in the deer feces 5 – 20 mm deep in soil from La Selva Biological Station. Six of the seeds had sprouted and opened their first set of leaves within ten days, thus showing that acacia seeds are still viable after passing through the gut of a deer.

DIURNAL ZOOPLANKTON DIVERSITY AND SPECIES COMPOSITION UNDER FOUR DOMINANT AQUATIC VEGETATION TYPES IN THE PALO VERDE MARSH

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Abstract: Because greater physical complexity of sub-surface habitat provides greater protection from visual planktivores, zooplankton diversity and abundance should increase with increasing complexity. We sampled zooplankton in four habitat types in the Río Tempisque marsh at Palo Verde National Park, Costa Rica, and found marginally significant differences in diversity between them, with highest diversity in the highest complexity habitat type and lowest diversity in the lowest complexity type. We also found patterns in copepod and cladoceran abundance which contradict predictions based on diel migration patterns in the temperate zone.

Key Words: cladocerans, copepods, diversity, Eichhornia crassipes, Typhus latifolia

INTRODUCTION

Predation, refuges and availability of resources may influence the spatial distribution of zooplankton in freshwater systems. Because zooplankton have visual predators, sub-surface structure of aquatic plants enhances refuge during daylight, with structure of higher complexity providing greater protection (Pennak 1978).

Thus, we hypothesized that zooplankton diversity, in patches of dominant aquatic plants in the Palo Verde marsh, would increase with the complexity of plant sub-surface structure. Specifically, we predicted that zooplankton diversity would be highest under water hyacinth, which has a relatively complex floating root system, lower under mixed-species vegetation (containing cattail, water hyacinth and other species), lower still under cattail stands, and least in open water. We also sought to compare our results with previous work in the Palo Verde marsh to elucidate effects of the decline of native plant assemblages on zooplankton populations.

METHODS

On 13 January 2005, we took three zooplankton samples under each of the four vegetation types in the Río Tempisque marsh at Palo Verde National Park, Costa Rica. Four types of floating and emergent vegetation were defined as (1) water hyacinth (*Eichhornia crassipes*), (2) cattail (*Typhus latifolia*), (3) mixed vegetation (cattail, water hyacinth, *Mimosa dormiens, Neptunia* spp., *Thalia geniculata, Heteranthera spicata* and other species) and (4) open water without emergent or floating vegetation.

At each patch, a tube sampler was lowered into the water column to a few cm above the sediment. Both ends of the tube were then stoppered, the water within the tube was homogenized, and a portion of the sample was poured into a container for later analysis. Depth at each sampling site

was recorded. We made qualitative assessments of the relative complexity of sub-surface vegetation structure for each vegetation type, by examining root and stem structures in the sampled areas of the marsh.

We preserved samples in isopropyl alcohol and counted and identified all zooplankton in a 15% subsample by volume, for each of the 12 samples. Cladocerans were classified by morphotype. Copepods were recorded as adult or nauplii stages or as parasitic morphotypes. No distinction was made among ostracod types. Rotifers were noted as present, but not counted. Diversity was calculated with a Shannon-Weiner diversity index. Several one-way ANOVAs and a multiple comparisons post-hoc test were performed using JMP 4.0.0.

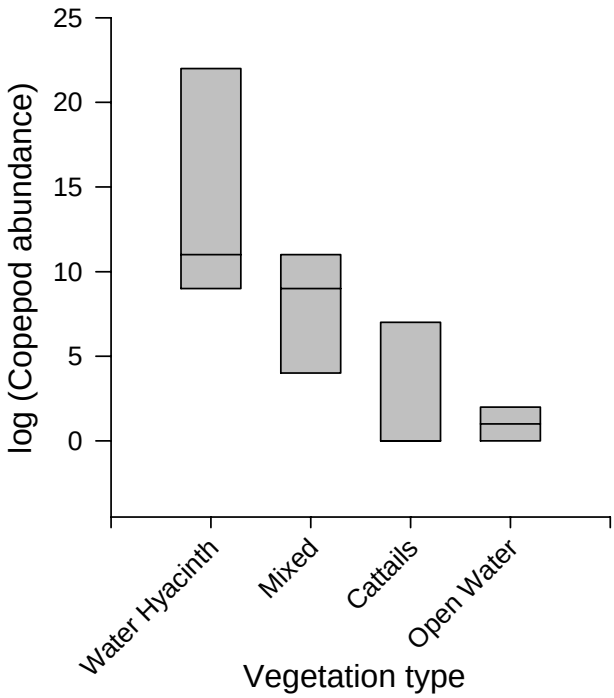

Figure 1. Zooplankton diversity assessed by counting morphotypes in three samples taken under each of four aquatic vegetation types in the Palo Verde marsh. Vegetation types on the x-axis are in order of decreasing sub-surface structural complexity. Diversity was quantified by the Shannon-Weiner index. Data were normalized by logarithmic transformation.

RESULTS

There was a marginally significant difference in log-transformed zooplankton diversity among the four vegetation types, with more complex vegetation supporting more diverse zooplankton assemblages ($F = 3.30$, $df = 3, 8$, $P = 0.08$; Fig. 1). Log-transformed abundance of total cladocerans did not differ among vegetation types ($F = 2.05$, $df = 3, 8$, $P = 0.19$), but log-transformed total copepod abundance was significantly greater in the water hyacinth patch than in the cattail and open water patches ($F = 7.52$, $df = 3, 8$, $P = 0.01$; Tukey HSD post-hoc, $\alpha = 0.05$; Fig. 2).

DISCUSSION

Though there was no significant difference in diversity among vegetation types for our limited sample, trends in the data were consistent with our predictions. Poulin et al. (1998) found greater zooplankton abundances in patches of chorizo (*Neptunia plena*) than in patches of water hyacinth, and identified chorizo as possessing a more complex floating root structure. Since 1998, invasive water hyacinth has replaced so much of the chorizo in the marsh that chorizo was not available to be tested in this study. Thus, the overall complexity of sub-surface structure in the Palo Verde marsh may have decreased with the decline of native plant assemblages. This trend may have, in turn, reduced zoo-

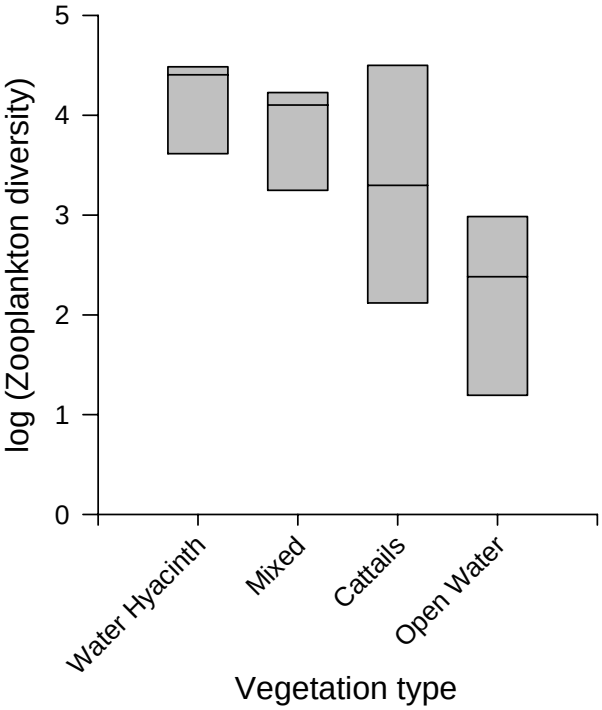

Figure 2. Copepod abundance assessed by counting individuals in three samples taken under each of four aquatic vegetation types in the Palo Verde marsh. Vegetation types on the x-axis are in order of decreasing sub-surface structural complexity. Data were normalized by logarithmic transformation.

plankton diversity or abundance in the marsh, by reducing refuge availability and increasing predation pressure.

In the temperate zone, cladocerans usually exhibit stronger diel migration than copepods because they are slower and more conspicuous, and hence experience stronger fish predation pressure (Pennak 1978). Because planktivorous fish occur in the Palo Verde marsh (Venegas 2002), we expected to observe the strongest effects of refuges on cladoceran abundance. Instead, we observed positive effects of structural complexity only on copepod abundance, in agreement with the observations of Poulin et al. (1998).

These results imply that some unstudied factor influences the distribution of zooplankton in the Palo Verde marsh. Copepods may be the more preferred or more easily-obtained prey in this system. Resource availability may have a greater influence on the diurnal distribution of zooplankton than predation pressure, or divergence in resource use between cladocerans and copepods may drive differences in their relative abundances in different microhabitats. Alternately, contrary to assumptions underlying our hypothesis, invertebrate predators of cladocerans may inhabit complex vegetative structures, displacing prey to less complex habitats.

Sampling for zooplankton in fish exclosures, or assessing the abundance of invertebrate predators of zooplankton among vegetation types, could reveal predation risks for copepods and cladocerans in this system. Measurement or manipulation of the distribution of phytoplankton, suspended detritus, and other important components of zooplankton diet, could shed light on the influence of food resources on zooplankton distribution.

LITERATURE CITED

Pennak, R.W. 1978. Fresh-water invertebrates of the United States: Second edition. John Wiley and Sons: New York.

Poulin, D. L., R. F. Douzinas, A. M. Eaken, J. R. Mooney and D.R. Rubenstein. 1998. Diurnal zooplankton distribution in relation to aquatic vegetation in a tropical marsh. Dartmouth Studies in Tropical Ecology, p. 11-13.

Venegas, M. M. 2002. Peces presentes en los humedales temporales del Parque Nacional Palo Verde, Guanacaste, Costa Rica. Escuela de Ciencias Biológicas, Universidad Nacional de Costa Rica: Costa Rica.

EFFECTS OF HABITAT STRUCTURE AND PREY AVAILABILITY ON ABUNDANCE OF THE LYNX SPIDER *PEUCETIA VIRIDENS*

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Abstract: To test the hypothesis that *P. viridens* abundance varies with habitat structure and insect abundance, we quantified habitat structure as well as numbers of insects and *P. viridens* caught with sweep nets. Spider abundance varied among habitats and increased with flower number. Neither habitat nor insect abundance in sweep net samples affected *P. viridens* abundance. *P. viridens* abundance may be driven more by pollinator abundance (which probably responds to flower number) than by the abundance of insects within the vegetation.

Key Words: oxyopidae

INTRODUCTION

Spider abundance may respond to physical habitat structure and prey abundance (Arango et al. 2000, Foelix 1996). Some spiders select habitats with greater prey abundance, though some do not (Foelix 1996). We hypothesized that abundance of *Peucetia viridans* (Oxyopidae), the green lynx spider, would increase with increasing prey abundance and would respond to differences in physical habitat structure. Because we focused on physical habitat structure and its effect on prey availability, we examined insects within the vegetation, rather than flying insects visiting the patch.

METHODS

We sampled four 1 m^2 plots in each of three habitat types at Palo Verde National Park in Costa Rica: areas dominated by *Justicia comata* (Acanthaceae), a mix of low grass and *J. comata*, and low grass only. *J. comata* was producing abundant flowers at the time of sampling. In each plot, we counted the number of flowers and visually estimated percentages of green and brown vegetative ground cover. To estimate mean plant height, we measured the height of three haphazardly selected plants in each plot. In *J. comata* plots, we counted the number of stems per plot. In mixed and low grass plots where this was not practical, we counted stems in three haphazardly placed quadrats of 222