DEFENSE ACTIVITY OF THREE ANT SPECIES ON *ACACIA COLLINSII* IN SUN AND SHADE

SARA M. HELLMUTH, PETER N. CHALMERS, MATTHEW T. KEMP,
HEATHER E. LAPIN AND PAUL A. MARINO

Abstract: Local abundances of three acacia-ant species, *Pseudomyrmex flavicornis, P. nigrocincta,* and *P. spinicola*, are differentially correlated with the light environment (shade vs. sun) of their host trees. We hypothesized that this is due to physiological differences among ant species in their metabolic responses to sunlight. However, we found no differences among species in how their defensive activity varies with sunlight. Alternative mechanisms to explain the observed distributional pattern include (1) differences among ant species in their metabolic response to air temperature and (2) interspecific competition among ants.

Key words: light gradient, myrmecophyte, Pseudomyrmex

INTRODUCTION

Acacia collinsii (Fabaceae) has a mutualistic relationship with ants in the genus *Pseudomyrmex*. The ants attack herbivores that disturb the host plant and they trim away neighboring competitive vegetation. The ants benefit from their association with the acacia tree by taking refuge in its thorns and consuming the plant's nectar and proteinaceous Beltian bodies (Janzen 1983).

Three species, *P. flavicornis*, *P. spinicola,* and *P. nigrocincta*, have been shown to vary in distribution between sun and shade habitats: *P. flavicornis* is more abundant in high-light environments; *P. nigrocincta* is found primarily on shaded trees; and *P. spinicola* is equally abundant in both light environments (Ermentrout et al. 2003). We hypothesized that this distributional pattern is the result of habitat selection to optimize metabolic activity. One indication of such optimized metabolic activity would be a heightened defensive response under light conditions in which they occur more abundantly. We predicted that defense activity, measured as the response to physical disturbance of the host plant, would be higher for *P. flavicornis* in high light environments than in the shade, whereas the response of *P. nigrocincta* would be higher in the shade than in the sun. We also predicted that *P. spinicola* would show an equal intensity of defensive response between habitats of sun and shade.

METHODS

This study was conducted in a dry tropical forest near the OTS Biological Station, Palo Verde National Park, Guanacaste, Costa Rica on 10 January 2004. For each of three ant species (*P. flavicornis, P. spinicola,* and *P. nigrocincta*) we sampled four trees that had a majority of their branches in the sun and four trees that had a majority of their branches in the shade. All study trees selected were 1 - 3 cm in trunk diameter and 2 - 3 m tall (an attempt to control for ant colony size).

On each tree, we selected the branch closest to 1.5 m from the ground and 1 m long to standardize the location of the disturbance among trees. Pre-disturbance ant activity was measured by counting the number of ants that crossed a line on the trunk level with this branch for 1 min. We then rapped sharply on the branch five times with a pen to simulate a disturbance, and counted ants crossing the same line during the next 1 min period.

We quantified defensive response to dis-

turbance as *DR* = [*post-dist* + 1]/[*pre-dist* + 1]), where *pre-dist* and *post-dist* = ant counts before and after disturbance, respectively. This metric standardized ant activity based upon pre-disturbance abundance of patrolling ants (adding 1 was to avoid division by zero). Differences in sun and shade response for each ant species were analyzed with a t-test. We also evaluated *DR* with a two-way ANOVA that included species, light environment, and species x light.

RESULTS

Both pre- and post-disturbance counts varied widely among trees (pre-disturbance range 0—119 ants/min; post-disturbance range 1—403 ants/min) (Fig. 1). Pre-disturbance ant activity was correlated with post-disturbance ant activity, and this correlation was not affected by light differences (Fig. 1). There were no differences in defensive response (*DR*) between sun and shade colonies of any ant species ($t < 1.02$, $df = 6$, $P > 0.34$; Fig. 2). ANOVA revealed no significant differences in defensive response among the three ant species ($F_{2,23} = 1.04$, $P = 0.37$) or between light environments ($F_{1,23} = 1.23$, $P = 0.28$; $F_{2,23} = 0.91$, $P = 0.42$ for species x light interaction).

DISCUSSION

Our results refuted the hypothesis that sunlight would have different effects on the defensive responses of three sympatric species of *Pseudomyrmex*. This suggests that the distribution patterns of ants, which are correlated with light gradients (Janzen 1983, Ermentrout et al. 2003), are not attributable to differences among species in their direct metabolic responses to sunlight.

Interspecific competition is an alternative hypothesis to explain the distributional patterns of *Pseudomyrmex* at Palo Verde. Beadell et al. (1996) showed that tree health is correlated to light availability. If *P. flavicornis* were competitively dominant over the other species in sunny environments, *P. flavicornis* may exclude other *Pseudomyrmex* species from the healthier (and

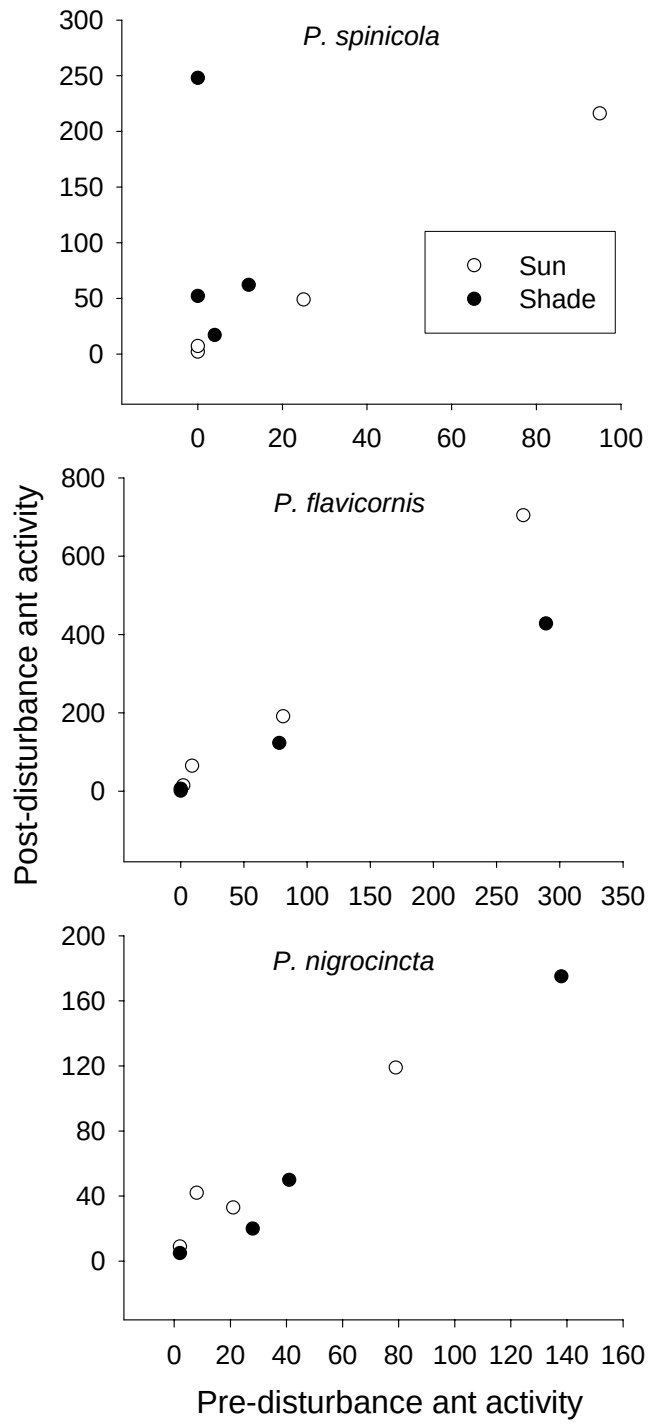

Figure 1. The relationship between pre-disturbance ant activity (number of ants) and post-disturbance ant activity (number of ants).

therefore presumably nectar-rich) sun trees. The other two species would then be forced into suboptimal (shadier) habitats. Under this hypothesis, *P. flavicornis* is predicted to win competitive interactions with the other two species.

Alternatively, temperature might explain the pattern in a way we have not examined. Ginsburg and Kaveeshwar (1995) found that *P. flavicornis* becomes more active and *P. spinicola* less active with increasing temperature. Because we took all of our measurements during one 3 h period in the morning, it is possible that the temperature difference between sun and shade was not great enough to elicit a difference in ant activity. It is possible that ant metabolic activity is influenced by temperature differences that are the result of the light environment, rather than light environment per se, which is how we defined our treatments. This could be tested with direct measurements of thoracic temperatures in ants as a function of air temperature and sunlight.

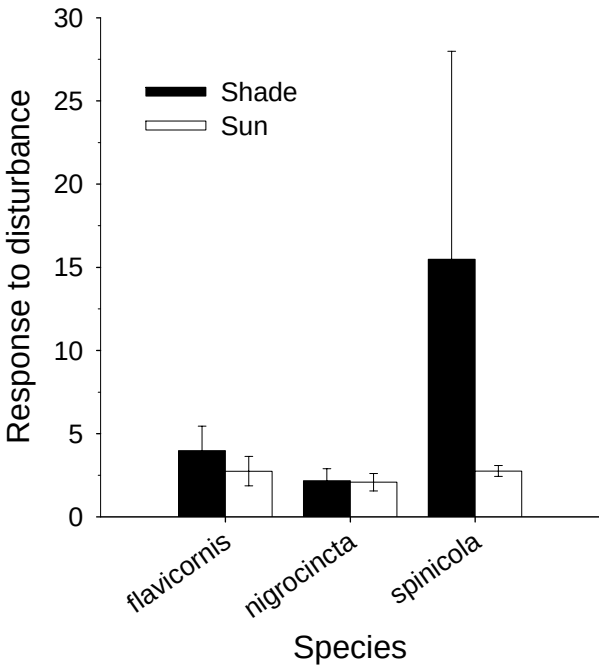

Figure 2. Response of three species of Pseudomyrmex ants to disturbance (mean ± SE) in two light environments on *Acacia collinsii* at Palo Verde, Costa Rica. N = 4 for each treatment for each ant species.

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RESOURCE ALLOCATION TO ANTS IN *ACACIA COLLINSII*

LUKE M. EVANS, JILL L. HARRIS, ELEANOR E. CAMPBELL,
SARAH E. B. FIERCE AND R. SCOTT CUSHMAN

Abstract: Young trees in the understory need to (1) grow quickly to outcompete nearby vegetation and (2) avoid or tolerate herbivory. Allocation of resources to these two strategies can vary with environmental conditions and age. We hypothesized that in a tropical dry forest, older *Acacia collinsii* trees would allocate proportionately more resources to defense than younger trees, and that trees in sunny locations would allocate proportionately more resources to defense than trees in shaded locations. We found no significant difference between old and young trees or sun and shade trees in nectary density. Young trees and old trees did not differ in their resource allocation to defense or competition, indicating that young trees appear to balance resources among defense, competition reduction, and growth. We found no significant differences in resource allocation between sunny and shaded trees in terms of either halo size or ant activity. However, ant activity tended to be higher in shaded trees, perhaps indicating more dire consequences of herbivory for shaded trees.

Key words: competition, herbivory, plant defense, Pseudomyrmex spinicola

INTRODUCTION

To reach available sunlight in the canopy, young trees in the understory need to (1) grow quickly to outcompete nearby vegetation and (2) avoid or tolerate herbivory. Plants have limited resources to allocate to growth vs. defense. The relative amount allocated to these two processes can vary depending on environmental conditions and age. For example, when water or mineral nutrients are limited, plants frequently allocate more carbon resources to defense (S. Martinson, pers. comm.). Also, plants that are older and larger often have more total carbon resources and less need for additional growth and so may allocate more resources to defense than younger plants.

We tested for effects of plant age and amount of sunlight on defenses of the ant acacia tree, *Acacia collinsii*. This tree's defense system is based on a symbiotic mutualism with ants, primarily *Pseudomyrmex spinicola*. *A. collinsii* supplies carbon-based nectar to the ants, which defend the plant from herbivory and reduce plant competition by cutting back surrounding competing vegetation (S. Martinson, pers. comm.) *A. collinsii* trees also have beltian bodies, which are a nitrogen-based food source for the ants, but we did not consider these in our study as they only rarely occurred on the *A. collinsii* at the time of our study. We hypothesized that young acacias, which should be under strong selection for rapid growth, would allocate proportionally fewer resources to defense than old acacias. We predicted that older trees would have more nectaries per m of branch, proportionally larger halos of removed vegetation, and that ant responses to disturbance would be greater in old trees than in young trees. We also hypothesized that trees in a sunny environment would have greater carbon resources by virtue of higher photosynthetic rates, and would therefore allocate more to defense than the trees in a shaded environment. We predicted that trees in the sun would have more nectaries per m of branch, larger halos of removed vegetation, and greater ant responses to disturbance than trees in the shade.

METHODS

We sampled 21 *A. collinsii* trees occupied

by *P. spinicola* ants in the dry tropical forest in Palo Verde National Park on 10 January 2004 at the beginning of the dry season. Study trees were chosen from within the area east of the OTS field station, between the marsh and the park entrance road (ca. 2 ha). We selected seven trees each to represent: (1) young trees in the shade, (2) old trees in the shade and (3) old trees in the sun. Tree size was assumed to be a surrogate for age; "young" trees were 1.5 - 2.2 m tall and "old" trees were 3.5 - 6.5 m tall. Shade environments were classified as those where the acacias were beneath an overhead canopy of taller trees; sun trees lacked such an overstory and their foliage received more direct sunlight per day than shade trees. For our analyses, old trees in the shade were used both for tests of (1) tree age, with light environment held constant, and (2) light environment, with tree age held constant.

To measure ant activity response to disturbance we simultaneously monitored four haphazardly chosen branches on each tree (one observer per branch). At 13 cm from the trunk each observer simultaneously counted the number of ants moving past a point for 1 min. The observers then simultaneously struck their branches with a pencil three times to disturb it, and again observed the number of ants moving past the same point for 1 min. We recorded the number of nectaries on each branch and the length of the branch. On each tree we also recorded tree height and distance to nearest vegetation along the ground (halo of removed vegetation).

Measurements of nectary density and ant activity were log-transformed to correct for heteroscedasticity. We tested for differences in nectary density between treatments using a nested ANOVA (trees within treatments and branches within trees with branch and tree as random effects). We hypothesized that post-disturbance ant activity would be related to pre-disturbance ant activity, and that the radius of the cleared halos would be related to tree height. Therefore we used regression analyses to compare the tree populations (sun vs. shade and old vs. young). In all cases, the statistical null hypothesis was that the populations did not differ in the slopes or intercepts of regressions (post-activity vs. pre-activity or halo area vs. tree height). F-tests of the null hypothesis follow Zar (1999).

Results

Old trees and young trees were broadly overlapping in pre-disturbance vs. post-disturbance ant activity ($F_{2,12} = 1.27$; Fig 1, upper left). Old trees were more than twice as tall as young trees, but their halo radii ranges were overlapping (0.4 - 1.0 m vs. 0.6 - 1.3 m; Fig 1, upper right). Thus halo sizes relative to tree size were somewhat larger in young trees compared to old trees, although the regressions were not statistically distinguishable ($F_{2,12} = 2.74$, $p = 0.11$).

Compared to sun trees, shade trees with low ant activity had larger increases in ant activity following disturbance ($F_{2,12} = 3.53$; Fig 1, lower left). Sun and shade trees were very similar in the size of cleared halos ($F_{2,12} = 0.93$, Fig 1, lower right).

Nectary density was similar (mean ± SD = 45.67 ± 24.27) on all trees and did not differ significantly between young trees and old trees ($F_{1,12} = 0.00$, $P = 1.00$) or between shaded trees and sunny trees ($F_{1,12} = 1.27$, $P = 0.28$).

Discussion

Our results refuted the hypothesis that old trees would have better ant defenses by virtue of allocating more resources to ants. If anything, young plants tended to have larger halos of cleared vegetation relative to their size. Assuming that there is a tradeoff between growth

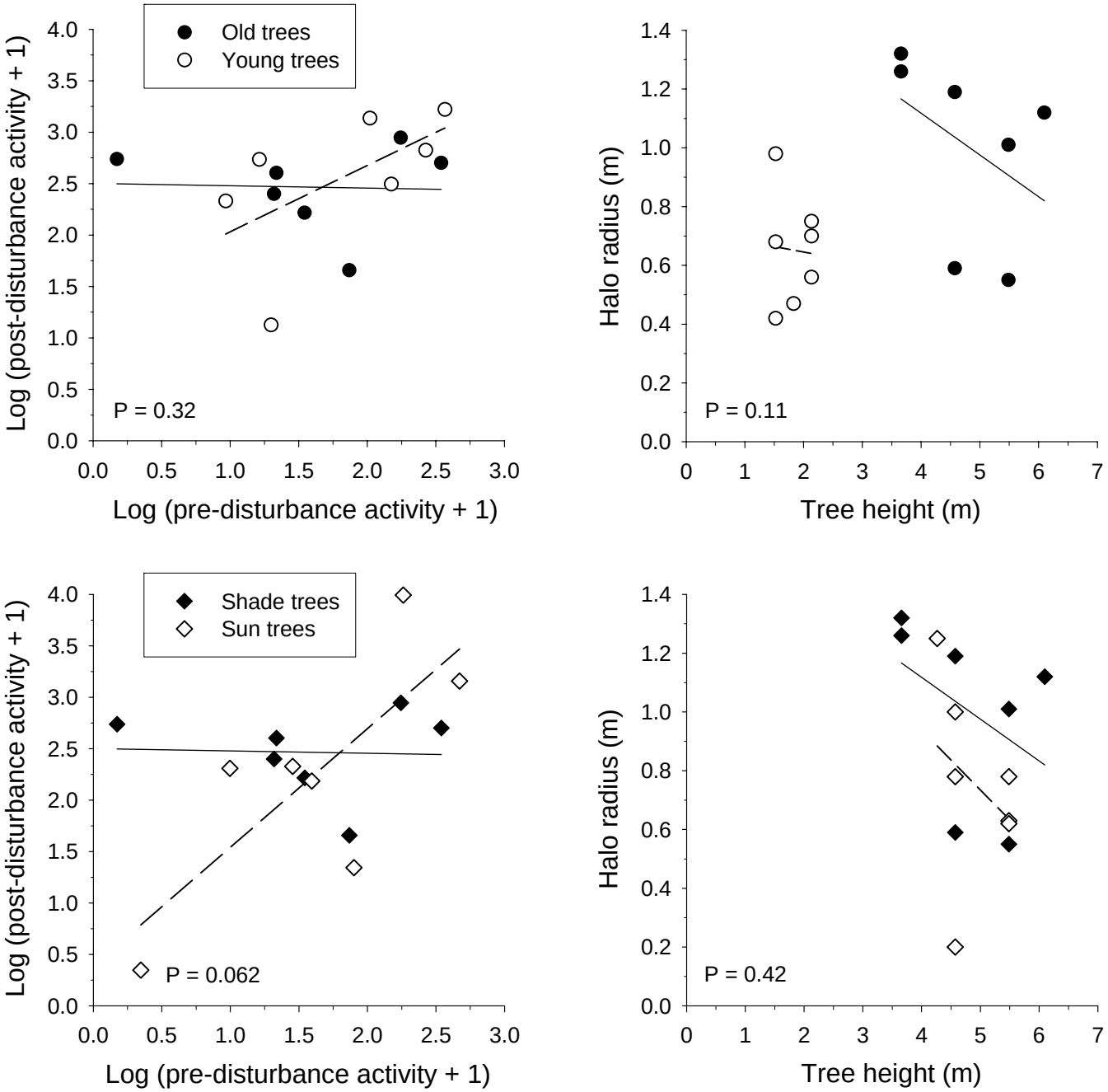

Figure 1. Comparison of old trees vs. young trees (top) and shaded trees vs. sunny trees (bottom) with respect to ant response to disturbance (left) and size of cleared halos around trees (right). P values are from tests of the null hypothesis that slopes and intercepts do not differ between the two populations. In all cases, x axis shows what was hypothesized to be a covariate of the variable of interest, although this was not generally substantiated (i.e., the only significant regression was for ant activity in sun trees).

and defense, this implies that the high herbivory in tropical forests forces young plants to invest quite heavily in defense, even at a cost to growth. This could be a feature of ant-based defenses, which unlike defenses based on secondary metabolism, can result in the elimination of potential competitors (by ants clearing nearby vegetation). This may mitigate the costs of reduced growth associated with increased investment in ants. An alternative explanation is that young plants commonly have more carbohydrates than can be invested in growth (because growth is primarily limited by water or mineral nutrients). In this case, there is not necessarily a growth-defense tradeoff.

Our results suggested a difference be-

tween sun trees and shade trees in the pattern of ant response to disturbance. This pattern could be adaptive because trees that are already shaded (and/or the ants that inhabit them) have relatively more to lose from losses of photosynthetic capacity due to herbivory. This hypothesis would be supported if photosynthetic rates were significantly greater in higher light environments.

The lack of a difference in halo sizes between sun and shade trees could be because ants have a limited ability to clear vegetation, or because there is a maximum beneficial halo size, beyond which returns to the tree and/or ants diminish. If so, halos around old trees, regardless of light environments, should be near their optimal size. However, there was a six-fold range in the radius of halos among similarly sized trees. Future studies could explore the causes and consequences of this variation.

Nectary density appears to be constrained by genetics and development. The proposition that ant activity is a function of nectar allocation remains untested. Direct measures of nectar production would have great value for future studies of acacia resource allocation to defense and competition.

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COLONIZATION AND DEFENSIVE ABILITIES OF ACACIA ANT SPECIES IN AN EARLY SUCCESSIONAL DRY TROPICAL FOREST

ELIZABETH V. WILSON, R. QUINN THOMAS, J. KHAI TRAN, STEPHEN WELLER AND BRENDA WHITED

Abstract: The ant species *Pseudomyrmex flavicornis*, *P. spinicola*, and possibly *Crematogaster brevispinosa* occur in a symbiotic relationship with *Acacia collinsii*. *C. brevispinosa* has been reported to occupy mostly dead or dying acacias (Janzen 1983), but Ermentrout et al. (2003) found that it was one of the two most common ant species on acacias in an early successional site. We hypothesized that *C. brevispinosa* may be a good colonizer of young acacias but a poor defender of their host plants, resulting in their disappearance in late successional stages. We quantified (1) the presumed colonizers of acacias by examining which ant species occupied young trees (defined as those ≤ 1 m tall), and (2) the defensive abilities of each ant species. *P. spinicola* was the most common ant species on small acacias (60%) with *C. brevispinosa* the second most common (31%). In our behavioral test, we found no difference between the defensive abilities of *C. brevispinosa, P. spinicola*, and *P. flavicornis* in response to disturbance. Thus, prevalence of *C. brevispinosa* in this early successional dry tropical forest is still largely unexplained, and further studies are needed to clarify its relationship with *A. collinsii*, as well as its patterns of occurrence and distribution.

Key words: Acacia collinsii, *defensive abilities*, Crematogaster brevispinosa, Pseudomyrmex flavicornis, Pseudomyr-

INTRODUCTION

Acacia collinsii exists in a mutualistic relationship with several species of ants including *Pseudomyrmex flavicornis*, *Pseudomyrmex spinicola*, and possibly *Crematogaster brevispinosa*. *P. flavicornis* appears to occupy acacias more frequently in open sun, *P. spinicola* occurs across all habitats, and *C. brevispinosa* has been reported to occupy mostly dying or dead acacias, presumably after the originally colonizing ant species has abandoned the tree (Janzen 1983:762). Assuming that a later successional forest should contain a higher proportion of dead or dying *A. collinsii*, Ermentrout et al. (2003) hypothesized that *C. brevispinosa* should occur more often in late successional sites where acacias may be less healthy or in various stages of dying. However, they found that *C. brevispinosa* was absent from the acacias they sampled in a later successional site, but represented a relatively high proportion (32%) of the ant species on both large and small acacias in an early successional site. A possible explanation for this finding is that *C. brevispinosa* is a good colonizer of young *A. collinsii* but is either a poor defender of acacias or is outcompeted by other acacia ant species before the forest matures. We thus hypothesized that acacia ant species differ in their colonizing abilities, predicting that *C. brevispinosa* would occur more frequently on young acacias than would other acacia ant species. We also hypothesized that acacia ant species would not be equally effective defenders of their host acacias. We tested the specific prediction that *C. brevispinosa* colonies would be poor defenders of their host acacias when compared to the other two common species of acacia ants.

METHODS

On 10 January 2004 from 0830 to 1130, we studied the ant-acacia system in Palo Verde National Park, Guanacaste Province, Costa Rica. Our study site was located 6 km from the OTS field station (4 km on the road from the station

Table 1. Frequency of occurrence (%) of the most common ant species occupying young *A. collinsii* (≤ 1 m tall) and on all *A. collinsii* in the study plot (from Ermentrout et al. 2003).

	C. brevispinosa	*P. flavicornis*	*P. spinicola*	Total colonies
Young acacia	30.8	9.6	59.6	52
All acacia*	32.4	40.5	27.0	37

*Calculated from raw data of Ermentrout et al. (2003). Data are the frequencies of the most common ant species on isolated acacias and on the largest acacias > 1 m tall within clusters occupied by unique ant species.

and 2 km on La Carreta road; GPS location 16P 068 5939, 1147437). It consisted of second growth vegetation, including many acacias approximately 4-6 m tall. The site was burned in 1994 - 1995 and was currently being grazed by cattle.

To determine which ant species colonize young acacias, we surveyed ant populations on acacias ≤ 1 m tall in areas surrounding the permanent transects established by Ermentrout et al. (2003). We surveyed trees located 1 m or more from large (> 5 cm in diameter) acacias. Fifty two sample trees were tagged, their ant species were identified, and the health of each tree assessed using a 0 - 2 scale (0 = dead or sparse foliage, 1 = widely scattered foliage, and 2 = dense, lush foliage). We used G-tests to evaluate the null hypothesis that (1) ant species occurred with the same relative abundance on young plants as in the tree population as a whole, and (2) ant species occurred at random with respect to tree health.

To assess the defensive response behavior of the ant species, we selected nine healthy acacia trees (2 - 5 m in height) occupied by each of the three ant species (total of 27 trees). On each tree, we counted the number of ants passing an imaginary line on a large horizontal branch for 10 s before disturbance and considered this the baseline rate of ant activity. After applying a series of ten rapid taps at the line, we counted the number of ants crossing the line in three 10 s intervals separated by 5 s each. The three post-disturbance counts were very similar so were averaged to yield one measure per tree of pre- and post-disturbance activity (ants / 10 s). We employed a one-way ANOVA (of log transformed counts) to compare ant species with respect to pre-disturbance and post-disturbance ant activity. We used regression analyses to test the null hypothesis that species were the same in the relationship between pre- and post-disturbance activity (i.e., same slopes and intercept; Zar 1999).

Results

P. spinicola occupied 59.6% of the small acacia trees (≤ 1 m tall), followed by *C. brevispinosa* (30.8%) and *P. flavicornis* (9.6%) (Table 1). These relative abundances of ant species on young acacias (≤ 1 m tall) differed significantly from equal frequencies ($G = 21.05$, $df = 2$, $P < 0.0001$) and from those reported by Ermentrout et al. (2003) for trees in the same site ($G = 32.74$, $df = 2$, $P < 0.0001$; Table 1). On young trees in 2004, compared to all trees in 2003, *P. spinicola* abundance was higher, *C. brevispinosa* abundance was similar, and *P. flavicornis* abundance was much lower (Table 1).

The distribution of ant species on small acacias was related to the apparent health of trees ($G = 10.57$, $df = 4,46$ $P = 0.03$). *C. brevispinosa* occurred relatively more than *P. spinicola* or *P. flavicornis* on acacias with sparse, mostly dead foliage (health = 0) and relatively less on lush, densely foliated trees (health = 2), while *P. spinicola* occurred with relatively high

frequency on trees with lush foliage (health = 2) (Fig. 1).

There was no difference between ant species in their activity prior to disturbance (back-transformed means = 1.8 vs. 1.3 vs. 2.1 ants / 10 s for *C. brevispinosa*, *P. spinicola*, *P. flavicornis* respectively; $F_{2,24} = 0.41$, $P = 0.67$). All three species increased activity following disturbance, but there was no difference between species in post-disturbance activity (7.0 vs. 11.0 vs. 15.0 ants / 10 s; $F_{2,24} = 1.82$, $P = 0.18$). There was also no difference in the relationship between pre-disturbance and post-disturbance activity (Fig. 2).

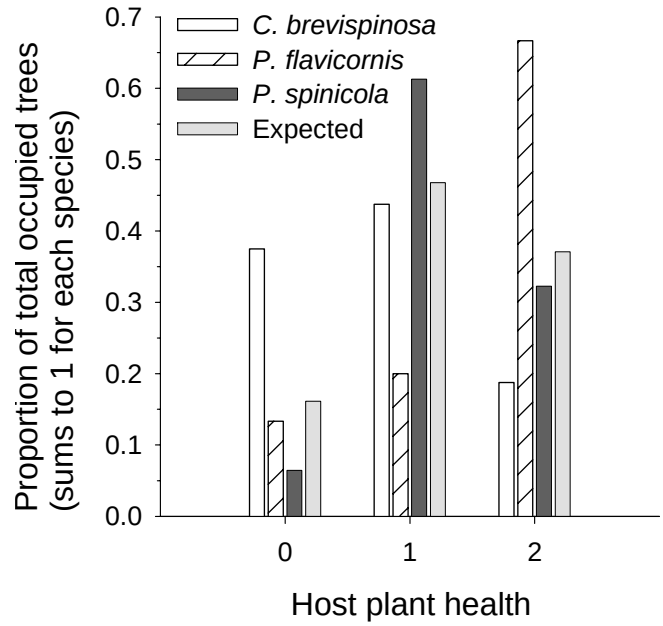

Figure 1. Frequency of ant species occupying acacia plants < 1 m tall of different health status (0 = foliage mostly dead/ very sparse (N = 10), 1 = foliage widely scattered/not dense (N = 29), 2 = foliage dense/lush (N = 23)). Expected values are based on the frequency of acacias in the three health categories.

DISCUSSION

According to our hypothesis that *C. brevispinosa* was the better colonizer of small acacias, we predicted that *C. brevispinosa* would be the most abundant species on young acacias ≤ 1 m tall. Instead, we found that *P. spinicola* was the most abundant, suggesting that *P. spinicola* is in fact the better colonizer in this early successional dry tropical forest site. However, *C. brevispinosa* did occupy 31% of the young acacias sampled, a relatively high percentage. Among these young acacias, *C. brevispinosa* occurred more often on unhealthy trees (health = 0), in accordance with Janzen's (1983) observations. The fact that many small and presumably young acacias were classified as unhealthy (health = 0) was unexpected, but this could account in part for the relatively high percentage of *C. brevispinosa* in our sample. Some *C. brevispinosa* were also found inhabiting healthy acacias (e.g. with health scores of 1 or 2). Therefore it is still unclear why *C. brevispinosa* occurred at such high frequency in both this year's sample of young trees and Ermentrout's transect samples of all trees in this early successional site. This requires future study.

The supposed symbiotic relationship be-

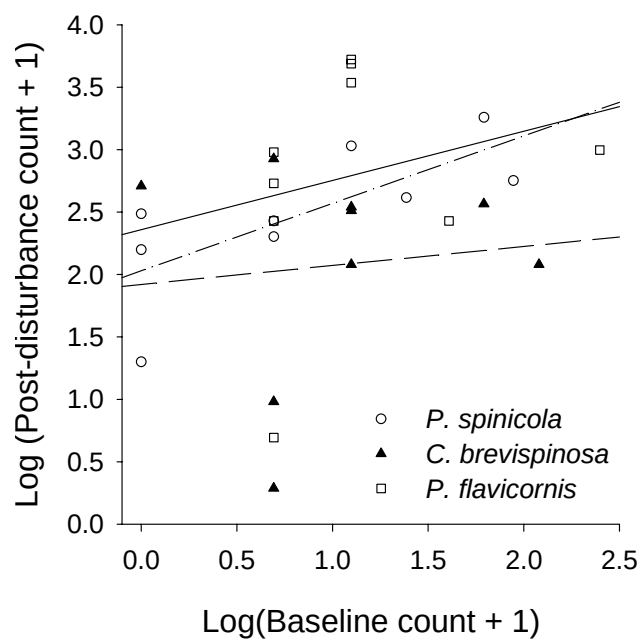

Figure 2. Comparison of ant species in their response to disturbance. In all species, activity was increased following disturbance, but there was no difference among species in the relationship between activity before and after disturbance. Best-fit regression lines are shown for each species separately (dash-dot line = *P. spinicola*; dashed line = *C. brevispinosa*; solid line = *P. flavicornis*), but regressions did not differ among species ($F2, 24 = 2.19$, $P > 0.10$).

tween *A. collinsii* and *C. brevispinosa* is also unclear. Although species differences were nonsignificant, *C. brevispinosa* was the least responsive to disturbance (Fig. 2), in accordance with our prediction that *C. brevispinosa* is a poor defender. It is unclear how much benefit acacia trees receive from *C. brevispinosa*, an ant species that may colonize dying trees and has a low defensive response to disturbance of its host tree.

An alternative hypothesis that we did not directly test is that *C. brevispinosa* may be outcompeted by other ant species as a forest matures. This would help explain why Ermentrout et al. (2003) found the species absent in their late successional forest site. Our measurement of aggressive response was not a measure of competitive ability, so we do not know the competitive ability of *C. brevispinosa* relative to other ant species. Further studies could use other methods, such as ant transplant experiments, to determine relative competitive abilities of acacia ant species, including *C. brevispinosa*.

Given that we tagged all the acacia trees in our sample, a future study could resample these trees in subsequent years to determine if there has been a change in tree health or the abundances of acacia ant species. More research is needed to explain the prevalence of *C. brevispinosa* at this early successional site and its potential symbiotic relationship with *A. collinsii*.

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FEMALE VIGILANCE IN HOWLER MONKEYS (*ALOUATTA PALLIATA*)

SARAH E. B. FIERCE, ELEANOR E. CAMPBELL, LUKE M. EVANS,
JILL L. HARRIS AND R. SCOTT CUSHMAN

Abstract: Group vigilance is one beneficial aspect of group living in howler monkeys (*Alouatta palliata*), where the responsibility of scanning for danger may be partitioned among individuals depending on their social roles. We hypothesized that vigilance among female howler monkeys should vary with the risk faced to their young. We observed scanning behavior of females in two howler monkey troops in Palo Verde, Costa Rica. We found no significant difference in the percentage of time spent scanning among females with juveniles vs. infants vs. no associated young. Furthermore, the amount of time a female spent scanning did not vary with the distance to her associated young, nor with the presence or absence of a nearby male. Our finding that the presence of young had little effect on female vigilance is consistent with one but not both previous studies of this population. Sometimes male vigilance in troops may be sufficient for the detection of danger.

Key words: group living, juveniles, predator detection, primate behavior, scanning behavior

INTRODUCTION

The daily activities of howler monkey (*Alouatta palliata*) troops involve foraging, resting, traveling and scanning for danger. A reduced need for individual vigilance is one of the potential benefits of group living. Nowak et al. (2002) supported this idea and found a negative correlation between troop size and individual time spent scanning. Other studies have examined characteristics of troop vigilance in relation to the sexes and ages of the members within it. For instance, Iwamoto et al. (2003) found that the distance to and sex of the nearest neighbor had no effect on the vigilance of an individual. The effects of the presence of young on vigilance have been less clearly defined. Two contradictory studies have observed females with and without young: Cover et al. (1997) found increased vigilance in females with associated young compared to those without, while Bird et al. (1996) found no significant differences.

To resolve these contradictory findings, we studied how the presence and nearness of young affected the vigilance of female howler monkeys. We hypothesized that maternal vigilance in howler monkeys should vary with the risk faced to their young. We tested three predictions: (1) focal females with associated young (of any age) will be more vigilant than females without young; (2) focal females with infants will be more vigilant than females with free-ranging young; (3) focal females will be more vigilant when their young (of any age) are far away and therefore more exposed to danger; and (4) focal females with young will be more vigilant when there are no males nearby.

METHODS

On the mornings of 11 - 12 January 2004, we located and observed two troops of *A. palliata* at Palo Verde National Park, about 1 km northwest of the OTS field station. We conducted two-minute focal samples of individual females, and recorded the amount of time each spent scanning the surroundings, feeding, moving, or engaging in other activities. For this study, we calculated the percentage of total time spent scanning. We recorded whether each female was associated with an infant or juvenile (within 5 m) and the distance to other conspecifics. Young in direct contact with a female at all times were considered infants, while free-

roaming young were considered juveniles. All females in each troop were observed once, and then, because of the scarcity of troops in the area, observations on the same females were made again after approximately 45 min.

The percent of time spent scanning was log-transformed to correct for non-normality and heteroscedasticity. We used ANOVA and t-tests to test for differences in the percent of time a female spent scanning depending on (1) whether or not she was associated with any dependent young, (2) whether she was associated with an infant, (3) the distance to her associated juvenile, and (4) whether she was within 5 m of a male.

RESULTS

We obtained a total of 33 scan samples, from approximately 12 females over two days. Most observations came from one large troop which had no infants, approximately nine females, five males and six juveniles. A second smaller troop had approximately three females, two males and two infants.

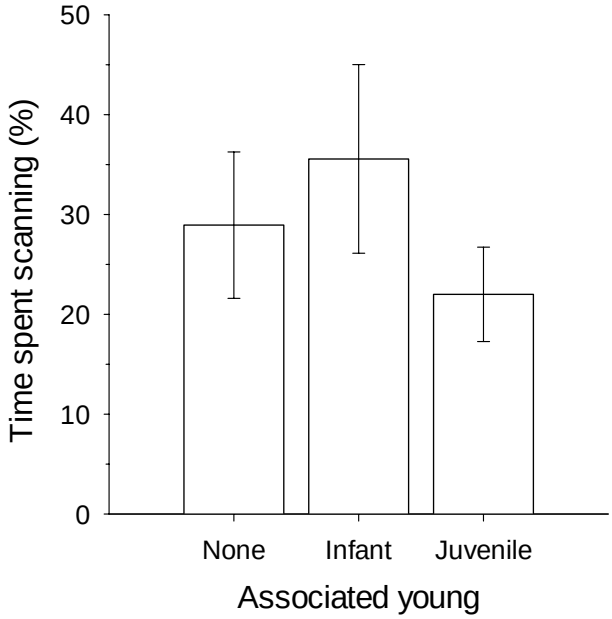

Figure 1. Mean percentage of time spent scanning (± SE) of howler monkey females with no young, an infant, or a juvenile. Young were considered to be associated when they were within 5 m of the female. Sample sizes are indicated above bars.

The vigilance of females was not significantly affected by the presence or nearness of any dependent young, or by the presence of a nearby male. There was no significant difference in the percentage of time spent scanning among females with juveniles vs. infants vs. no young ($F_{2,32}$ = 0.77, P = 0.47; Fig. 1). Females with young at distances that were near (≤ 2 m) vs. medium (2 - 5 m) vs. far (5 - 10 m) did not differ in percentage of time spent scanning ($F_{2,21}$ = 0.02, P = 0.98; Fig. 2). Among females with young at any distance, those near a male (≤ 5 m) scanned less often than those that were not near a male (Fig. 3), but the difference was not significant (t = 0.25, df = 19, P = 0.81; Fig. 3).

DISCUSSION

Female howler vigilance was not significantly affected by the presence, age class or distance of associated young. These findings are consistent with those of Bird et al. (1996), who found no difference in vigilance among females with and without young, but contrast with those of Cover et al. (1997).

We defined the nearness of each female to her conspecifics using distances that may not be biologically relevant on the scale of a howler monkey troop. We assumed that juveniles within 5 m of a female belonged to that female, but this association may not be valid for juveniles old enough to be free-roaming. Additionally, for more mobile young, the social structure of the troop may be such that communal vigilance is more important than individual maternal vigilance. It is still possible that females with dependent infants are more vigilant than females with juveniles, but too few females with infants were included in our sample to provide

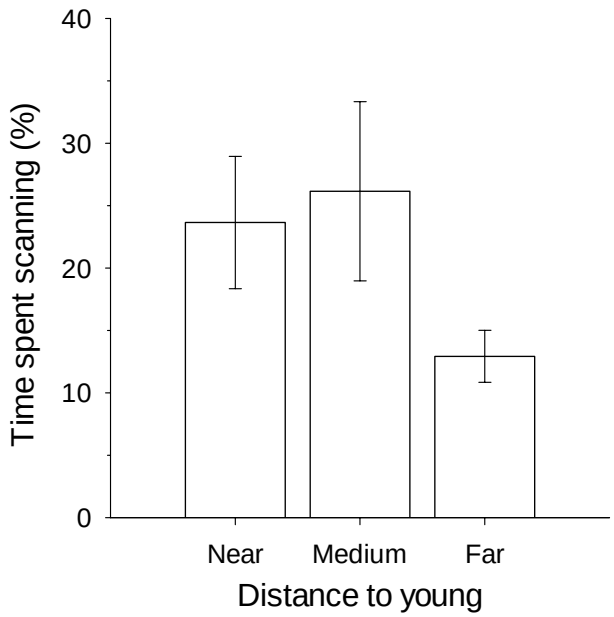

Figure 2. Mean percentage of time spent scanning (± SE) of females with young that were at a near (< 2 m), medium (2 - 5 m), and far distance (5 - 10 m). Sample sizes are indicated above bars.

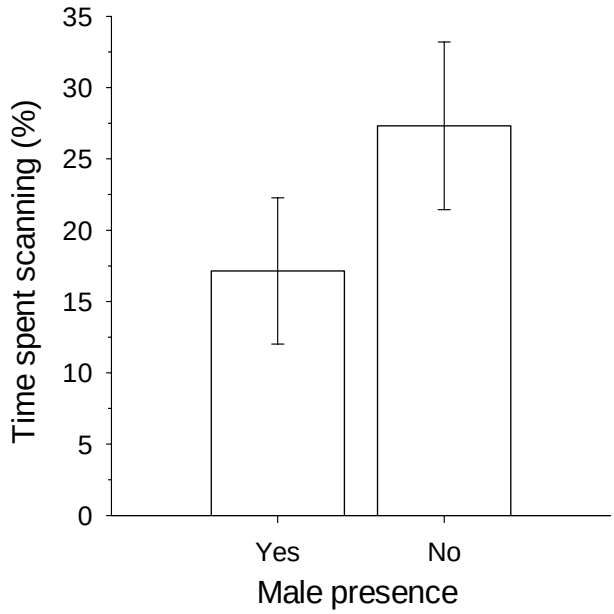

Figure 3. Mean percentage of time spent scanning (±) SE of females with young when males were and were not present within 5 m. Sample sizes are indicated above bars.

a robust test. Future studies of howler monkeys could further explore maternal vigilance by observing more females with infants. Although nearby males did not affect female howler vigilance in our study, the presence of males anywhere in a troop may ensure maternal and juvenile safety, and thus affect female vigilance. Females may relax their vigilance once a threshold number of males per female in the troop has been reached. In our study, we assessed the effect of males only within 5 m of a female. This distance may not be biologically relevant to howler monkeys, whose troop members often roam for dozens of meters in any direction. Further studies could explore this characteristic of troop vigilance. Finally, some sampling difficulties, especially low sample size, may be responsible in part for our findings. The variability in time spent scanning was so large that a greater number of samples might be necessary to detect a difference in vigilance rates. The number of individuals and troops scanned was low, and the majority of our scans came from one large troop with no infants.

Given that Nowak et al. (2002) showed that troop size has a negative effect on individual vigilance, using data primarily from a single large troop may not be representative of female vigilance in all situations. Ideally, several troops of varying sizes and compositions should be studied to address the question of female vigilance.

Earlier studies indicate that the responsibility of scanning for danger is divided among troop members (Nowak et al. 2002). Our study suggests that females may not be solely responsible for the protection of their young and that vigilance by the troop as a whole, and perhaps by adult males in particular, may have a greater role. Future studies should explore more precisely how vigilance responsibilities are divided among howler monkey troop members.

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RELATIONSHIPS BETWEEN BUTTERFLY FLIGHT AND WING COLORATION AND PATTERNING

BRENDA M. WHITED, R. QUINN THOMAS, J. KHAI TRAN,
STEPHEN T. WELLER AND ELIZABETH V. WILSON

Abstract: Butterflies use several different defense systems against predators including camouflage and bright coloration that warns of chemical defenses. Butterflies lacking either of these defense systems may have to rely on evasive flight behavior. We quantified several aspects of flight pattern of 21 Costa Rican butterfly species to determine how individuals with different wing patterns and coloration respond to a simulated predation event. Solid colored butterflies with neither camouflage nor bright coloration exhibited faster, more evasive flight traits. These results suggest that butterflies with neither crypsis nor aposematism depend on evasive flight to avoid predation.

Key words: aposematism, butterflies, camouflage, chemical defenses, crypsis, flight patterns

INTRODUCTION

Butterflies are subject to attacks from numerous predators, which has led to the evolution of defense mechanisms such as camouflage, chemical defenses, and evasive behavior. Camouflage functions to blend the organism into the background, making it difficult to detect (DeVries 1987). This can take the form of matching natural objects such as a leaf litter and ground cover or disruptive patterning that breaks up the butterfly's outline making it difficult to detect (Sbordoni 1998). Chemical defenses involve the butterflies' incorporation of toxins that make them distasteful. Chemically defended butterflies tend to advertise their toxin with bright red and orange coloration, such as the Monarch butterfly (*Danaus plexippus)* with its bright orange color (DeVries 1987). Certain butterflies lack camouflage and chemical defense, and may avoid predators through evasive behavior (Chai et al. 1990).

In this study, we examined the evasive behavior of butterflies in relation to their predator avoidance strategies. We hypothesize that butterfly species vary in flight pattern according to their need for predator protection. Based on pattern, indicating lack or presence of camouflage, and coloration, indicating lack or presence of chemical defense, we predict differences in turning frequency, flight duration, relative speed, and average height of flight. Specifically, butterflies lacking camouflage and chemical defense should exhibit more evasive flight traits than those with camouflage or warning coloration.

METHODS

We visually assessed the behavior and appearance of butterflies encountered haphazardly on the morning of 12 January 2004 near the OTS field station at Palo Verde National Park, Guanacaste, Costa Rica. We observed butterflies in three different habitats: an open field near a marsh, a forested area near the water hole approximately 3 km east of the field station, and the lower slope of the tropical dry forest behind the field station. We measured flight traits of each individual butterfly after being disturbed (prodding with a meter stick) from a perched position. These measurements included number of mid-air turns (> ~ 90° change in direction), relative speed (0 = slow, 1 = medium, 2 = fast), average height of flight (0 - 1 m, 1 - 2 m, and > 2 m above ground), and total flight time, as responses to disturbance.

We used descriptive keys to identify

morphospecies and to categorize by pattern and coloration (DeVries 1987, Rainforest Publications 2001). Patterns were grouped into three categories: mottled, disruptive, and solid. "Mottled" characterized butterflies that resembled ground cover such as leaf litter, and tended to have different shades of brown and white that occurred in variegated spots and stripes. *Anartia jatrophae* is an example of a mottled butterfly (DeVries 1987: plate 28). "Disruptive" characterized butterflies with intermittent blotches of two or more colors, creating many distinct lines that functioned to break up the butterfly's entire outline. Disruptive also included those species with one bright stripe, often white, running across the wing that also functioned to break up the outline. *Siproeta stelenes biplagiata* is an example of a disruptive butterfly (DeVries 1987: plate 28). "Solid" characterized butterflies that had no patterning, and those we observed were all white or all yellow. The butterflies of the *Eurema* genus exemplify solid butterflies (DeVries 1987: plate 10). Coloration categories were determined by the amount of red and orange color of the butterfly's wings. Butterflies with > 50% red/orange coloration were considered to be a potentially toxic butterfly, and all others with < 50% red/orange were categorized separately. *Euides isabella* is an example of a predominately red/orange colored butterfly (DeVries 1987: plate 31).

Across all three habitats, we observed a total of 21 species (N = 5, 9, and 7 each for disruptive, mottled and solid butterflies respectively; N= 4 and 17 each for red/orange and non red/orange butterflies). We observed one to twelve individuals per species (mean = 5).

Analyses were conducted with JMP 5.0 (SAS 2003) with method EMS (traditional). We used a nested analysis of variance (ANOVA), with species as a random effect nested within pattern and coloration. Tests for pattern and coloration were based upon the number of species in each category that were observed. Statistical inferences from nested ANOVA regarding pattern and coloration were the same as with one-way ANOVAs of species means, but the nested model also provided tests of the extent to which individuals within a species showed repeatable flight pattern. Flight duration and number of turns were log-transformed to correct for heteroscedasticity.

RESULTS

All measured flight patterns were reasonably repeatable within a species; significant effects of species indicated that there was less variance among individuals of the same species than among individuals of different species (Tables 1, 2)

Table 1. Results from nested ANOVAs comparing flight traits among butterfly species with mottled, disruptive, or solid wing pattern.

		Log(time)		Log(turns/s)		Speed		Height	
Source	DF	MS	F	MS	F	MS	F	MS	F
Pattern	2	0.290	2.28	0.754	3.38*	3.494	5.80**	0.625	0.56
Species (pattern)	18	0.165	2.49**	0.318	4.42**	0.734	1.87*	1.589	4.62**
Error	83	0.066		0.072		0.392		0.344	

* P < 0.05, ** P < 0.01

Table 2. Results from nested ANOVAs comparing flight traits among butterfly species with red/orange coloration vs. others.

		Log(time)		Log(turns/s)		Speed		Height	
Source	DF	MS	F	MS	F	MS	F	MS	F
Color	1	0.733	7.03*	0.574	3.59†	1.100	1.67	5.569	8.24**
Species (color)	19	0.190	2.86**	0.360	5.00**	1.269	3.24**	1.435	4.17**
Error	83	0.066		0.072		0.392		0.344	

* P < 0.05, ** P < 0.01, † P = 0.0655 (marginally significant)

Flight duration

Flight duration did not vary across pattern, but did vary with red/orange coloration (Table 1, 2); red/orange butterflies had longer-flight duration that non red/orange butterflies (Fig. 1).

Turning frequency

Disruptive butterflies had significantly fewer turns per second than mottled and solid butterflies (Fig. 4, Table 1). Red/orange butterflies showed fewer (marginally significant: P = 0.065) turns per second than non red/orange butterflies (Fig. 2, Table 2).

Speed

Disruptive butterflies flew significantly slower that mottled and solid butterflies (Fig. 5, Table 1). Speed did not vary with coloration (Table 2).

Height

Height of flight did not vary with pattern, but did vary with red/orange coloration (Table 1, 2); red/orange butterflies flew significantly higher than non red/orange butterflies (Fig. 3).

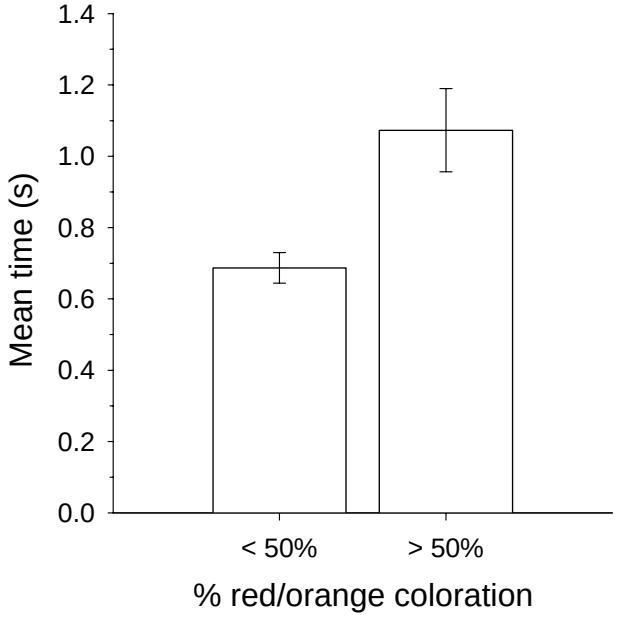

Figure 1. Flight duration of butterfly morphospecies with different coloration. Bars show means ± S.E, calculated from species means.

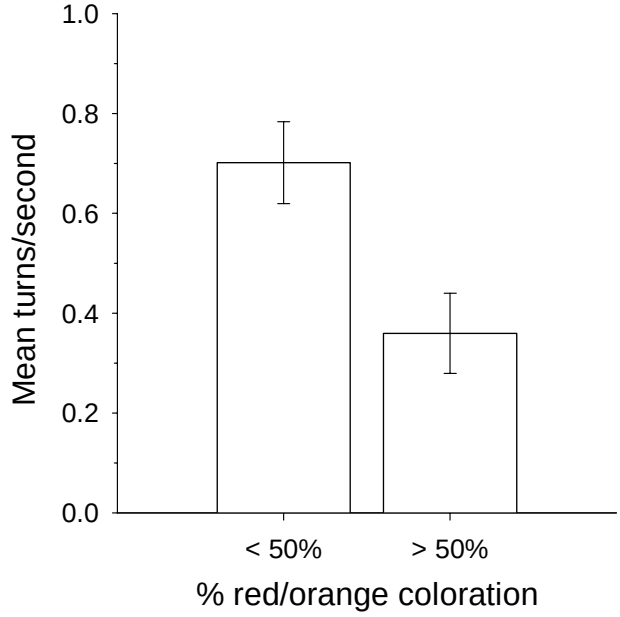

Figure 2. Turning frequency of butterfly morphospecies with different coloration. Bars show means ± S.E, calculated from species means.

DISCUSSION

Our analysis of butterfly flight pattern showed differences in measured flight traits among butterflies of different patterns and coloration. This suggests that butterflies lacking both camouflage and bright coloration rely more on evasive flight as a defense strategy, although not every flight trait measured showed significant differences.

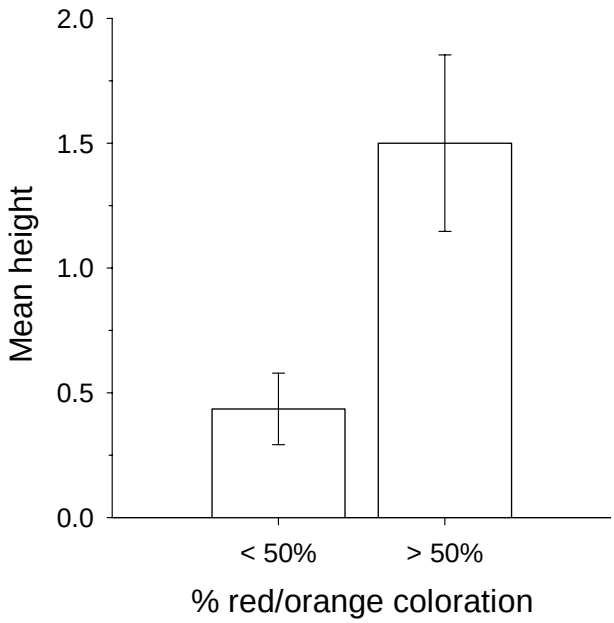

Figure 3. Mean height of flight of butterfly morphospecies with different coloration. Bars show means ± S.E, calculated from species means.

Disruptive butterflies tend to fly straighter and slower that mottled and solid butterflies. The camouflage of disruptive butterflies may be most effective in flight. As a disruptive butterfly flaps its wings, its outline can flash in and out of visibility, causing a predator to easily lose sight of its potential prey. Thus, fast, evasive flight has probably not evolved in this butterfly. In contrast, mottled butterflies may benefit more from landing and blending into the background. When in flight, the mottled butterfly may be just as visible as the solid butterfly lacking patterning, thus explaining their fast, evasive flight. Like mottled butterflies, solid butterflies have fast, evasive flight. These butterflies may rely on flight as an escape method because they lack any form of camouflage.

Butterflies with > 50% red/orange coloration had higher flight durations, lower turning

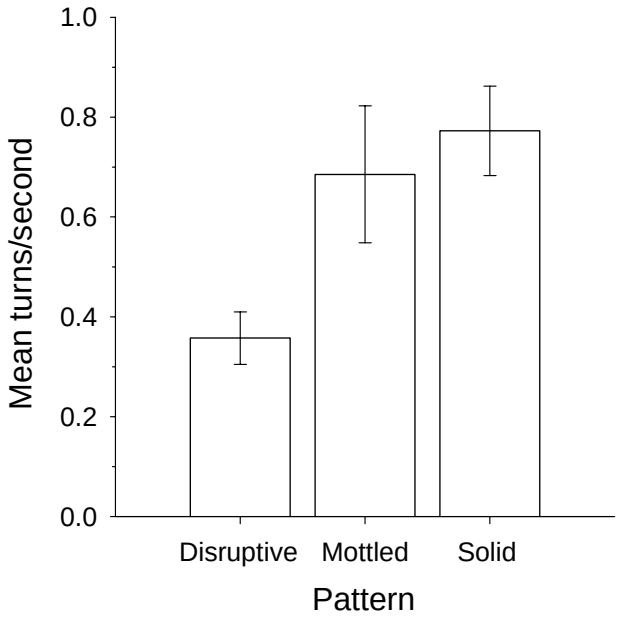

Figure 4. Turns per unit time of butterfly morphospecies with different wing pattern types. Bars show means ± S.E, calculated from species means.

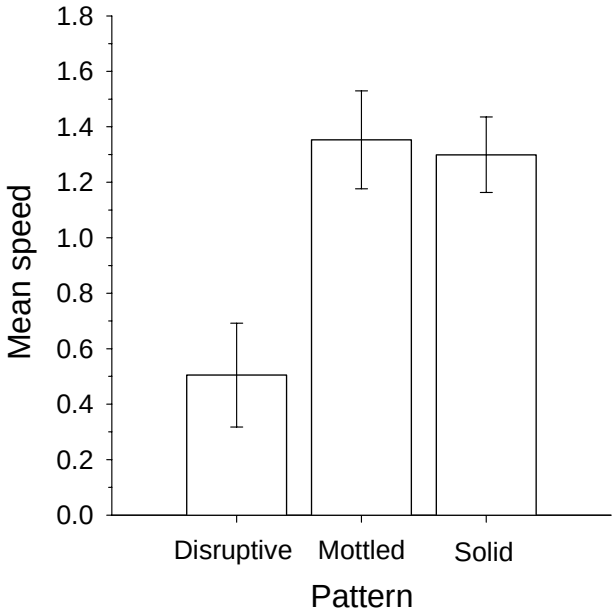

Figure 5. Relative speed of butterfly morphospecies with different wing pattern types. Bars show means ± S.E, calculated from species means.

frequency, and a relatively high level of flight. If these butterflies contain chemical defenses, they might not need to use flight as a mechanism of predator evasion. In fact, a direct, long, high flight should function to more effectively display warning coloration to a predator.

The camouflage of mottled and disruptive butterflies may be indicative of crypsis, a defense strategy that causes predators to lose sight or become confused about the location of the potential prey (DeVries 1987, Sbordoni 1998, Janzen 1983). The coloration of red/orange butterflies may be indicative of aposematism, a defense strategy where chemical defense is advertised with a brightly colored warning (DeVries 1987). Numerous studies show that crypsis and aposematism are effective forms of defense in many types of organisms, with butterflies being commonly cited examples (Begon et al. 1990). Thus butterflies lacking both crypsis and aposematism would logically have evolved other forms of defense. Our study suggests this alternate form of defense may be evasive flight.

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MORPHOLOGICAL AND PHYLOGENETIC PATTERNS IN DIURNAL VS. NOCTURNAL SPIDERS

HEATHER E. LAPIN, MATTHEW T. KEMP, PETER N. CHALMERS,
SARA M. HELLMUTH AND PAUL A. MARINO

Abstract: Nocturnal animals share traits adaptive to being active at night, sometimes as a result of convergent evolution. We hypothesized that nocturnal vs. diurnal grassland spiders would differ in their morphological characteristics and phylogeny. However, we found no difference between nocturnal and diurnal spiders in body size, eye number, cryptic coloring or foraging behavior; neither was there a difference in the proportional representation of different families of spiders found during the day versus those found at night.

Key words: Araneae, *convergent evolution, temporal distribution*

INTRODUCTION

Convergent evolution occurs when ecological or evolutionary pressures select for similar morphologies and behaviors among different phylogenetic groups (Begon et al. 1990). For example, streamlined form for movement through water has been selected for in most fish, some mammals, and even some birds. Similarly, large eyes have evolved independently in at least three different families of nocturnal birds: e.g., the boat billed heron, owls, and potoos (Stiles and Skutch 1989).

There are at least six spider families present at Palo Verde National Park (Babineau et al. 1999). Families of spiders may exhibit convergent evolution as a result of differential selective pressures on spiders that are active in day vs. night. It could be that spiders that are diurnal vs. nocturnal have repeatedly evolved to be morphologically similar to each other and different from spiders active at the other time. Alternatively, eye morphology and hunting strategy, which serve as diagnostic traits in distinguishing spider families (Kaston 1973), may be so evolutionarily conserved that day vs. night activity is primarily determined by phylogeny. In this case, hunting strategy might be dictated by evolutionary history, as opposed to the case where hunting strategy is relatively plastic, and morphology evolves accordingly. We predicted that night-active spiders would be relatively larger (because they are less vulnerable to visual predators), less cryptic, have more eyes and display different foraging behavior than day-active spiders.

METHODS

We sampled the diurnal and nocturnal spiders in an open grass field bordering the marsh at Palo Verde National Park, Costa Rica on 12 January 2004. We established six 10 m transects spaced 5 ft apart and examined 6 in on either side of the transect once during the day (0930 - 1100) and once during the night (2130 - 2300). For all spiders we recorded size, coloration (camouflaged or not), activity, and presence or absence of a web. In the same location we also set 15 pitfall traps evenly spaced on a 25′ x 15′ grid, filled halfway with soapy water. We emptied pitfalls after 10 h of day collecting and 10 h of night collecting. We recorded size, coloration, number of eyes, sex and family for each spider collected in pitfall traps.

RESULTS

We collected 22 spiders representing eight families from the night pitfall traps and seven spiders representing four families from the day pitfall traps. Three families were repre-

sented in both day and night samples (Table 1). Neither body size ($t = 0.27$, $df = 27$, $P = 0.79$), sex ($X^2 = 1.21$, $df = 1$, $P = 0.27$) nor eye number ($t = 0.77$, $df = 27$, $P = 0.45$) differed between day and night spider communities.

We found 51 spiders during the day transect and 28 spiders during the night transect (Table 2). Day and night communities were very similar with respect to occurrence of camouflage and webs. Spiders found at night were larger than those found during the day, but this might have been the result of detection bias and was not supported by the pitfall data. Spiders found during the day were somewhat more likely to be active than those found at night.

Table 1. Number of spiders from each family found in 15 pitfall traps run during one day and one night. Bold indicates families found in both night and day samples.

Family	Day	Night	Total
Agelinidae	**2**	**7**	**9**
Araneidae	**1**	**2**	**3**
Caponiidae	0	1	1
Hahniidae	0	2	2
Lycosidae	**3**	**7**	**10**
Lyssomonidae	0	1	1
Pisauridae	0	1	1
Salticidae	1	0	1
Zoropsidae	0	1	1
Total	7	22	29

Discussion

Surprisingly, we found no difference in size, coloration, or eye number between spiders found during the day vs. night, suggesting that these morphological characteristics are not unique to nocturnally or diurnally active spiders. There may, however, be other morphological adaptations that differentiate nocturnal and diurnal spiders that we did not measure.

Because there was no clear pattern of family assemblage between spiders found during the day and night, our data suggest that adaptations necessary for nocturnal vs. diurnal lifestyles are evolutionarily labile within families.

For several reasons the results of our study were somewhat inconclusive. Limited captures in the pitfalls precluded statistical tests for associations between time of activity and spider taxonomy. The pitfalls were probably most effective at capturing ground foraging spiders and least effective at capturing spiders in orbs or jumping spiders (Salticidae). Day and night transects were not easily comparable because detection ability varied between night and day and because lights were needed to conduct nighttime search, potentially changing the spiders' activity patterns. The fact that we found larger spiders at night might be because larger spiders react more to invasive lights and are then easier to see. The lights may also have caused spiders to freeze, which would explain the higher proportion of activity found among spiders detected during the day transects.

The apparent lack of taxonomic or morphological patterning of spiders with respect to

Table 2. Characteristics of spiders detected during surveys conducted in the day vs. night along six 10 m transects.

	# present	Mean size (mm)	Percent with camouflage	Percent with web	Percent active
Day	51	3.21 ± 0.43	35	22	67
Night	28	4.86 ± 0.56	43	21	43

nocturnal vs. diurnal activity suggests that other ecological factors might be more important than time of activity. For example, the morphological characteristics that we measured may be more representative of habitat type (e.g. forest vs. grass and underbrush) and prey within habitat type (e.g. Homopterans vs. Orthopterans) rather than traits unique to nocturnal or diurnal activity. Future studies could compare morphological, behavioral and taxonomic affiliations between habitats.

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FACTORS INFLUENCING THE OUTCOME OF BEHAVIORAL ENCOUNTERS IN *CTENOSAURA SIMILIS*

J. KHAI TRAN AND JILL L. HARRIS

Abstract: Ctenosaura similis exhibits territorial behavior, often resulting in conflicts between individuals. To assess whether individuals differ in their abilities to compete socially, we examined two factors thought to influence the outcomes of such encounters, body size and role as instigator/non-instigator. The "victor" of encounters was usually the larger individual and also the instigator. The instigator also tended to be the larger individual. Given that the victor of an encounter gains certain benefits (i.e., space or mates), we suggest that these factors may affect the fitness of individuals, and thus have evolutionary significance.

Key words: aggression, dominance, size, social interactions, territoriality

INTRODUCTION

Ctenosaurs (*Ctenosaura similis*), large territorial iguanid lizards, are common in Palo Verde National Park (Fitch and Hackforth-Jones 1983). Ctenosaurs sometimes display similar behavior in territorial and in courtship displays, often involving head-bobbing and species-specific postures (Savage 2002). During initial observations of ctenosaur groups, we witnessed multiple encounters between individuals. To investigate factors that may determine the outcome of these encounters, we tested the hypothesis that individuals differ in their abilities to compete socially. In areas of high ctenosaur density, territories may overlap and a social hierarchy may be established, generally with larger males dominating females and smaller males (Janzen 1983). Sex is difficult to determine in smaller individuals, so rather than differentiating between males and females, we first predicted that larger individuals would win encounters more often than smaller individuals. In many species, once an individual has established a territory, it is rarely ousted (Curtis and Barnes 1983). Based on this idea, we then predicted that non-instigators would win encounters more often, since we assumed that they would be the territory holders.

METHODS

We observed two groups of *C. similis* in Palo Verde National Park, one on the grounds of the Organization for Tropical Studies (OTS) field station and one approximately 1 km away, next to the park headquarters. Groups were observed from 0800 to 1600 on 14 January 2004. Encounters were defined as any observable interaction between two or more individuals. We noted the size and roles of the individuals involved and the outcomes of encounters. For multiple interactions between the same pair of individuals, only the first encounter was included in the analysis to avoid bias. We observed all encounters for their full duration, noting which individual was larger and which was the instigator. The instigator was defined as the individual that approached the stationary non-instigator. The victor was defined as the individual who did not move away from the location of the encounter.

Chi-squared tests were used to determine if the proportion of encounters that larger animals were victorious and the proportion of encounters that the non-instigators were victorious were significantly different from 0.5. In an attempt to differentiate between territorial and courtship behavior, we grouped the encounters

by speed of movement. Fast encounters were defined as encounters which involved running by one or both ctenosaurs. Slow encounters were defined as encounters which did not involve running.

Results

We observed three main types of encounters. A typical fast encounter involved one individual running towards another, with the other fleeing rapidly, sometimes pursued by the first. A second type of encounter, a type of slow encounter, involved an individual moving through an area, resulting in a nearby individual moving slowly away from the area. The third type, also a slow encounter, involved one individual, assumed to be a male, slowly approaching another, assumed to be a female, that would slowly move away, slowly pursued by the first; these encounters sometimes resulted in copulation events.

Overall, larger individuals were the winners more often (11 of 14 observed encounters) than smaller individuals ($c^2 = 4.57$, df = 1, P = 0.03), and the instigator won encounters more often (14 of 17) than the non-instigator ($c^2 = 7.12$, df = 1, P = 0.008). The larger individual was the instigator in every encounter (N = 13). Sample sizes differed since not all encounters involved a size difference or had a clear instigator.

Larger individuals and instigators won all of the fast encounters (N = 6). For slow encounters, the larger individual and the instigator still won more often (5 of 8 and 8 of 11, respectively), although results were not significant ($c^2 = 0.50$, df = 1, P = 0.48, and $c^2 = 2.27$, df = 1, P = 0.13, respectively).

Discussion

Our findings support the hypothesis that there exists a difference in *C. similis* individuals' abilities to compete socially: larger individuals and instigators won more encounters. Larger individuals appeared physically superior to smaller animals and would probably inflict injury upon another individual should actual fighting occur. For smaller individuals, selection may favor those that yield to larger, stronger individuals. Future studies could seek to demonstrate physical superiority of larger individuals, perhaps by assessing injuries afflicted in actual fighting and comparing them between larger and smaller individuals.

Our finding that the instigator would lose the encounter more often than the non-instigator was opposite of our prediction. We assumed that non-instigators would be the territory holders, since they would, by definition, remain stationary. However, this assumption appears to be incorrect, and in fact we guess the instigator was usually the territory holder. We did not consider that an individual may react to another individual in areas beyond its immediate surroundings, but within its presumed territory, and take chase. More needs to be known about the size and temporal stability of territories.

Since we found that the larger individual was always the instigator and also found that the larger individual won encounters more often, by extension, the instigator would win more often. Conflict, and movement in general, is energetically costly. Individuals may minimize activities involving movement, especially aggressive encounters, unless some benefit is gained. Since larger individuals are more likely to be victorious in encounters, they would be more likely than smaller individuals to instigate an encounter.

Victorious individuals must gain some benefit from winning encounters, such as territory, mates, or reduced competition for resources. Therefore, individuals that are large and aggressive, with these two traits probably

being linked, would have higher fitness.

Our results may have been confounded by the combination of mating and non-mating behaviors combined into one data set. In general, encounters classified as slow appeared to be courtship-based, because the two individuals remained in close proximity for long periods of time and several encounters of this type ended in copulation events. The ability to distinguish between sexes would be beneficial to future studies.

Future studies could investigate additional factors that may influence the outcome of encounters, such as health, sex, age, reproductive status, or aggression independent of size. We did not examine the magnitude of size differences. However, two similar-sized individuals may have a greater degree of escalation than two individuals of greatly disparate sizes. Further studies could also seek to confirm assumptions of the costs and benefits of encounters.

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DENSITY-DEPENDENT GROWTH OF THE COLUMNAR CACTUS, *LEMAIREOCEREUS ARAGONII*

STEPHEN T. WELLER AND ELIZABETH V. WILSON

Abstract: Intraspecific competition for resources often results in density-dependent growth. The columnar cactus *Lemaireocereus aragonii* has waxy rings that can be used to determine annual growth rate. We examined the effects of plant density on cactus growth rates. Cactus growth rate decreased with increasing cactus density in the presence of woody plants but was unrelated to cactus density when woody plants were absent. Elevation was unrelated to cactus growth rate. Further studies are needed to understand how density-dependence of growth translates into demographic effects on fecundity and survival.

Key words: Palo Verde, waxy growth rings

INTRODUCTION

Density-dependent growth in plants occurs when resources are limited. At high densities, individuals must share resources, and thus a smaller amount of a given resource is available to each individual. Competition for resources may affect growth rate, development, and reproduction (Begon et al. 1990). In this study we investigated the effects of varying conspecific and woody plant densities on the growth rate of the columnar cactus *Lemaireocereus aragonii.*

L. aragonii grows in the deciduous dry forests of Costa Rica, usually on steep limestone cliffs and outcroppings. *L. aragonii* grows primarily during the dry season when light availability is high, using internally stored water from the wet season. A waxy coating is deposited at the plant's meristem during the wet season, forming rings that can be used to measure annual extension growth of the cacti over time (Buskirk and Otis 1994).

These cacti and other woody plants growing on rocky outcroppings might compete for limited resources such as space, nutrients, and water. If so, the growth of *L. aragonii* would be negatively related to the neighborhood density of competitors, including conspecifics and woody plants.

METHODS

On 13 - 14 January 2004, we collected data on *L. aragonii* near the OTS field station in Palo Verde National Park, Guanacaste, Costa Rica. We sampled five discrete populations of cacti that were each located on different limestone outcroppings (about 5 - 250 m^2 each). Sample sites were located at the north end of the Sendero Mapache, as well as along the trail to the Mirador Guayacan west of the Sendero El Cactus.

For each cactus plant, we measured the number, height, and diameter of cactus stalks, the distance between each of the five most recent growth rings, altitude, the categorical presence or absence of woody plants (> 1 cm in diameter) within a 1 m radius, and the number of other cacti growing within a 1 m radius. We calculated the annual growth rate over the last five years by averaging the height of the five most recent growth rings. Because the condition of growth rings varied from cactus to cactus (the oldest having faded beyond recognition), we collected growth data only from cacti that had the five most recent rings visible enough to measure accurately. We measured cacti < 3 m in height that had at least five rings visible. Cacti with > 10% surface area damaged (i.e. brown, mottled, rotten, or scarred sections) were ex-

cluded from our study.

We log-transformed average annual growth to improve normality and homoscedasticity, and then used linear regression to model the relationship between cactus growth rate and cactus density in the presence and absence of woody plants. We also evaluated all possible regression models that included elevation.

RESULTS

Cactus growth rate decreased with increasing cactus density in the presence of woody plants ($F_{1, 24} = 6.33$, $P = 0.02$), but was unrelated to cactus density when woody plants were absent ($F_{1, 31} = 0.00$, $P = 0.96$; Fig. 1). Elevation was unrelated to cactus growth rate (or the residuals of cactus growth rate as a function of cactus density) in the presence or absence of woody plants ($P > 0.40$ for effects of elevation in all possible regression models).

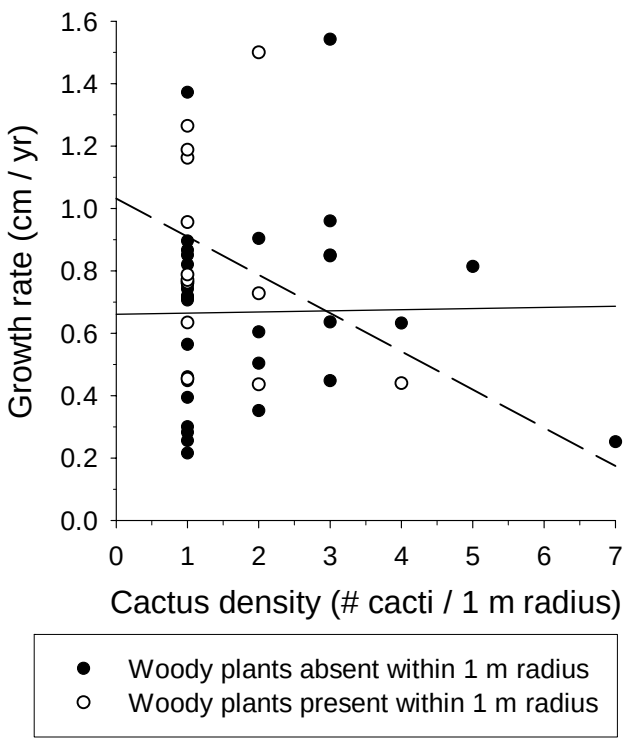

Figure 1. Relationship between cactus density and growth rate in the presence and absence of woody plants. Solid line = regression with woody plants absent; dashed line = regression with woody plants present. Cactus growth rate decreased with increasing density of conspecifics in the presence of woody plants ($y = 1.03 - 0.12x$, $r^2 = 0.10$) but not in the absence of woody plants.

DISCUSSION

Cactus growth rate was negatively density-dependent as predicted if there is resource limitation, but only in the presence of woody plants. In the absence of trees, cactus density may not be high enough for density dependent growth to occur. Although we did not quantify dispersion, the cacti appeared to be uniformly dispersed, so perhaps this spacing is sufficient to preclude resource limitation. The fact that density-dependence only emerged in the presence of woody plants suggests that woody plants are depleting one or more of the resources that can be limiting for cacti (perhaps water, nitrogen, or phosphorus).

Although we measured growth rate of *L. aragonii* as an indicator of density dependence, the ultimate effects of competition are on fecundity and survivorship (Begon, et al. 1990). There may be additional effects of density on cacti that are not apparent through our study. Long-term demographic studies could look at the fecundity and survivorship of cacti to further test for density-dependent effects on *L. aragonii*.

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SPATIAL DISTRIBUTION OF WATERBIRDS IN A RECENTLY MOWED SECTION OF TROPICAL MARSH

MATTHEW T. KEMP, LUKE M. EVANS AND BRENDA M. WHITED

Abstract: The Palo Verde marsh is undergoing a restoration program that involves mowing overgrown vegetation, mainly *Typha* and *Thalia*. It is unclear how marsh bird species will respond spatially to these newly opened areas. Because some marsh birds may require dense vegetative cover for feeding or protection, we hypothesized that in a large area of open water, bird density would vary spatially, with many species remaining near edges with denser vegetation. We collected abundance data and monitored habitat use by focal individuals in a recently mowed area in the marsh and found that 11 of 14 species had higher densities within 10 m of the edge than in the central, more open habitat. Three of the five species for which focal individuals were monitored spent more time foraging in the edge habitat. These results suggest that large open areas may not be optimal habitat for several species of water birds, though further mechanistic studies are needed to understand the patterns we observed.

Key words: egret, gallinule, heron, limpkin, Palo Verde marsh, restoration, waterbirds, wetlands

INTRODUCTION

The Palo Verde marsh, located along the Tempisque River in Palo Verde National Park, is one of the most extensive areas of wetland in northwestern Costa Rica and provides important habitat for a variety of waterbird species. Since the late 1970's, the historically open-water marsh has become choked by cattails (*Typha* sp.), which have created a homogeneous habitat limiting bird diversity and abundance (Holmes, pers. comm.). In 2003, OTS and partners began a restoration program to reopen some cattail-dominated sections of the marsh (E. Gonzalez, pers. comm.). An early study suggested that the newly created open-water space increased the abundance of some waterbird species (e.g., black-bellied whistling-duck, *Dendrocygna autumnalis;* Licona et al. 2003).

Other marsh birds, however, may require some amount of dense vegetation (e.g., *Thalia, Typha*) as cover from predators, foraging substrate, or nesting sites. Thus, large areas lacking vegetative cover, such as those created by restoration activities, could be detrimental to such species. These adverse effects could be manifest on a variety of scales, from daily foraging behavior—the scale we examined—to reproductive success. To test the hypothesis that marsh species favor areas with nearby cover, we quantified bird abundance in a recently mowed sector of the Palo Verde marsh. We predicted that marsh birds would be more abundant in edge areas (i.e., closer to cover), than in more open habitat.

METHODS

Our study location was Laguna de Palo Verde, Palo Verde National Park, Costa Rica. On 13 January 2004, marsh vegetation (mainly dense *Thalia* stands) just west of the OTS station's observation tower was mowed by a tractor (Appendix 2). This created 28,000 m^2 of open water with patches of floating, uprooted vegetation, bordered by dense, 2 m high *Thalia* and *Typha* on all sides. The edge between the open area and uncut vegetation was abrupt. We defined any point within the mowed area < 10 m from the cut edge as "edge" habitat and any point > 10 m as "open" habitat. We believed that 10 m was an appropriate distance for our purposes because any bird within this range would be able to reach cover quickly. Also,

greater proximity to the edge might reduce visibility of marsh birds to potential predators.

On 14 - 15 January, MK conducted three surveys per morning (ca. 0745 - 0815, 0830 - 0900, 0915 - 0945) during which he counted all individuals of each bird species that were foraging or sitting within the mowed area. The location of each individual was categorized as edge or open habitat. All abundance data were weighted according to the total area of each spatial category, producing a per hectare measure of density of individuals. We did not record flying individuals or species such as snail kite (*Rostrhamus sociabilis*) and red-winged blackbird (*Agelaius phoeniceus*) that were not continuously utilizing the area at the level of the water or floating vegetation. We analyzed density data with a full factorial two-way ANOVA, with habitat and species as main effects. For each individual species, we also used a chi-square test to evaluate whether birds occurred in edge vs. open habitat more or less often than expected based on the relative area of the two habitats; for this we used the average of the six counts (which guarded against inflating our observations with repeat measurements of the same individuals).

On the same mornings, LE and BW monitored focal individuals of five species (glossy ibis, great egret, limpkin, little blue heron, northern jacana). They observed each individual for 10 min (n = 8 for all species except limpkin, n = 5), recording total time spent in edge and open habitat. Focal individuals were selected randomly from a pool of all birds within the mowed area. These data provided time-budget measures of habitat use for a subset of species to complement our abundance measures. The proportion of time spent by each bird in edge habitat was evaluated with a t-test against the null hypothesis of 0.255 based upon the proportional area.

RESULTS

We recorded 19 species of birds foraging or sitting within the newly opened area of marsh (Appendix 1). Common gallinule, great blue heron, least bittern, roseate spoonbill, and white ibis were rare (< 5 sightings) and excluded from the analyses. For the remaining 14 species (Fig. 1), the two-way ANOVA revealed signifi-

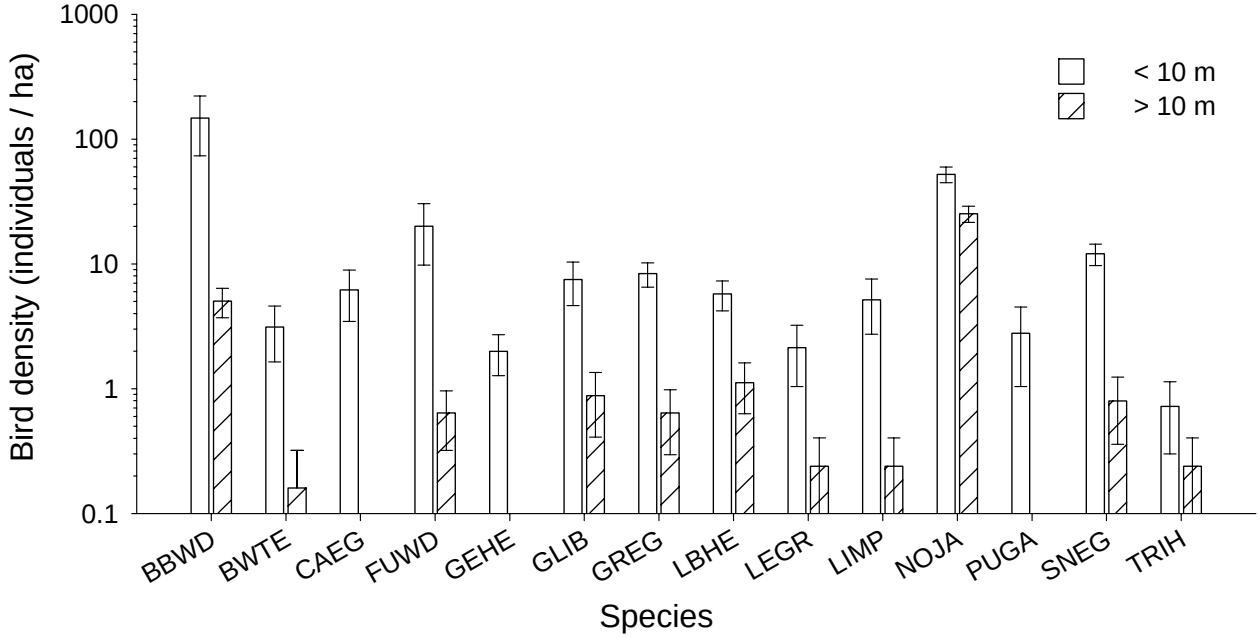

Figure 1. Comparison of the density of individuals (mean ± SE; n = 6 censuses; note log scale) of each species recorded in edge and open habitat. Codes, latin names, and total count numbers for each species are in Appendix 2.

cant effects of both species ($F_{13,14}$ = 11.76, P < 0.0001) and habitat ($F_{1,14}$ = 62.82, P < 0.0001), but not the species-habitat interaction ($F_{13,14}$ = 0.79, P = 0.68). In the chi square analysis, 11 of 14 species showed significantly higher density of individuals in the edge zone than in the open habitat, while the other four species showed no significant difference in density between edge and open areas (Table 1).

Three of the five species for which we obtained focal sample data spent significantly more time foraging in the edge versus the open area than would be predicted by available area in each category (great egret, t = 13.90, df = 7, P < 0.0001; little blue heron, t = 4.96, df = 7, P = 0.0008; limpkin, t = 2.50, df = 4, P = 0.03; Fig. 2).

Table 1. Chi-square comparisons of bird abundance in edge vs. open habitats in the Palo Verde marsh. Species in bold had significantly more individuals in edge habitat than expected under the null hypothesis that abundance is proportional to area (df = 1 for all species). See Appendix 1 for full species names.

Species	X^2	P
BBWD	**318.76**	**< 0.001**
BWTE	**7.21**	**< 0.01**
CAEG	**8.70**	**< 0.005**
FUWD	**44.9**	**< 0.001**
GEHE	3.07	< 0.10
GLIB	**13.30**	**< 0.001**
GREG	**12.00**	**< 0.001**
LBHE	**5.07**	**< 0.05**
LEGR	2.29	< 0.25
LIMP	**6.56**	**< 0.025**
NOJA	**15.35**	**< 0.001**
PUGA	**5.01**	**< 0.05**
SNEG	**19.10**	**< 0.001**
TRIH	0.67	< 0.50

The other two species did not show a significant difference in time spent between the two habitats (glossy ibis, t = 1.40, df = 7, P = 0.10; jacana, t = 1.44, df = 7, P = 0.10).

Discussion

Our results showed that marsh birds were generally more abundant and spent more time near edges than in open areas. Mechanisms for the observed patterns include foraging habitat preferences and the need for nearby cover from predation, probably from raptors (e.g., peregrine falcons, *Falco peregrinus*), but the relative importance of these may vary among species. The foraging of least grebes, which are open water divers, should not be affected by the edge; furthermore, this species' diving ability reduces the need for vegetation as predation cover. The three duck species (black-bellied whistling-duck, fulvous whistling-duck, blue-winged teal), in contrast, used the mowed area for resting rather than foraging, so their use of

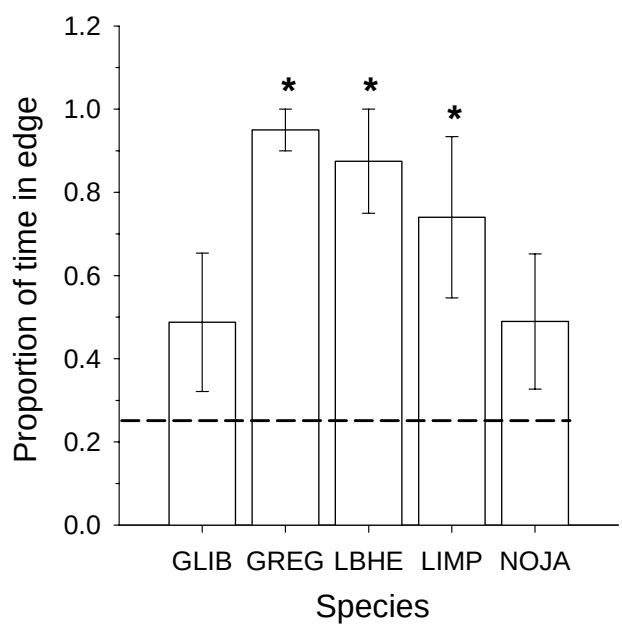

Figure 2. Proportion of time spent < 10 m from the edge (mean ± SE). Stars indicate a significant difference from the expected value based on proportionate area of edge habitat (0.255, represented by dashed line).

the edge habitat is probably related to reducing vulnerability to predators.

Eight out of the ten wading species (three egret species, little blue heron, ibis, jacana, limpkin, gallinule) showed significantly higher densities in edge habitat; the other two (green heron, little blue heron) showed a similar trend. Individuals of these species are generally solitary foragers, so they might benefit from nearby vegetation as a refuge from predators. Alternatively, the edge may simply have provided better foraging sites for wading birds, even though qualitative characteristics such as water depth and density of floating vegetation did not differ between the edge and open habitats.

Because of the unique, recently disturbed nature of our unreplicated study site, management implications of our results are presently unclear. Nevertheless, we suggest caution in aggressively pursuing large-scale mowing activities throughout the marsh, because our data suggest that some bird species favor edge habitat, and some may in fact be more abundant within the densely vegetated portions of the marsh. Further studies should examine whether the distributional pattern we observed holds for all large open areas of the marsh, as well as explore potential mechanisms for this pattern on a species by species basis. Also, long-term census data in mowed and unmowed areas would be useful in determining the effects of restoration activities on the overall abundance of marsh birds.

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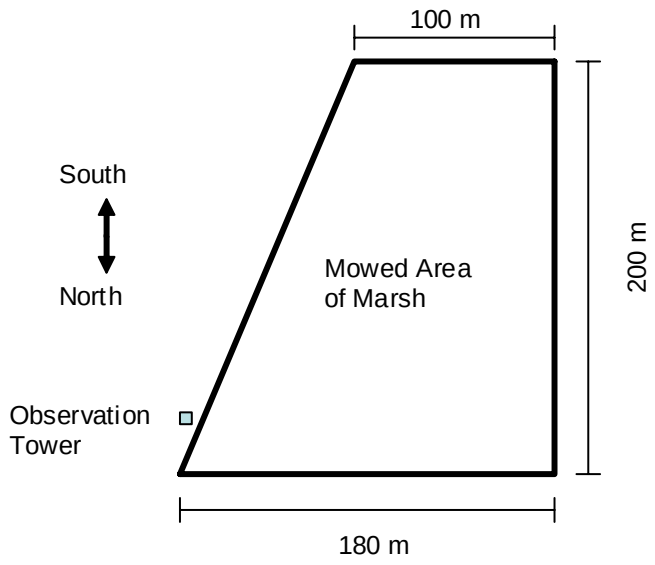
Appendix 1. Shape and dimensions of the census plot. Surveys were conducted from the observation tower.



Appendix 2. Codes, common names, and Latin names of marsh bird species recorded during the census periods, with mean and maximum count (in parentheses) of six censuses.

Symbol	Common name	Latin name	Census mean (max)
BBWD	Black-bellied whistling duck	*Dendrocygna autumnalis*	130.3 (260)
BWTE	Blue-winged teal	*Anas discors*	3.2 (7)
CAEG	Cattle egret	*Bubulcus ibis*	2.8 (7)
COGA	Common gallinule	*Gallinula chloropus*	0.2 (1)
FUWD	Fulvous whistling duck	*Dendrocygna bicolor*	18.0 (54)
GBHE	Great blue heron	*Ardea herodias*	0.3 (2)
GEHE	Green heron	*Butorides striatus*	1.0 (3)
GLIB	Glossy ibis	*Plegadis falcinellus*	8.5 (16)
GREG	Great egret	*Casmerodius albus*	7.0 (12)
LEBI	Least bittern	*Ixobrychus exilis*	0.2 (1)
LBHE	Little blue heron	*Egretta caerulea*	6.3 (8)
LEGR	Least grebe	*Tachybaptus dominicus*	1.8 (4)
LIMP	Limpkin	*Aramus guarauna*	3.3 (13)
NOJA	Northern jacana	*Jacana spinosa*	91.3 (113)
PUGA	Purple gallinule	*Porphyrula martinica*	1.5 (6)
ROSP	Roseate spoonbill	*Ajaia ajaja*	0.7 (2)
SNEG	Snowy egret	*Egretta thula*	9.2 (13)
TRIH	Tri-colored heron	*Egretta tricolor*	1.2 (2)
WHIB	White ibis	*Eudocimus albus*	0.2 (1)

TEMPORAL PARTITIONING OF FEEDING IN TROPICAL MARSH FISH OF LAGUNA PALO VERDE

R. SCOTT CUSHMAN AND PAUL A. MARINO

Abstract: Several fish species co-occur in the tropical marsh system of Laguna Palo Verde. We hypothesized that these fish temporally partition feeding activity in the relatively small areas of open water. We tested this hypothesis by comparing fish abundances and gut contents at dawn and in the afternoon. All the fish showed the same pattern of high feeding and abundance in the afternoon, and low feeding and abundance at dawn. This pattern is probably due to the co-incindence of lower predation pressures and higher feeding efficacy in the afternoon.

Key words: Cichlidae, competitive exclusion, niche

INTRODUCTION

According to the competitive exclusion principle, coexistence of species requires a differentiation of realized niches, a "partitioning of resources" (Begon et al. 1990). In lentic aquatic systems, resources can be partitioned in at least three ways: spatially, as fish occupy their preferred habitats; by prey type, as fish choose different food items; and temporally, as fish feed at different times.

Several fish species coexist in Laguna Palo Verde, a large wetland in Palo Verde National Park, in Guanacaste province of northwest Cost Rica. These species include *Herotilapia multispinosa, Achrocentrus nigrofasciatus, Astatheros longimanus, Parachromis managuensis,* and *Oreochromis nilotica* (Cichlidae), *Astyanax aeneus* (Characidae) and *Poecilia gillii* (Poecillidae) (Vargas et al. 2002, unpub. manuscript).

These fish may partition prey types (Bussing 1998). For example, *P. managuensis* possesses large sharp teeth adapted to a partly piscivorous diet, while *H. multispinosa*, a species of similar size, has tricuspid teeth better suited for consuming algae and detritus (Bussing 1998).

Fish may partition the marsh spatially among preferred microhabitats, as has been shown for the marsh's zooplankton (Poulin et al. 1998). Alternatively, open water, which is uncommon in the marsh relative to the area covered by aquatic vegetation, may be preferred by fish species because of the potential for efficient foraging (Bussing 1998). In this case, temporal partitioning of feeding (e.g. day vs. night) could help minimize interspecific competition among fish.

We tested for temporal partitioning in open water areas by measuring diel patterns in the abundance and feeding intensities of the fish species that co-occur within this habitat.

METHODS

We took three samples with a seine net at mid-afternoon (1500) and three in the morning (0600). We restricted our measurements to *H. multispinosa, A. longimanus, P. managuensis, A. aeneus* and *P. gillii*. Samples were taken in open water areas, all in a long strip that was 4 - 6 m wide. This strip of open water was bordered on both sides by a mix of floating vegetation and thick patches of *Thalia geniculata* and *Typha dominguensis*. Two of us dragged the net for approximately 8 m, while two associates attempted to drive fish into the net from the opposite direction. Fish were identified, counted, and released in the field. To evaluate feeding intensity, we dissected 17 fish that died during the netting (four to eight per species); we visu-

ally inspected the contents of each fish's gut, and assigned a gut fullness ranking of zero, one, two, or three. *P. gillii* was not evaluated for gut fullness because of its small size.

We used 2 - way ANOVAs to test for the effect of time and species on abundance (catch size) and gut fullness. Catch sizes were log transformed to correct for heteroscedasticity.

RESULTS

Mean catch sizes were significantly larger in the afternoon ($F_{1,16}$ = 15.58, P = 0.0012; Fig. 1). Catch sizes differed significantly among the four species ($F_{3,16}$ = 6.33, P = 0.005): *P. gillii* was the most abundant, followed by *A. aeneus*, *H. multispinosa*, and *P. managuensis* (mean catch size = 28.5, 12.7, 5.3, 0.7). There was no significant interaction between sampling time and species in catch size ($F_{3,16}$ = 0.76, P = 0.53).

Fish guts were generally empty in the morning and relatively full in the afternoon. Mean gut fullness index was significantly higher in the afternoon ($F_{1,11}$ = 24.30, P = 0.0005; Fig. 2). Gut fullness did not differ among species ($F_{2,11}$ = 0.49, P = 0.62), nor was there a significant interaction between time of day and species ($F_{2,11}$ = 0.93, P = 0.42).

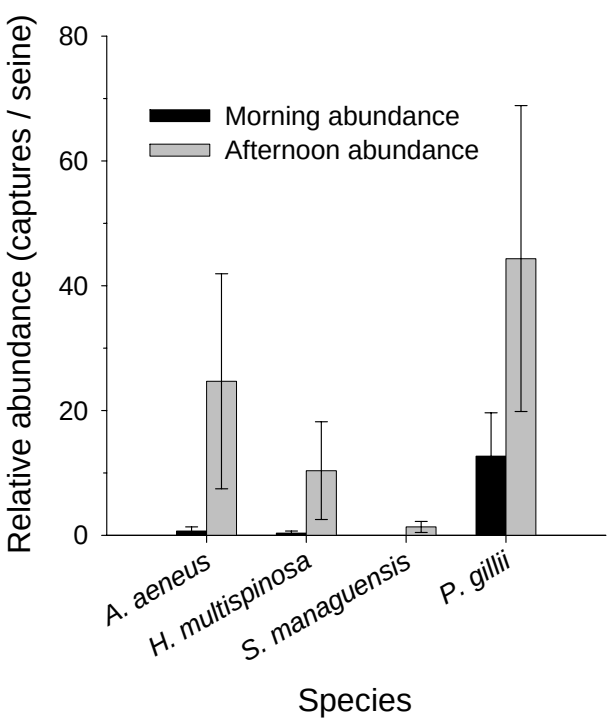


Figure 1. Relative abundances (± SE) in morning and afternoon of four species of fish in Palo Verde Marsh.

DISCUSSION

Our data indicate temporal trends in fish feeding and activity, but argue against temporal partitioning of feeding activity among species. Higher captures and higher gut fullness in the afternoon indicate that these fish feed on a similar schedule, in the same environment.

Visual feeding and predator avoidance are two likely explanations for this pattern. These fish are all visual feeders and may rely on direct sunlight to locate prey in the turbid marsh water. Major predators of fish in the marsh include crocodilians, fishing bats, and birds (potentially, herons, egrets, storks, osprey,

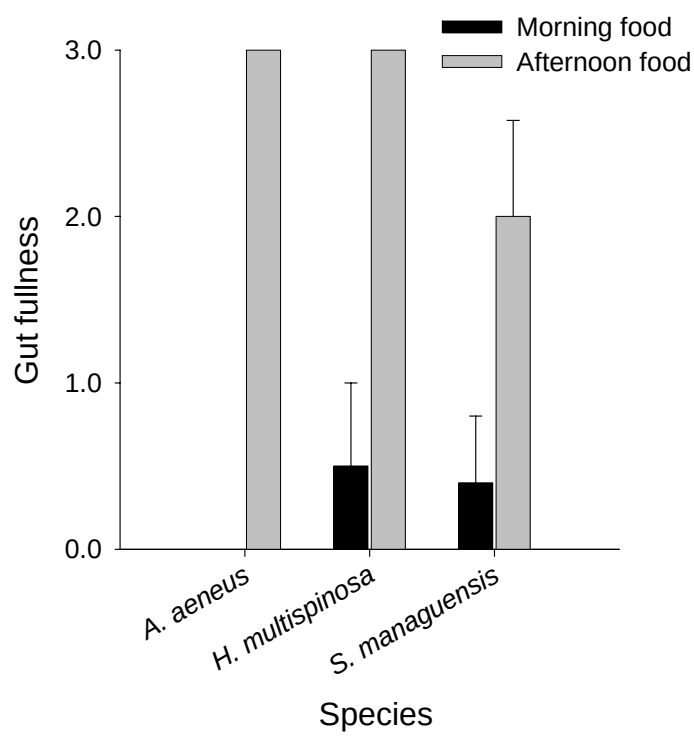


Figure 2. Mean gut content ranking on a scale of 0 to 3 for morning and afternoon samples of three fish species in Palo Verde Marsh. Samples sizes (from left to right) = 2, 2, 4, 1, 5 and 3.

and kingfishers). Predation by crocodilians and fishing bats is highest at night, and bird predation may peak in the early morning when birds are most active (M. Kemp, pers. comm.). Thus, feeding efficacy and predator avoidance may both favor the concentration of feeding activity in the afternoon. Such an alignment of feeding and predator avoidance pressures contrasts with the situation of many organisms, such as dielly migrating zooplankton, which must compromise between activity schedules that maximize feeding rate or minimize predation risk.

Our analysis was limited to shifts of fish abundances within just one marsh habitat type, open water. A future study that utilizes minnow traps, for example, could compare temporal patterns in fish abundances between microhabitats such as open water and floating vegetation. Our interpretation of the data reported here predicts that fish have a diel pattern of migration between open water and protective cover.

The hypothesis that this pattern is caused by both high predation pressures and low feeding efficacy at night and in the early morning would be falsified if predation pressures were actually higher during the day. Any visually feeding piscivorous fish in the marsh and many birds might prey more heavily on fish during the day. Future studies could seek to quantify the strength and diel patterns of predation from specific predators in Laguna Palo Verde.

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MICROHABITAT SELECTION OF *NOROPS* LIZARDS IN RELATION TO TEMPERATURE

SARA M. HELLMUTH, SARAH E. B. FIERCE AND ELEANOR E. CAMPBELL

Abstract: Small lizards that employ a sit-and-wait foraging strategy tend to be thermal conformers whose body temperature corresponds to that of the environment. Given that the metabolism of thermal conformers depends on surrounding temperatures, we postulated that temperature is a major influencing factor on their microhabitat distributions. We studied the distribution of two thermal conforming lizard species, *Norops cupreus* and *Norops sericeus*, predicting that they would be most abundant in the warmest available microhabitats. This prediction was supported but we did not demonstrate that the distributions were different from random with respect to temperature.

Key words: foraging efficiency, temperature distributions, Norops cupreus, Norops sericeus, *thermal conformers*

INTRODUCTION

Lizards employ two kinds of foraging strategies: sit-and-wait, and active searching (Janzen 1983). A lizard's ability to maintain a particular body temperature through thermoregulation is affected by its foraging strategy. Active-searching predators often have body temperatures 4 - 10 °C higher than the surrounding temperature (Janzen 1983). Sit-and-wait predators, in contrast, spend most of their time perching and tend to be thermal conformers, which have body temperatures only 1 - 2 °C above surrounding temperature (Janzen 1983). Given the dependence of sit-and-wait strategists on the surrounding temperature to regulate their metabolism, we hypothesized that small lizards employing this foraging strategy would have habitat preferences based on local ambient temperature.

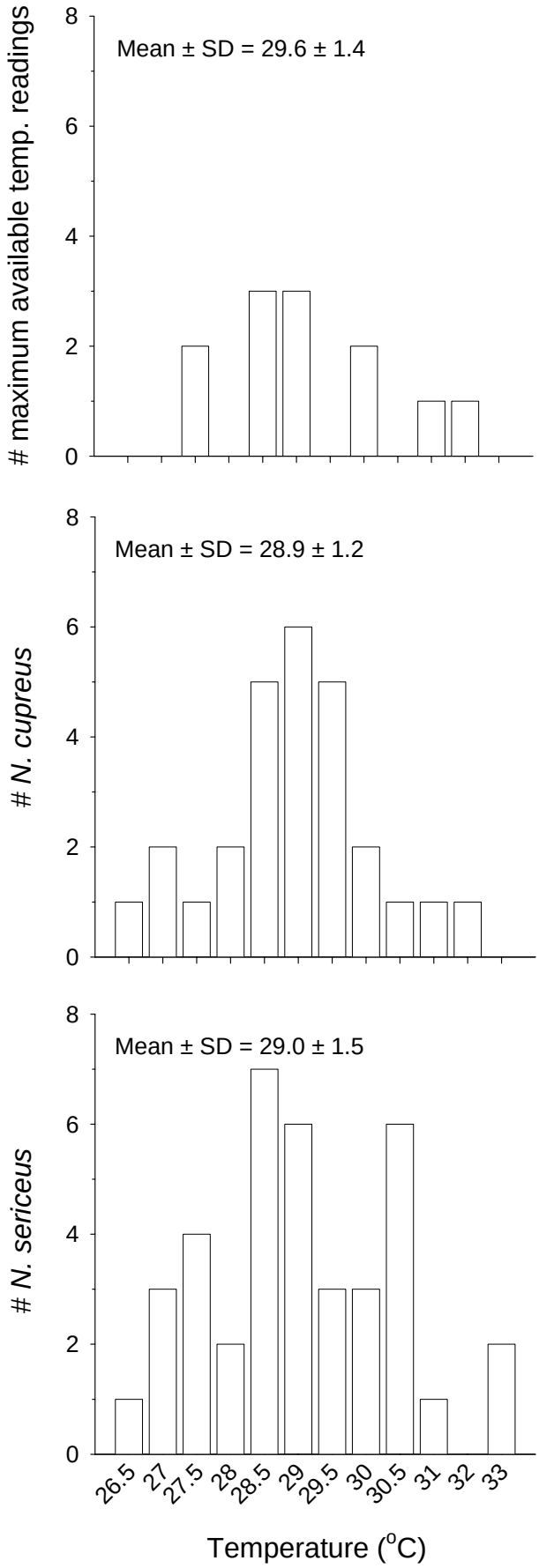
Two species of thermal conforming *Norops* lizards occur commonly in the tropical dry forest at Palo Verde. We predicted that *Norops* would be found in the warmest microhabitats available at a given time of day, where they would best be able to raise their metabolism and thus their activity level. We tested this prediction for two anole lizard species, *Norops cupreus* and *Norops sericeus*, which are both examples of thermal conforming, sit-and-wait predators that generally hunt invertebrates in leaf litter (Savage 2002).

METHODS

Throughout the day on 14 January 2004, we examined the distribution of *N. cupreus* and *N. sericeus* among microhabitats around the OTS field station at Palo Verde National Park, Costa Rica. We noted the time at which we first encountered each individual lizard, the temperature at that location (lizard location temperature), and the height above ground at which the lizard was initially observed. At 30 min intervals we estimated the maximum air temperature (maximum available temperature) within the area of recent lizard readings (ca 15 x 15 m) by measuring air temperatures within patches receiving direct sunlight. We used a one-way ANOVA to compare lizard location temperatures for the two species and maximum available temperatures. We also performed a visual evaluation of these three frequency distributions of temperatures to compare variance.

RESULTS

Mean lizard location temperatures did not differ from maximum available temperatures, nor did they differ between lizard species



($F_{2,77}$ = 0.61, P = 0.55). All three frequency distributions of temperatures appeared to be very similar in all respects (Fig. 1). Lizard height above ground did not differ significantly between species: mean ± SE = 23.4 ± 6.04 vs. 28.2 ± 6.79 cm for *N. sericeus* vs. *N. cupreus* (t = 0.53, df = 59, p = 0.60).

Discussion

Both *N. cupreus* and *N. sericeus* occurred in microhabitats that were as warm as the maximum available temperatures. Most of the lizards were found in a typical foraging position, perching on tree trunks less than 1 m above the ground (Janzen 1983). Presumably, lizards can maintain high metabolic activity, and therefore have high foraging efficiency, by positioning themselves in warm microhabitats.

One caveat to our conclusions is that we did not measure the temperatures of randomly selected microhabitats within these environments. Thus we do not know if lizard location temperatures or our estimates of "maximum available temperature," as measured just from sun patches, would have differed from randomly selected microhabitats. It may be that there was little difference in this forest between the average ambient temperature and maximum available microhabitat temperatures. In this case, we could have obtained the data in Fig. 1 even though lizards were positioning themselves at random with respect to microhabitat temperatures.

Future studies of the temperature distribution of lizards should use thermometers with rapid response times such as the BAT-12 telethermometer. With this, it would be possible to

Figure 1. Frequency distributions of maximum available temperatures (upper) and local lizard temperatures for *N. cupreus* (middle) and *N. sericeus* (bottom). The means and the variances were very similar among distributions.

measure the shaded air temperature as well as the temperature of an inert black body (e.g. a 2 x 2 cm of black foam rubber) to estimate solar warming potential. This would be the best way quantify the energy available to lizards in different microhabitats, and correlate it to their habitat preferences.

It is interesting to note the similarity in microhabitat preferences between the two species given that they are highly territorial (Savage 2002). Field observations indicated that more *N. sericeus* were active at dusk, suggesting that the two species partition the habitat temporally. Future studies could compare the temporal activity patterns of the two species, and determine how niche differentiation occurs.

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NOT SINGING IN THE RAIN: *NASUTITERMES CORNIGER* RESPONSE TO TRAIL DISTURBANCE IN THE PRESENCE OF WATER

R. QUINN THOMAS, HEATHER E. LAPIN AND PETER N. CHALMERS

Abstract: Termites in tropical wet regions, but not elsewhere, build covered trails to food sources. It is not known why termites build these trails. We tested the hypothesis that covered trails have evolved for rain protection by comparing the efficacy of trail repairs with and without simulated rainfall and found termite rebuilding ability to be significantly hampered in wet conditions. Contrary to the hypothesis, trail repair required at least 77% longer in the presence of water. We propose three alternate explanation for the trails existence: (1) to provide a microclimate for the termites, (2) to protect against predation, and (3) to protect pheromone-based communication systems within the colony.

Key words: arboreal nests, communication, pheromones, termite

INTRODUCTION

Termites occur worldwide, but tropical termites build nests using carton, fecal glue that the workers secrete (Borrow and White 1970). Additionally, it appears that only termites in rainforests and seasonally wet forests build carton trails to food sources, but the trail's function is unknown (Lubin 1983 and Holmes, pers. comm.) Rainfall is an important abiotic factor in the rainforests and dry deciduous forests where trails are found. Therefore, water may be a threat to the colony and affect the behavior of termites. We hypothesized that trails are built to protect the termites from the threat of water, and predicted that termites will rebuild a trail breach quicker under wet conditions. To test this prediction we examined how the rebuilding of a trail breach by *Nasutitermes corniger* differed under wet and dry conditions.

METHODS

We measured the breach rebuilding ability of 19 colonies of *N. corniger* in Palo Verde National Park, Costa Rica on 14 - 15 January 2004. We made a breach of ~ 1.5 mm in the trail at a measured distance from the nest. We measured the time at which the first soldier appeared at the breach (discovery time), the time elapsed after discovery before the first worker deposited carton (recruitment time), the subsequent number of carton deposits per minute to repair the breach (building rate), and the time until the breach was repaired (completion time), to a maximum of 15 min. We performed these measurements twice on each nest, once on each of two consecutive days (at the same time). On one day, the breach was dampened with water (~ 2 mL) every minute, and the other day was a control. Treatment and control were applied in randomized order. This matched-pair design standardized for differences in rebuilding rate due to differences in colony traits.

RESULTS

The time until trail breaches were discovered by *N. corniger* was unaffected by water additions (mean ± SE = 29 ± 7 vs. 53 ± 18 seconds for control vs. water addition; paired-t = 1.26, df = 18, P = 0.89). With the addition of water, recruitment time was longer (paired-t = 3.31, df = 18, P < 0.004; Fig. 1) and building rate was faster (paired-t = 6.71, df = 18, P < 0.001; Fig.1). Consequently the total time to repair trail breaches

was longer in the presence of water additions (mean ± SE = 900 ± 0 vs. 692 ± 44 seconds; paired t = 4.70, df = 18, P < 0.001). Building rate was unrelated to distance from the nest in the absence of water (P = 0.12; Fig. 2), but increased with distance from the nest with the water addition treatment (r^2 = 0.44, df = 18, P = 0.002; Fig. 2).

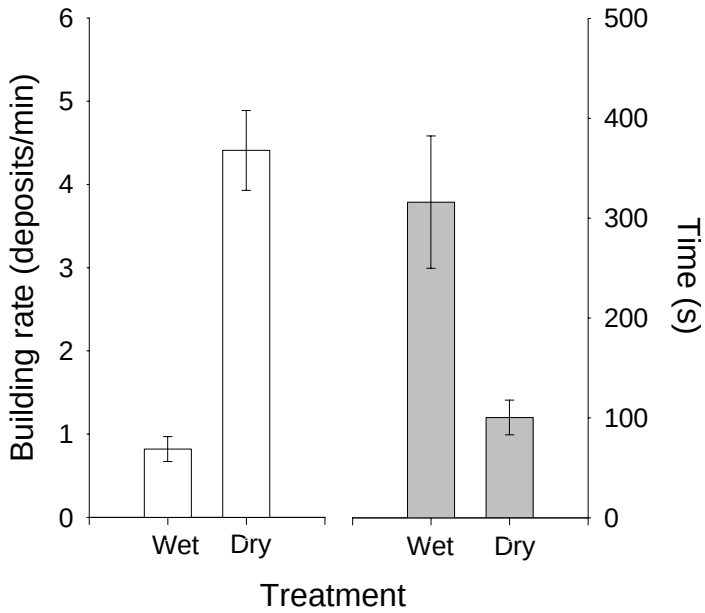

Figure 1. The rate (left) at which *N. corniger* rebuilds disturbed trails in wet and dry conditions and the time between when *N. corniger* soldiers discover a disturbance and when they recruit builders to fix it in wet and dry conditions (right). Mean (± SE) of rates and times are reported.

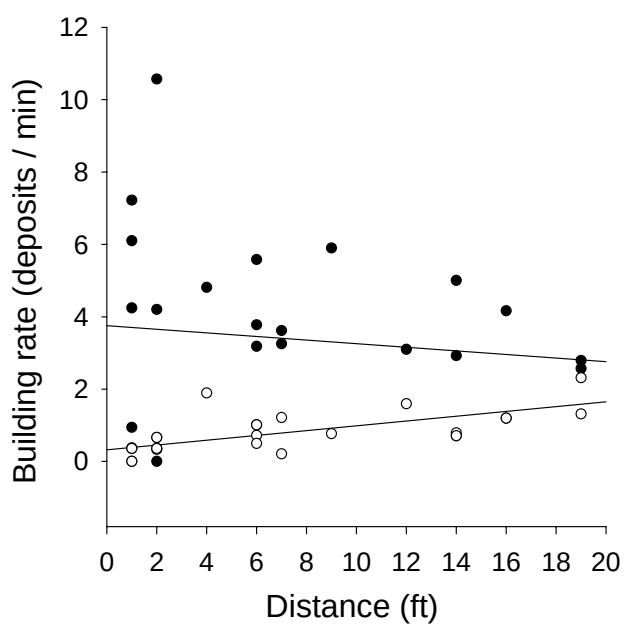

Figure 2. The rate at which *N. corniger* rebuilt trail breaches versus distance between the breach and the nest in wet (open circles) and dry (closed circles) conditions. Regression line shown for wet conditions.

Discussion

Our prediction that termites will rebuild trail breaches faster under wet conditions because water presents a threat was not supported. This suggests that trails are built for reasons other than protection from rain. We suggest three alternative hypotheses to explain why *N. corniger* builds protected trails.

First, termites may not build trails as protection from rain, but to preserve a more humid microclimate. Our wet treatment may have preserved the optimal level of humidity within the trail, so rebuilding quickly was not necessary to prevent desiccation. Altering the humidity without adding water could test this alternate hypothesis.

Another explanation could be that trails are built to protect against predation. For example, a soldier may generate alarm signals (presumably a pheromone) if the threat, like the continual application of water, remains present after the initial breach. This alarm signal may repel vulnerable soft-bodied workers and attract large-jawed, unpalatable soldiers (Lubin 1983). If the water addition treatments generated a sustained alarm, it could have caused recruitment time to increase and building rate to decrease, as we observed. This could also explain our finding that, under wet conditions, building rate increased as distance from the nest increased. A breach farther from the nest may pose less of a threat to the colony and would therefore be less likely to cause an alarm. This could explain the increase in building rate with increasing distance from the nest in the water addition treatment. Breaching trails at varying distances from the nest under both treatments

and counting the number of soldiers that appear at the breach could test this possibility.

Finally, the water-insoluble trails could specifically protect water-soluble communication pheromones from rain (Gribble, pers. comm.). The wet treatment could have diluted or altered the activity of pheromones that trigger repair behavior. Applying a treatment that disrupts pheromones without altering the microclimate could test this hypothesis.

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