A FAILED MUTUALISM BETWEEN *ACACIA CORNIGERA* AND ITS RESIDENT ANTS

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Abstract: The ant-acacia mutualism at Palo Verde National Park has been well studied for *Acacia collinsii*, but not *A. cornigera*. We examined the relationship between *A. cornigera* and its associated ants and found it was not consistent with well-documented ant-acacia mutualisms. The plants appeared healthy and provided abundant resources to ants (Beltian bodies, nectaries and thorns). However, the ants did not fully use these resources, and only 8% of the ant colonies on *A. cornigera* responded aggressively to prolonged disturbance. *P. flavicornis*, the only ant-acacia mutualist we found on *A. cornigera*, was far less aggressive than on nearby *A. collinsii*. Thus, the mutualism between these species appears to be dysfunctional, at least at our study site.

Key Words: Acacia cornigera, Acacia collinsii, *mutualism*, P. flavicornis, *defense*

INTRODUCTION

The ant-acacia mutualism at Palo Verde National Park has been well studied for *Acacia collinsii*, but not *A. cornigera*. Both species provide resident ant colonies with hollow thorns to inhabit, carbohydrates in the form of nectaries, and protein and lipids in the form of Beltian bodies. In return for these investments, mutualistic ant species provide aggressive defense against natural enemies (Janzen 1983).

Aggressive defense of *A. collinsii* by *P. spinicola* and *P. flavicornis* has been recorded repeatedly and consistently in the literature (e.g. Janzen 1983, annual reports in Dartmouth Studies in Tropical Ecology). Janzen (1983) suggests that the ant mutualisms with *A. cornigera* and *A. collinsii* are similar. We decided to test this assertion. We censused a local *A. cornigera* population and investigated the presumed mutualistic relationship with its resident ant colonies.

METHODS

During the late morning 8 January 2006, we censused a spatially well-defined population of *A. cornigera* in the open, cattle-grazed area between the marsh edge and the fence, in front of the OTS field station at Palo Verde. We measured the height of each tree and recorded the density of Beltian bodies on a 0-3 scale. A value of 3 signified higher than typical density (based on general observations of *A. collinsii* at Palo Verde), 2 represented a more typical density, 1 was less than typical, and 0 signified absence. We recorded the presence of holes in the thorns, indicating whether a tree had been colonized.

We classified visible ant density and activity on the same 0-3 scale. We then simulated vertebrate herbivory by manually removing leaves and stems, and noted the change in activity of the ant colony, which we again ranked on a 0-3 scale (0 represented no change in activity, 3 a dramatic increase). Aggression was ordered on a scale of 0-3 based on the ants'

propensity to sting when disturbed: 3 represented an immediate sting or bite, 2 an intermediate response (bites and/or stings), 1 required extreme provocation (prolonged simulated browsing) before a sting or bite, and 0 represented no bite or sting. We collected a sample morphotype of each resident ant colony and identified the morphotype to species.

RESULTS

Over a three-hour period we sampled 43 *A. cornigera* trees. Most trees (n=35) hosted only one species, but more than one ant species was found on 2 trees. Only 7.7% of the 39 ant colonies present showed any aggressive response. Among the 12 *P. flavicornis* colonies (each of which had sole occupancy of a tree), only 25% showed an aggressive response (i.e. aggressiveness of 1, 2 or 3 on our scale). In the Dartmouth long term ant-acacia study at Palo Verde, *P. spinicola* is common on *A. collinsii*, yet we found no *P. spinicola* in our study area (Table 1).An informal survey of ant species on *A. collinsii* within 50 m of the study site revealed the presence of several aggressive *P. spinicola* colonies. We found a higher frequency of *P. nigropilosa* (an ant-acacia parasite) than has been found in past studies (Table 1). Further, 18.6% of previously colonized *A. cornigera* had been abandoned. Yet, these abandoned *A. cornigera* appeared to be healthy, based on abundant nectaries and Beltian bodies, green, shiny foliage and large thorns, compared to the normal appearance of *A. collinsii* at Palo Verde.

DISCUSSION

Four observations indicate a failure of the mutualism between *A. cornigera* and its resident ants: (1) low aggression in the usually aggressive *P. flavicornis*, (2) a high frequency of non-aggressive and parasitic *P. nigropilosa* and the absence of *P. spinicola* (Table 1), (3) a high frequency of abandoned *A. cornigera* trees, and (4) a high density of Beltian bodies on *A. cornigera* at the study site. It is clear that the ants were not providing defense for the tree even though the tree was providing resources for the ants. Despite the lack of defense, the trees appeared in good health.

The presence of nearby *A. collinsii* trees indicates that a comparative study of

TABLE 1. Comparison among three sites at Palo Verde of ant species occupying acacia trees. Marsh edge (*Acacia cornigera*) was a cattle-grazed site with no canopy. Study A (*A. collinsii*) was a grazed site with no canopy, 4 km from our site. Study B (*A. collinsii*) was an ungrazed site with a canopy, 0.2 km away from our site. Percentage values represent percent of trees colonized by each species.

	A. cornigera (Marsh edge)	*A. collinsii* (Study A**)	*A. collinsii* (Study B**)
Total no. of *Acacia*	43	63	74
P. flavicornis	27.9%	12.7%	0.0%
P. nigropilosa	39.5%*	1.6%	5.4%
P. spinicola	0.0%	15.9%	55.4%
Crematogaster	4.7%*	55.6%	5.4%
Other spp.	18.6%	9.5%	21.6%
No ants present	14.0%	4.8%	18.9%

*In both instances of *Crematogaster* species, *P. nigropilosa* was also found on the plant

**Study A and Study B data are from a Dartmouth College long- term acacia-ant study (C. Layne, pers. comm.)

the two acacia species in the area is possible. Thus, it would be possible to investigate experimentally whether ant mutualists preferentially colonize *A. collinsii* rather than *A. cornigera.* In the meantime, the puzzle remains: why has the mutualism failed in this study area?

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RELATION BETWEEN *A. COLLINSII* NECTARY DENSITY AND DISTURBANCE-INDUCED ACTIVITY OF *P. SPINICOLA*

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Abstract: Acacia collinsii produces nectaries on leaf petioles for the mutualistic *Pseudomyrmex spinicola* ants that defend them. We examined the relationship between the density of nectaries and ant activity, hypothesizing that ant activity would increase with nectary density. We measured ant activity and nectary density on small (<1 m tall), medium (1-2 m tall), and large (2-3 m tall) ant acacia trees. Ant activity increased with nectary density on small and medium trees, suggesting that higher tree investment resulted in greater ant defense. However, we found that large trees with the same nectary density had less ant activity than small and medium trees, suggesting a lower return on investment as trees grow larger than 2 m tall.

Key Words: Acacia collinsii, Pseudomyrmex spinicola*, mutualism, plant defense, nectary*

INTRODUCTION

In the obligate mutualism between the ant, *Pseudomyrmex spinicola*, and the tree, *Acacia collinsii*, the ant receives food and shelter from the tree in return for defense against herbivores and competing plants (Janzen, 1983). One reward for ants is a sugar solution at nectaries on leaf petioles. We reasoned that ants would defend most vigorously those plants that provide the greatest reward. Thus, we predicted that as the investment in the reward (nectary density) increased, the investment return (ant activity) would also increase. We used ant activity as a proxy for the level of defense provided by the ants.

METHODS

On 9 January 2006, we sampled 26 *A. collinsii* trees in a heavily cattle-grazed area, northeast of the OTS station in the tropical dry forest of Palo Verde National Park, Costa Rica. This area has been used for ant-acacia research in several studies by the Dartmouth Tropical Studies FSP (e.g. Iwamoto et al., 2003). On trees containing the mutualist ant species *P. spinicola,* we haphazardly chose 4 branches on each of 10 small (0 - 1 m tall) and 10 large trees (2 - 3 m tall), and 3 branches on each of 6 medium trees (1 - 2 m tall). We visually estimated tree height and chose branches representative of the entire tree. We counted the number of nectaries on the leaf petioles along various branch lengths (4 - 103 cm), measuring on each branch from the first node with green leaves to the last node with green leaves.

We quantified nectary density as the number of nectaries/cm along branches. We measured ant activity by tapping for 5 seconds at an arbitrary point near the middle of the sampled length on each branch. We counted the number of ant crossings at that point over 1 minute immediately after tapping each branch. We defined investment return as ant activity/nectary/cm. We analyzed the

relationship between ant activity and nectary density using linear regression in JMP 5.0.1. We then used an ANOVA to determine if return on investment varied among tree sizes.

RESULTS

Ant activity increased with nectary density (r^2= 0.21, df=1, P=0.02; Fig. 1). Return on investment depended on tree size ($F_{2, 24}$= 7.35, P=0.0032; Fig. 2). Medium trees (1-2 m) had the highest return on investment (52.56 ± 7.00 ant ativity/nectary/cm; mean ± SE), followed by small trees (< 1 m; 43.46 ± 2.90), and then large trees (2-3 m; 24.30 ± 5.88).

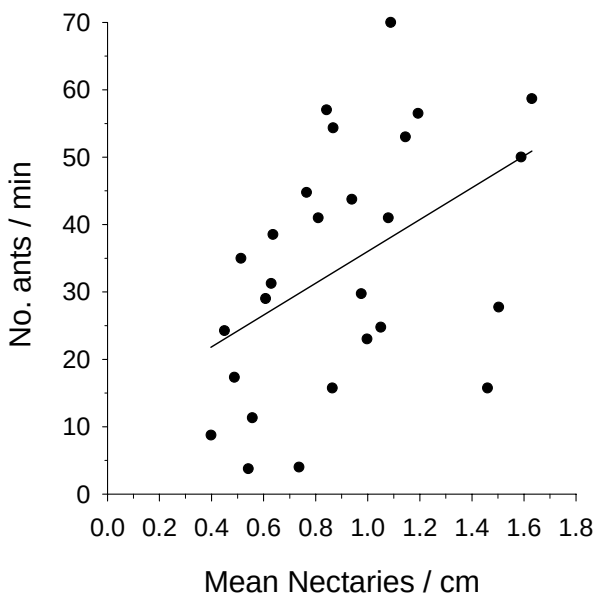

Figure 1. The relationship between *Pseudomyrmex spinicola* ant activity (measured as number of ant crossings on a point after branch disturbance) and nectary density on *Acacia collinsii* in Palo Verde National Park, Costa Rica (r2=0.21, df=1, P=0.02).

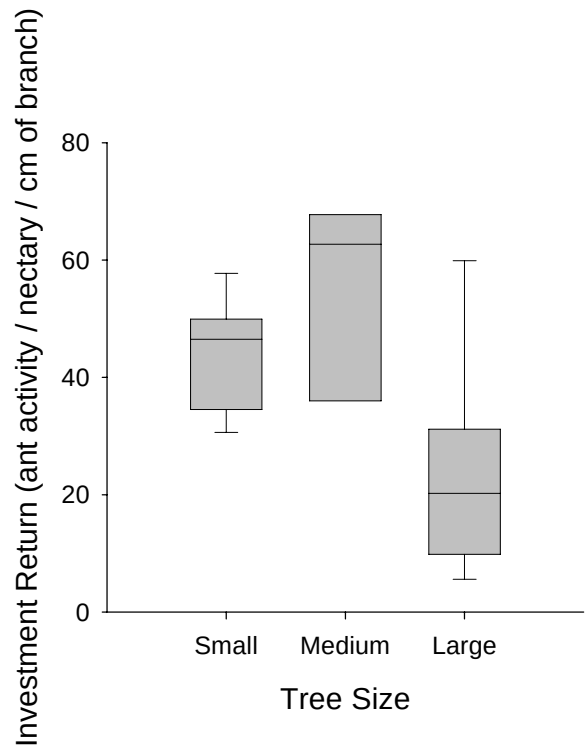

Figure 2. Differences in investment return in ant defense among size classes of *Acacia collinsii* at Palo Verde, Costa Rica. Small trees were < 1 m tall, medium trees 1-2 m tall, and large trees 2-3 m tall. Investment return was defined as the activity of mutualist *Pseudomyrmex spinicola* ants per nectary per meter of branch supporting green growth. See Figure 1 for definiton of ant activity. Error bars represent 95% confidence intervals. (Error bars on medium trees coincide with horizontal bars.)

DISCUSSION

Our results supported our hypothesis that greater plant investment would lead to more effective defense by ants. However, in the largest trees, investment return was less than expected. Because the amount of nectar per nectary does not depend on tree size (Matsuura et al. 2005), lower ant activity in large trees cannot be explained by lower nectar availability. We do not have a good alternative hypothesis. However, large

trees may be subject to different constraints (due to different ratios of photosynthetic/non-photosynthetic tissue).

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AGGRESSIVE RESPONSES OF *P. SPINICOLA* TO NUMBERS OF INTRODUCED *P. FLAVICORNIS*

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Abstract: Pseudomyrmex spinicola, which form colonies in *Acacia collinsii* trees, use a variety of aggressive responses against heterospecific ants that come into contact with their host tree. We hypothesized that *P.spinicola* would tend to expel but not kill introduced ants when few ants were introduced, but would grapple with and kill ants when many heterospecific ants were introduced. Our data supported our hypothesis and suggests that *P.spinicola* has been under selection to respond with more effective, but more costly behavioral response only when the colony may be seriously threatened by invasion.

Key Words: invasion, aggressive response, P. spinicola, P. flavicornis

INTRODUCTION

Pseudomyrmex spinicola and *P.flavicornis* are two species of ants that have obligate mutualist interactions with *Acacia collinsii* at Palo Verde National Park, Costa Rica. The ants protect their host trees from invasion by other ant species, using several aggressive responses to repel the invaders (Janzen 1983).

In this study we examined a threat of invasion to *A.collinsii* trees inhabited by *P.spinicola* by introducing different numbers of *P.flavicornis* ants onto the host tree. We hypothesized that although prolonged attacks are more costly, they would be more efficient in disabling larger numbers of introduced ants. Rapid expulsions, which are less costly, would tend to occur when few ants were introduced. We therefore tested for a relationship between the type of aggressive reponse and the number of invading ants. Specifically, we identified two types of aggressive response that apparently differ in energy costs; 1) the rapid expulsion of intact introduced ant from the host tree (with the possibility of expelled ants returning to the host tree) and 2) prolonged attack on introduced ants which permanently disables them.

METHODS

We sampled *A. collinsii* along a belt transect of the main access road 5 km east of the OTS station in Palo Verde National Park, Costa Rica. The transect spanned 30 m on either side of the road and extended for ca. 1 km.

Using aspirators, we collected *P. flavicornis* from three *A. collinsii* trees and applied them in arbitrarily chosen numbers (1 to 10 individuals) to 16 *A. collinsii* trees, each with active resident colonies of *P. spinicola*. On each tree, the *P. flavicornis* individuals were placed simultaneously at a height of approximately 1.3 meters (or at the top for smaller trees), near the central trunk. We monitored each tree for five minutes after the introduction and recorded

the time of each expulsion and the start of each prolonged attack.

We performed all analysis in JMP 5.0.1.2.

RESULTS

The number of prolonged attacks per introduced ant increased significantly with number of introduced ants (multivariate, non-parametric Spearman's Rho, P=0.05). Neither the number of expulsions per introduced ant (Spearman's Rho, P=0.18), nor the average time to either expulsion or prolonged attack (Spearman's Rho, P=0.23), was influenced by the number of introduced ants.

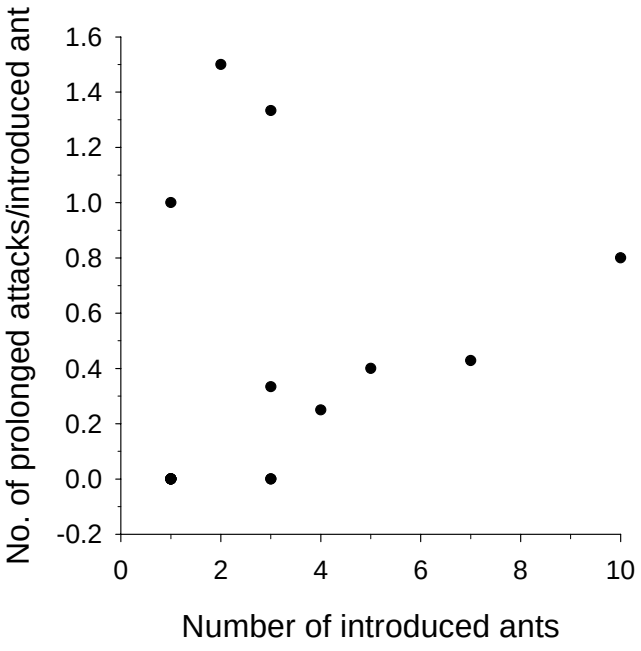

Figure 1. Number of prolonged attacks per introduced *P. flavicornis* ant by resident *P. spinicola* as a function of the number of ants introduced, in 16 *A. collinsii* trees in Palo Verde National Park (Spearman's Rho, P=0.05)

DISCUSSION

As hypothesized, *P.spinicola* tended to use the more energy-demanding, but more effective prolonged attacks when they encountered a large number of introduced ants. In contrast, when they encountered few *P.flavicornis* they tended to use the less demanding, but less effective expulsion response. *P.spinicola* has apparently been under selection to respond with the more effective but costly behavioral response only when the colony may be seriously threatened by invasion.

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COMPARISON OF DEFENSES AND STEM DENSITIES OF WOODY PLANTS BETWEEN CATTLE-BROWSED AREAS AND PROTECTED AREAS AT PALO VERDE NATIONAL PARK

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Abstract: We expected differences in woody plant defenses and stem density between heavily cattle-browsed areas and protected areas in Palo Verde National Park, Costa Rica. We predicted that there would be a higher density of woody plants with thorns, tough leaves, or aromatic chemical defenses (assessed by a smell test) in browsed areas. We also predicted that the density of woody plants in size classes accessible to cattle would be less in the browsed than the protected area. We found a significantly higher thorniness index in the plant community in the browsed area. We also found significantly greater densities of woody plants in the protected area in the smallest (0.5-1 cm diameter) woody plant size class.

Key Words: herbivory, cattle browsing, plant defense, thorns

INTRODUCTION

Cattle browsing has played an important role in the history and recent management of Palo Verde National Park, Costa Rica. The marsh and the understory of the dry forest on the lower slopes were subject to cattle browsing until 1981, when all cattle were removed. In 1987, cattle were reintroduced within a fenced zone near the marsh, to aid in the control of cattails. Thus, we can compare areas of forest understory that have been browsed for the past 19 years with areas protected from cattle during that time. Stewart et. al (1995) found significant differences in the morphotypes of small shrubs between the currently browsed and protected areas, but did not examine differences in plant defenses.

We examined three common defenses in which woody plants invest: thorns, tough leaves, and volatile secondary metabolites. We hypothesized that these defenses are an advantage in areas browsed by cattle, while in protected areas, plants that put more of their resources into growth outcompete plants that invest in defense. Thus, we predicted that the woody plants in the currently browsed area would have more defensive traits than those in the currently protected area, and that the densities of the smallest size classes (plants with twigs and leaves at an accessible height for cattle browsing) would be greater in the area protected from cattle browsing.

METHODS

We sampled on 10-11 January 2006, within 1 km of the marsh edge, ca. 1 km east of the OTS Field Station, Palo Verde National Park, Costa Rica. The study site was a 200 m x 50 m plot, bisected lengthwise by a cattle fence (Fig. 1). We divided the plot into four 50 m x 50 m

sectors. In each sector, using stratified random sampling, we selected a random point on the fence, and ran a transect perpendicular to the fence into both the currently browsed area and the protected areas. For the first transect, we sampled along its full 25 m length in the browsed area. To expedite sampling and increase replication, further transects were sampled along randomly chosen 10 m lengths in the browsed and protected areas (Fig. 1).

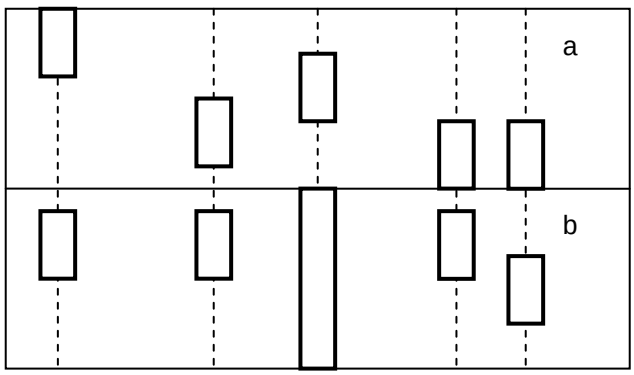

Figure 1. Diagram of the protected (a) and currently browsed (b) study areas (borders denoted by heavy black line) at Palo Verde National Park, Costa Rica. The center line represents the fence and each dashed line represents a transect.

We sampled woody plants for thorniness, toughness, and smell (as a crude indication of the presence of aromatic compounds) along each transect. We counted stems in the following diameter classes: 0.5-1, 1-5, 5-10, 10-20 cm, continuing in 10 cm intervals up to 70 cm. In the currently browsed area, we counted the plants in the 0.5-5 cm size classes within 3 m of the transect, plants in the 5-20 cm size classes within 5 m, and plants in the 20+ cm size classes within 10 m of the transect (sampling on both sides). In the area protected from browsing, sampling was similar, except that stems in the 0.5-5 cm size classes were counted within 2 m of the transect. Thorniness was ranked from 0 (no thorns) to 3 (dense thorns); toughness was ranked from 1 (easy to tear and crush) to 3 (difficult); and smell was ranked from 0 (normal "green foliage" smell) to 3 (strong smell). Smells were qualitatively variable, ranging from "garlic" to "cooked crab."

We obtained an index of foliage density at ca. 1.3 m height by having a subject in a white shirt walk 15 m from the fence along each transect, in both browsed and protected areas. For each observation, five observers estimated the percent exposed area of the white shirt from a single vantage point on the fence. We omitted the visual estimate that deviated most from the mean of the five values, retaining four for data analysis. Data from the 25m-length belt transect were standardized to be comparable to the 10m-length belts. We ran one-way ANOVAs to compare differences in defense indices, basal areas, and stem densities between the currently browsed and protected areas.

RESULTS

Individuals (all size classes combined) had a higher thorniness index in the currently browsed area than in the protected area (Fig. 2, $F_{1,8}$=5.43, P=0.05). Neither smell ($F_{1,8}$ = 0.15, P = 0.71) nor toughness ($F_{1,8}$=2.12, P=0.18) differed significantly between the browsed and protected areas (Fig. 2).

The ratio of mean thorniness (currently browsed/protected) increased with increasing diameter over the smallest three size classes (Table 1). There were no differences between the currently browsed

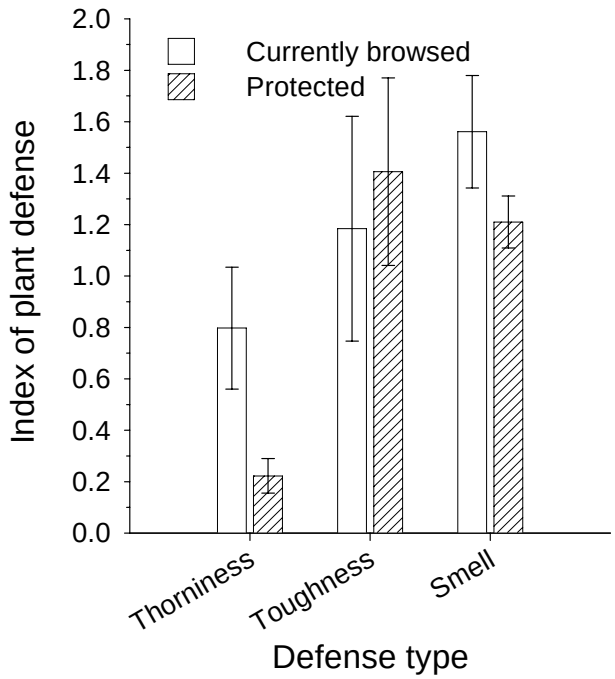

Figure 2. Index (mean ± 1 S.E.) of plant defense (thorniness, leaf toughness, and smell of crushed leaves, all rated on a scale of 0-3) in areas with different cattle browsing histories at Palo Verde National Park, CostaRica.

and protected areas for smell and toughness (although toughness for the 1.0-5 cm size class was marginally significant, Table 1).

The smallest two size classes accounted for most stem density (Fig. 3). The protected area had significantly higher stem density in the 0.5-1.0 cm size class (mean=1.67/m^2) than the currently browsed area (mean=0.81/m^2, $F_{1,8}$=5.29, P=0.05, Fig. 3).

The visual index of foliage density was greater in the protected area (mean=51%) than in the currently browsed area (mean=23%, $F_{1,8}$=4.66, P=0.06).

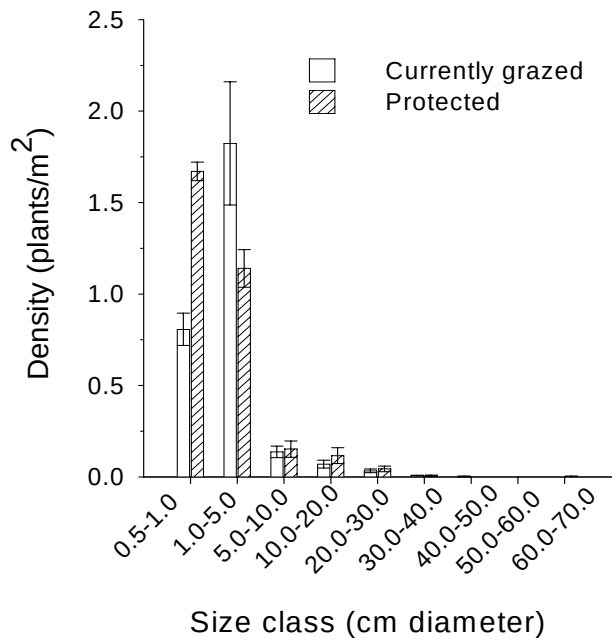

Figure 3. Mean density of woody plants by size class in areas with different cattle browsing histories at Palo Verde National Park, Costa Rica (± 1 S.E.). Differences in density between areas were significant in the 0.5-1 cm size class and marginally significant in the 1-5 cm size class (see text for details).

TABLE 1. Mean indices of plant defense (thorniness, leaf toughness, and smell of crushed leaves, all rated on a scale of 0-3) and mean basal area for the 3 smallest size classes of woody plants in currently cattle browsed (referred to as browsed) and protected areas at Palo Verde National Park, Costa Rica. See text for details of statistical analysis. All values are ± 1 S.E.

Size class		Mean Thorniness Index	Mean Toughness Index	Mean Smell Index	Mean Basal Area (cm^2)
0.5-1.0 cm	Browsed	0.3540 ± 0.1025	1.3689 ± 0.1587	1.2300 ± 0.4759	0.3563 ± 0.0388
	Protected	0.2557 ± 0.0740	1.3346 ± 0.1636	1.3717 ± 0.5054	0.7378 ± 0.1612
	P-value	0.2595	0.3750	0.5802	0.0437
1.0-5.0 cm	Browsed	0.9793 ± 0.3118	1.6738 ± 0.2665	1.2374 ± 0.5107	12.8837 ± 2.3890
	Protected	0.2337 ± 0.0930	1.2032 ± 0.1141	1.1633 ± 0.4028	8.0582 ± 1.0801
	P-value	0.0626	0.0766	0.7416	0.1897
5.0-10.0 cm	Browsed	0.5489 ± 0.1167	1.1317 ± 0.0633	0.6686 ± 0.1746	6.0436 ± 1.3874
	Protected	0.1667 ± 0.0697	1.0000 ± 0.0000	1.2613 ± 0.1533	6.7152 ± 1.9678
	P-value	0.0342	0.1059	0.1353	0.8002

DISCUSSION

The greater dominance of thorny plants in the currently browed area indicates that thorns are an effective defense against cattle browsing. The degree of dominance of thorny plants increases with increasing size in the currently browsed area compared to the protected area, indicating greater survival of thorny plants under browsing pressure. The impact of browsing on smaller plants is further shown by the significantly higher stem density in the 0.5-1 cm size class in protected areas, compared to currently browsed areas.

Of the three defense types quantified, thorniness seems the most directly relevant to vertebrate browsers and was also the easiest for us to assess directly in the field. Leaf toughness, in contrast, may be most effective against insect browsers and less effective against ruminant herbivores. Further, we did not have a leaf penetrometer available for more precise measurements in the field. The smell data may not adequately represent chemical defenses effective against cattle.

Cattle have clearly had an effect on community structure in browsed areas of Palo Verde National Park, changing stem densities, morphotype frequencies, and foliage density of the understory.

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DENSITY DEPENDENCE OF HERBIVORY ON *RUELLIA INUNDATA* AT SMALL SPATIAL SCALES

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Abstract: We investigated density-dependence of herbivory on *Ruellia inundata* in Palo Verde National Park in Costa Rica. We hypothesized that the proportion of leaves with herbivore damage would be positively related to stem density / m^2. However, our results suggest no relationship between stem density and herbivore damage at the 1 m^2 scale, or leaf density and herbivore damage at the stem scale.

Key Words: Ruellia inundata*, density dependence, herbivory, scale*

INTRODUCTION

Ruellia inundata is a common, multi-stemmed herbaceous perennial occurring in patches of varying density (# stems / m^2) in Palo Verde National Park, Costa Rica. Patches with higher stem densities provide more concentrated food resources for herbivores. Therefore, herbivores may forage longer or in higher numbers in high density patches, causing more leaf damage. Thus, we predicted that herbivore damage would increase with stem density at the 1 m^2 scale. We also predicted that herbivore damage to leaves would increase with the density of leaves per stem.

METHODS

On 9 January 2006, on the former airstrip in front of the OTS station in Palo Verde National Park, Costa Rica, we haphazardly selected 1 m^2 plots (n = 32) of *R. inundata* and counted the number of green stems in each plot as a measure of stem density. We haphazardly sampled 5 stems in each plot, recording the total number of leaves on each stem, and herbivore damage. We calculated herbivore damage as the proportion of leaves on the plant missing partial leaf area. We analyzed the relationship of herbivore damage (proportion of leaves damaged) to stem density at the 1 m^2 scale, and also at the leaves/stem scale, using linear regression analysis in JMP 5.0.1.

RESULTS

R. inundata stem density ranged from 5 to 173 stems / 1 m^2. Stems sampled within each plot contained between 4 and 58 leaves/stem. Herbivore damage was not significantly related to stem density at the scale of 1 m^2 ($r^2 = 0.05$, df = 1, 158, P = 0.20; Fig. 1). Although we found a significant positive relationship between the number of leaves damaged and leaves/stem (df = 1, 154, $P < 0.001$), the proportion of leaves damaged did not change significantly with increasing leaves/stem ($r^2 = 0.01$, df = 1, 153, P = 0.18; Fig. 2).

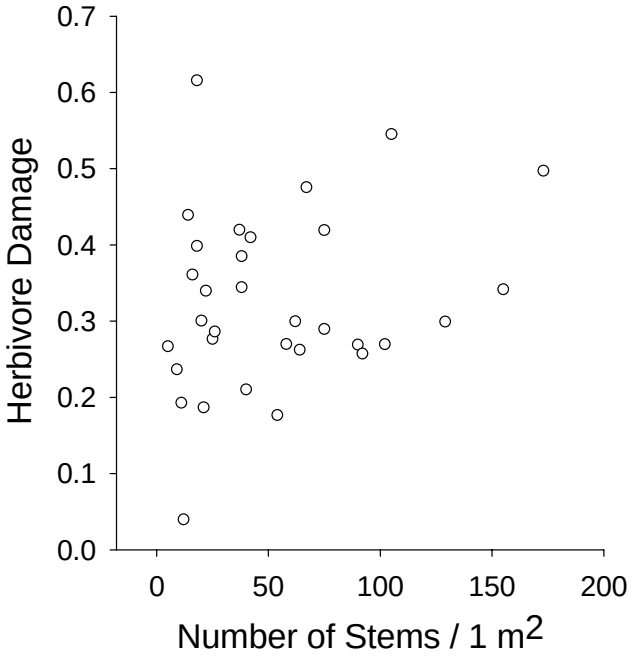

Figure 1. The relationship between the number of stems and herbivore damage in 1 m^2 plots of *Ruellia inundata* in Palo Verde National Park, Costa Rica (r^2=0.05, df=1, 158, P=0.20). Herbivore damage was defined as the proportion of leaves in the plot missing partial leaf area.

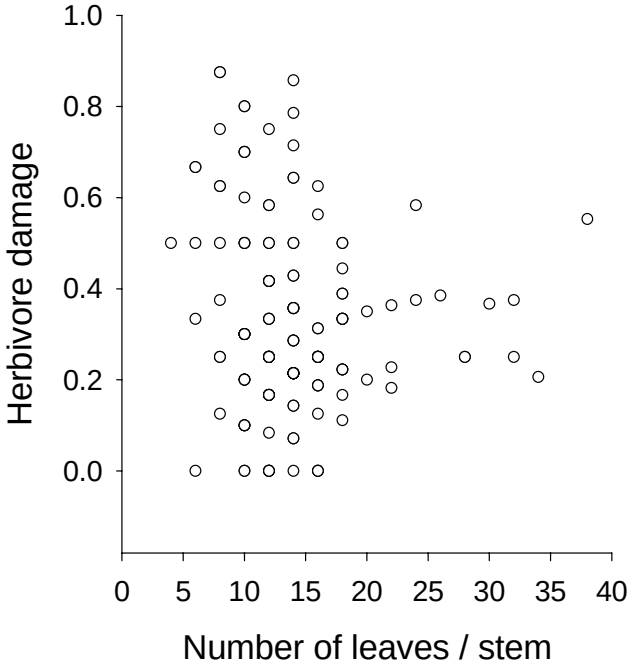

Figure 2. The relationship between the number of leaves and herbivore damage, per stem, in 1 m^2 plots of *Ruellia inundata* in Palo Verde National Park, Costa Rica (r^2 = 0.01, df = 1, 153, P = 0.18). Herbivore damage is defined as the proportion of leaves per stem missing partial leaf area.

DISCUSSION

We found no support for our prediction that herbivore damage would increase with higher stem density at the 1 m^2 scale, or with the number of leaves per stem. The effect host plant density has on intensity of herbivore damage should depend on the scale at which herbivores make foraging decisions. Grasshoppers, which were present in the study plots, are potential *R. inundata* herbivores capable of making foraging decisions across areas larger than 1 m^2. They are also generalist herbivores, and if they do not preferentially feed on *R. inundata*, they may not respond to the density of this species.

EFFECTS OF LITTER TYPE AND DEPTH ON ARTHROPOD DIVERSITY IN A TROPICAL DRY FOREST

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Project design: Elizabeth M. Wolkovich. Faculty editor: David R. Peart

Abstract: Because plant litter provides nutrients and structural habitat for arthropods, we hypothesized that arthropod abundance and diversity would increase with the depth, quality, and structural heterogeneity of litter. We compared two litter types, non-grass and grass, at two depths. We predicted that: 1) deeper litter would support higher abundance, biomass and diversity of arthropod species, and 2) non-grass leaf litter, which apparently provides greater structural complexity, would have a higher diversity of arthropods than grass litter. We found that grass litter had a significantly higher arthropod biomass than leaf litter, but there were no other significant differences among depths and litter types, in arthropod abundance, richness, or diversity.

Key Words: plant litter, arthropod, diversity

INTRODUCTION

Forest litter provides both structural habitat and nutrients for arthropods. Prior to leaf fall, deciduous trees resorb some of their nutrients, but structural defenses and some chemical defenses persist, probably reducing digestibility by litter arthropods. We expected grass litter to have more nutrients and fewer chemical and structural defenses, and thus have higher quality than non-grass ("leaf") litter. However, we also expected leaf litter to support a higher diversity of arthropod species than grass litter, by providing a more complex physical structure. Thus, we predicted that: 1) deeper litter would support higher abundance and biomass and diversity of arthropod species, and 2) leaf litter, which apparently provides greater structural complexity, would have a higher diversity of arthropods than grass litter.

METHODS

The overstory of our study site along the Serena El Pizote-La Martilla trail, northwest of the OTS research station in Palo Verde National Park, Costa Rica, was dry-deciduous forest. In the understory there were several small (up to 25 m^2) patches dominated by grass. We tested two litter types, grass and deciduous leaf, at two depths, deep and shallow, including four replicates of each of the four treatments (leaf shallow, leaf deep, grass shallow, grass deep) for a total of 16 sites. "Grass sites" were in grass dominated patches, while "leaf sites" were in understory areas without grass.

On the afternoon of 7 January 2006, we set pitfalls at eight sites. At each site, we placed three pitfalls roughly 1 m apart in a triangular formation. Pitfalls were 50 mm centrifuge tubes filled with 20 ml of a detergent/table salt and water mixture, and

set flush with the ground. We installed pitfalls at the remaining eight sites on the morning of 9 January.

On the morning of 10 January 2006, we collected pitfalls and measured the length and width of each litter patch and estimated the average litter depth (taken at 3 random points), at each site. We sorted samples to order and morphotype, and measured the length and width of each arthropod. We indexed individual biomass by multiplying length by width, and used this biomass proxy for each morphotype in the calculation of the Simpson's diversity index. We trapped arthropods from two sets of 24 pitfalls over a 40 hour period, and estimated abundance and biomass using numbers of arthropods per hour.

Using three two-way ANOVAs, we evaluated the effects of litter type and litter depth on numbers, biomass, and species richness. We used three *a priori* linear contrasts to determine differences in diversity between litter treatments. We used JMP 5.0.1 for all analyses.

RESULTS

We collected 1,153 total arthropods distributed among 54 morphotypes. We found ten total orders: Arachnida, Blattaria, Coleoptera, Diptera, Hemiptera, Hymenoptera, Isoptera, Microcorpyphia, Neuroptera, and Orthoptera. Grass litter had a higher arthropod biomass than leaf litter ($F_{1,14}$=4.77, P=0.05), but there was no effect of litter depth on biomass ($F_{1,14}$=0.54, P=0.48). There was no effect of the interaction between litter depth and litter type on biomass ($F_{1,14}$=0.40, P=0.54).

The ANOVA for Simpson's diversity index was not significant overall ($F_{3,12}$=0.77, P=0.53), nor was there a significant effect of litter type ($F_{1,14}$=0.00, P=0.10) or litter depth ($F_{1,14}$=2.10, P=0.17). Furthermore, we found no interaction between litter type and depth ($F_{1,14}$=0.22, P=0.65) nor any difference in our linear contrasts between leaf-shallow and grass-shallow ($F_{1,12}$=0.75, P=0.11), or leaf-deep and grass-deep ($F_{1,12}$=0.11, P=0.75). Based on a power analysis, we could have detected a difference of 1.0 in Simpson's diversity index with a probability of 0.90.

The ANOVA for abundance was not significant overall ($F_{3,12}$=0.80, P=0.52). Nor was abundance significantly affected by litter type ($F_{1,14}$=0.29, P=0.60), litter depth ($F_{1,14}$=0.17, P=0.69), or their interaction ($F_{1,14}$=1.96, P=0.19).

DISCUSSION

Arthropod biomass was greater in grass litter, which we suggest may be due to greater nutrient availability. However, our results did not support our hypotheses for differences in arthropod diversity, numbers, or species richness across litter types and depths. The similarity in arthropod communities across litter type and depth has at least two plausible explanations: 1) at the end each wet season deciduous leaf litter falls, reducing the dominance of grass litter in grass patches, or 2) even if grass litter tends to generate distinct arthropod communities, these local communities would be surrounded by a much larger litter arthropod community characteristic of deciduous tree litter. Thus, migration of individuals across the boundaries of grass patches would tend to

homogenize the litter arthropod community in space, blurring the distinction between grass patches and the surrounding habitat.

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NEST, WE HAVE A PROBLEM: *NASUTITERMES* TERMITE'S BEHAVIORAL RESPONSE TO TRAIL DAMAGE AT VARYING DISTANCES FROM NEST

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Abstract: Nasutitermes sp. termite colonies use chewed wood and fecal glue to construct a nest with radiating trails. When trails are damaged, worker termites rapidly locate the damaged area and begin repair. We examined how distance from the nest affected the onset of trail repair. Trail repair at damaged areas began sooner closer to the nest, and repair was initiated most frequently by ants moving from the direction of the nest. We infer that *Nasutitermes* colonies recruit workers and soldiers from the nest, for repair and for defense against predation at the repair site.

Key Words: Nasutitermes, *termites, colony repair, behavioral response*

INTRODUCTION

Termites of the genus *Nasutitermies* construct nests with radiating trails using carton, produced from chewed wood and fecal glue. Construction and defense of the nest and trails shows coordination of activity between the two sterile castes of termites: soldiers and workers. Soldiers protect the colony using a strong-smelling sticky secretion that impedes arthropod predators and is unpalatable to vertebrate predators such as anteaters. Workers are blind, relying on tactile and chemical signaling to coordinate nest and trail construction and repair. Soldiers respond in greater abundance to nest damage than to damage on trails farther from the nest (Lubin 1983).

We examined two responses: (1) the distance of trail damage from the nest relative to the time repair activity began and (2) the direction from which repair was initiated after damage. We hypothesized that these responses would be consistent with centralized coordination of repair from the nest. Thus, we predicted that repair would begin sooner for trails located closer to the nest and that repair activity would be initiated by ants moving from the direction of the nest. Termites have a highly organized social structure, which may require a centralized response, even in cases where damage occurs far from the nest.

METHODS

We used shears to cut gaps approximately 3 cm long in termite trails. We cut each trail at two distances from the nest, as follows. We randomly determined whether the proximal or distal cut would be made first. We generated a random number between 1 and 100 to determine the distance in cm that the proximal cut would be made, while the distal cut was made twice that distance from the nest. We watched the first cut until repair began. If we saw no termites at the damaged site for 10 minutes, we considered the colony abandoned and omitted it from our sample.

Ten minutes after making the first cut, we made the second cut and monitored them until repair began. We recorded the start time of repair, as well as the direction from which the first termite worker came to perform the repair.

We performed an ANCOVA between distance and time, with cut number as the covariate, a one way ANOVA of location vs. time, and a Contingency test of direction vs. location, using JMP 5.0.1.2 for all analysis.

RESULTS

Termites took longer to start repair on cuts farther from the nest (Fig. 1). The order of the cuts did not affect repair initiation time (F_1 = .09 P = .79) nor was there a significant interaction between cut order and distance from the nest (Analysis of Covariance, F_3 =4.12, P = .11).

Termites began trail repair on the cut closer to the nest, regardless of which cut was made first. Termites began repairing distal cuts after 333 $\pm$ 22 seconds and proximal cuts after 242 $\pm$ 15 seconds.

The distance of the cut from the nest did not affect the direction from which the termites arrived (Contingency test, $\chi^2_{1,50}$ = .31, P = .58). Termites arrived to repair trail damage on the side closest to the nest in 83% of all cuts.

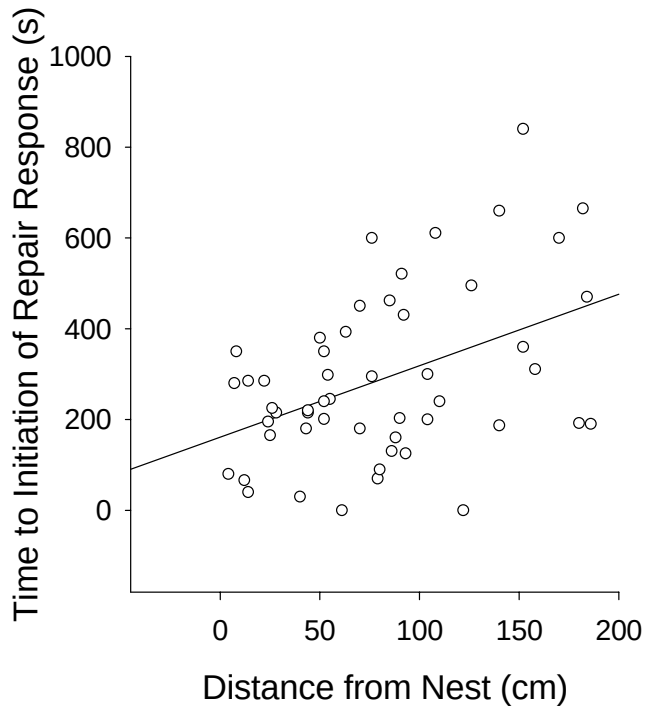

Figure 1. Relationship between the distance from the nest and the time of the repair response, for experimentally damaged trails of *Nasutitermes* termites at Palo Verde, Costa Rica (F_1=11.7, p = .0012)

DISCUSSION

The slower initiation of repair farther from the nest suggests that the workers travel from the nest to reach damaged areas. Moreover, within a trail, repair began earlier on cuts made closer to the nest than on cuts farther away. The direction from which the termites began repair activity did not depend on distance from nest, suggesting that the workers are recruited from the nest even if workers already in the trail are nearer to the damaged area.

Trail damage can result from predator attack. Thus, in the evolution of termite behavior, coordination of repair from the nest may have been favored by the benefits of recruiting soldiers for defense along with workers for the repair. Lubin

(1983) reported that *Nasutitermes* soldiers were found in greater abundance at damaged areas closer to (or on) the nest rather than at damaged areas farther from the nest. This distance-dependent pattern in the numerical recruitment response (which we did not examine) also indicates central control of recruitment from the nest.

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FORAGING EFFICIENCY AND GROUP BEHAVIOR IN NORTHERN JACANAS

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Abstract: Group-oriented behavior may entail both costs and benefits to the individual; we examined one possible cost. Northern Jacanas (*Jacana spinosa)* are tropical shorebirds that forage both individually and in groups. Adults defend territories aggressively, especially at dawn and dusk. We hypothesized that foraging activity would be lower for group foraging than for solo foraging, due to lower costs of aggressive interactions with conspecifics in solo foraging. Our results support this hypothesis, and suggest that increased aggression towards conspecifics reduces foraging activity.

Key Words: Jacana spinosa, *foraging activity, conspecific aggression, group dynamics*

INTRODUCTION

The Northern Jacana (*Jacana spinosa)* is a tropical shorebird found in freshwater marshes of Guanacaste Province, Costa Rica. Jacanas spend much of their time foraging in floating vegetation for insects, small fish, and invertebrates (Janzen 1983). Jacanas also defend breeding territories aggressively, with energy-demanding behavior that includes attacking, fleeing, wing-raising and vocalizations. The birds are most aggregated and active during the early morning and late evening, scattering during the day (Jackson and Kopplin 1996). Higher densities may increase aggressive behavior among individuals. We hypothesized that foraging activity per individual would be higher in solo foraging than in grouped foraging, due to less time spent by solo birds in aggressive interactions.

METHODS

We conducted our study on 10, 11 and 12 January 2006 in a freshwater marsh 0.5 km southwest of the OTS Field Station in Palo Verde National Park, Guanacaste, Costa Rica. We observed 20 individual Jacanas between 0500 and 0700 hours, and 23 individuals between 1600 and 1900 hours, along 0.5km of marsh edge with floating vegetation, between the observation tower and the bridge. We haphazardly chose each adult Jacana and monitored its foraging activity continuously for 5 minutes. Foraging activity was measured as mean peck rate in 30-second intervals. In each interval, we also counted the number of adult Jacanas within a 2 m radius of the focal individual, as well as the level of severity of aggressive behavior exhibited by the individual toward other Jacanas. Aggressiveness was recorded on a 0-3 qualitative scale, with zero representing the absence of aggression, and 3 representing prolonged, intense aggressive behavior.

For the 32 individuals that exhibited both solo and grouped foraging, we performed a one-tailed t-test of the difference between solo and group foraging activity. For the 11 birds that exhibited

either exclusively solo or exclusively group foraging, we performed a t-test between the foraging activity of solo and group foragers. Additionally, for all birds that foraged in groups, we performed an ANOVA to determine if foraging activity decreased with increased aggression towards conspecifics.

RESULTS

Birds foraged more when alone than when in groups. Mean peck rate was greater (by 2.15 pecks/interval) for solo than for group foragers, for individuals foraging both solo and in groups (one- tailed t-test, t_{30} =1.66, P=0.05). We also found a significantly higher foraging activity for individuals foraging exclusively alone than for those foraging exclusively in groups (t_{17} =6.97, P=0.02; Fig. 1). Additionally,

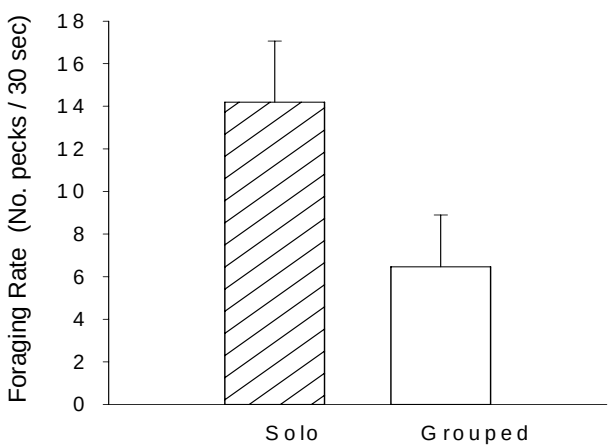

Figure 1. Mean foraging rate (measured as peck rate, mean ± SE) for Northern Jacana individuals foraging alone (striped) and in groups (white), at Palo Verde, Costa Rica. (t_{17}=6.97, P=0.02).

we found a significantly reduced foraging activity, for individuals foraging in groups, with increased severity of aggression toward conspecifics (ANOVA, $F_{1, 29}$=4.17, P=0.05; Fig. 2).

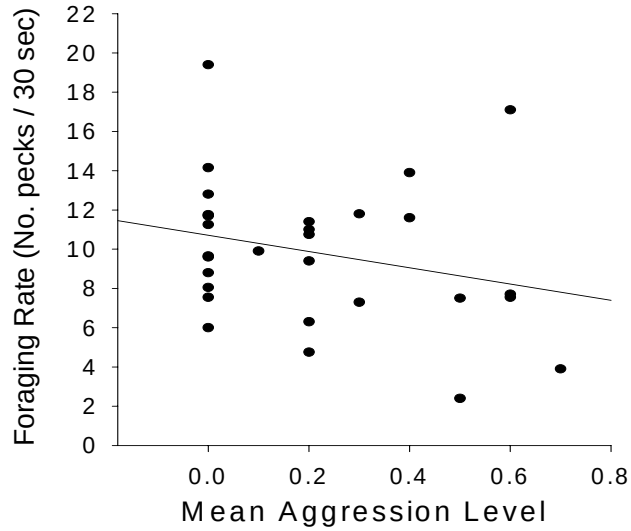

Figure 2. Mean foraging rate (measured as peck rate) for Northern Jacana individuals with increased aggression level at Palo Verde, Costa Rica (ANOVA, $F_{1, 29}$=4.17, P=0.05). See text for definition of aggression level.

DISCUSSION

Group foraging for these Jacanas results in lower foraging activity than foraging alone and is therefore a cost to individuals in groups. However, Jacanas in groups may benefit from enhanced detection of predators and defense against predator attacks, balancing the reduced foraging rate in groups.

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HABITAT DISTRIBUTION OF COMMON PAURAQUES AND THEIR PREY IN AN OPEN FIELD AT PALO VERDE

BRIAN D. BATES

Research advisors: Faculty and graduate students. Faculty editor: David R. Peart

Abstract: The Common Pauraque (*Nyctidromus albicollis*) is a nocturnal insectivorous bird, abundant in partly open habitats. Its distribution within these habitats is poorly studied, but is likely driven by either prey availability or predation risk. I examined pauraque distribution and the distribution of potential insect prey at night in a large mowed field In Palo Verde NP, Costa Rica. I found pauraques exclusively in localities close to trees or forest, but insect abundance did not differ between the forest edge and the middle of the field. Predation risk may be driving pauraque distribution, although it is unclear whether proximity to cover reduces predation risk to these birds.

Key Words: Nyctidromus albicollis, Common Pauraque, *distribution*

INTRODUCTION

Like other members of the family Caprimulgidae, the Common Pauraque (*Nyctidromus albicollis*) is a nocturnal insectivore. Pauraques typically hunt from the ground, sallying to catch moths or beetles and landing in the same spot a few seconds later. They are most common in partly open environments, such as brushland or open woodland (Janzen 1983), but their distribution within these open habitats is poorly described.

I set out to describe and explain the distribution of pauraques around a mowed field. Based on previous sightings, I suspected the birds hunt near the cover of forest or a tall tree. As pauraques were not breeding at the time of my observations, their distribution was probably driven by either prey availability or predation risk. I hypothesized that prey abundance drives their distribution. I quantified flying insect abundances to evaluate this hypothesis.

METHODS

I observed pauraques on January 11-13 at the former airstrip at Palo Verde National Park, Costa Rica. Pauraques do not breed at this time of year. The site, a 400 m x 35 m mowed field, is surrounded by closed forest on 3 sides. The field's southern border is a row of scattered tall trees along the shore of the Palo Verde marsh. A gravel road follows the forest edge on the opposite side of the field.

I observed pauraques between 8:30 pm and 1:30 am over the three nights. I located birds by systematically scanning the study site with night-vision binoculars to spot eyeshine. I recorded the substrate (grass, gravel road, bare ground) from which the bird hunted and the location of the bird relative to the edges of the field. I measured the distance to nearest cover, defined as forest or a tall tree. I used a one-tailed t-test to compare the mean distance from birds to cover to the mean distance to cover from random points in the field.

I investigated the distribution of flying insects (mainly moths) at the study site, by comparing abundances between the middle of the field and the edge of the field. For each count, I used night-vision binoculars and recorded how many insects flew through the field of vision in a 5-minute period. I stood 2 meters from the forest edge and looked along the edge for the edge count, and stood in the middle of the field looking down the length of the field for the middle count. I performed three such counts each, for the middle and edge of the field, and used a one-way ANOVA to determine if the abundance of insects differed between the forest edge and the middle of the field.

RESULTS

I encountered 14 pauraques throughout the study, including at least 5 different individuals. Their distribution was highly non-random: I found no individuals more than 6 m from the perimeter of the field (i.e. from cover), even though the field was 35 m wide.

Pauraques hunted only from either bare ground or gravel road, even though these substrates, which were almost exclusively near cover, covered a small proportion of the study site (visually estimated as 10%). Six of 14 observed birds hunted from a gravel road bordering dense forest. The birds that hunted from the gravel road were not randomly distributed within the road, showing a significant preference for proximity to cover (t_5=2.14, $P<0.0001$).

I found no significant difference in the abundance of insects between the forest edge and the middle of the field (ANOVA. F_5=4.57, P=0.10). Mean number of insects per five-minute count was 34 ±1.53 at the forest edge and 29.7 ±1.33 in the middle of the site.

DISCUSSION

The distribution of the Common Pauraque within the study site is apparently not driven by the distribution of insect prey. There is no clear reason why foraging efficiency would be higher closer to cover for reasons other than insect abundance. Due to the birds' cryptic coloration and sit-and-wait hunting style, it seems unlikely that insect prey can detect birds better in more open environments.

As insect abundance does not seem to drive pauraque distribution, reduced predation risk is a likely alternative. However, it is unclear whether nearby cover actually reduces predation risk to birds. If owls are the major predators, for example, pauraques would likely be more susceptible to attack in open environments, and therefore prefer forest edges. But pauraques did not fly into the forest when I flushed them, suggesting that they do not use it as a refuge from predators. Furthermore, proximity to forest edges could increase susceptibility to ground predators.

Further work on prey abundance may be informative. Although not significant with the small sample size, the mean number of insects per five-minute count was higher at the forest edge than in the middle of the site. My counting technique may have missed smaller insects, which could be an important food source

for pauraques, and may be more abundant near the forest edge.

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THE EFFECTS OF CATTAIL MANAGEMENT ON THE AQUATIC FOOD WEB OF THE PALO VERDE WETLAND

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Abstract: Palo Verde National Park implemented a management strategy to control cattail populations in the wetlands of Palo Verde National Park, Costa Rica, by crushing cattail stems with a tractor. We compared dissolved oxygen, zooplankton abundance, and fish abundance across three sites with different management histories: never managed, managed twice (2000, 2003) and managed eight times (1998-2005). We reasoned that decomposition of large inputs of organic matter in infrequently managed sites demands more oxygen than respiration of standing cattails. In frequently managed sites, low cattail abundance would reduce respiration of decomposing cattails. Therefore we predicted dissolved oxygen, zooplankton abundance, and fish abundance would increase in the following order: site managed twice, unmanaged site, and most frequently managed site. While fish abundancewas similar at the unmanaged site and the site managed twice, it was much higher at the most frequently managed site. Dissolved oxygen and zooplankton abundance trends were consistent with our predictions. Our findings suggest that repeated cattail management can improve productivity of the aquatic food web; this may, in turn, benefit bird populations.

Key Words: cattails, dissolved oxygen, zooplankton, fish, management

INTRODUCTION

A dramatic increase in cattail abundance in the Ramsar Wetlands in Palo Verde National Park, Costa Rica, led the Organization for Tropical Studies to implement a management strategy that involves the crushing of cattails by tractor. After crushing, the cattails are left at the marsh bottom. Their decomposition may reduce dissolved oxygen (DO) in the water column. Without management, high respiration levels in habitats with high cattail biomass may also lower water column DO. We hypothesized that decomposition of abundant organic matter in managed sites demands more oxygen than respiration of standing cattails. However, with frequent cattail management the standing cattail biomass and annual productivity could decrease--reducing inputs of cattail detritus to the marsh bottom.

Water column DO may directly and positively affect zooplankton, which in turn can increase fish abundance. We chose three sites with different management histories (never managed, managed twice and managed eight times) and compared DO, zooplankton abundance, and fish abundance across sites. We predicted that the most frequently managed site would have the highest DO, zooplankton abundance, and fish abundance, and that the site managed twice would have the lowest DO, zooplankton abundance and fish abundance, due to the larger input of crushed cattails.

METHODS

On 11 January 2006 we selected three sites in the Palo Verde Ramsar Wetland, based on site-specific history of cattail management. Site 1, ca. 600 m west of the airstrip and 100 m south of the marsh shore, has never been managed; site 2, 500 m south west of the end of the airstrip, was managed twice (2000, 2003); and site 3, located 10 m south east of the observation tower directly south of the OTS station, has been managed every year since 1998 (Table 1).

We set four passive fish traps at each site in a rectangular formation in the open water. We sampled three times at each site, from the morning of 12 January to the morning of 13 January. After our first sampling, we used wood props to raise three of four fish traps in site 1 and 2 to ensure that the height of the traps in the water column did not limit DO available to the fish. We sampled DO and temperature at five points (once at each trap and once in the middle of the site), with a DO meter at three depths. We sampled zooplankton twice at the undisturbed midpoint of each site. For each sample, we extracted 980 ml of water into a tube (ca. 60 mm diameter), and then filtered the contents on site with a 35 μm mesh screen. After fixing the zooplankton with alcohol, we counted them under a dissecting microscope. We identified, counted, and released fish in the field.

TABLE 1. GIS coordinates for sample sites in the Ramsar Wetlands in Palo Verde National Park, Costa Rica.

Site Number	Site Description	Longitude	Latitude
1	Unmanaged	11.44000°	68.1175°
2	Managed twice	11.43850°	68.1275°
3	Managed eight times	11.43785°	68.1800°

RESULTS

Zooplankton abundance was highest at the most frequently managed site and lowest at the site managed twice (Table 2). Dissolved oxygen was also highest at the most frequently managed site and lowest at the site managed twice (Table 2). Fish abundance was 10-20 times higher in the most frequently managed site than at the other two sites (Table 2).

TABLE 2. Number of fish captured in traps, mean number zooplankton/ L and mean DO across three sites with difference management histories in the Ramsar Wetlands in Palo Verde National Park, Costa Rica. Total fish is number caught at each site over three sampling occasions.

Site description	Total fish	Zooplankton (#/liter) (Mean ± 1 SE)	DO (mg/liter) (Mean ± 1 SE)
Unmanaged	5	24.29 ± 1.44	1.39 ± 0.11
Managed twice	10	13.26 ± 0.72	1.17 ± 0.20
Managed eight times	119	38.27 ± 5.41	1.73 ± 0.13

DISCUSSION

Our data were consistent with the hypothesis that decomposition of large inputs of organic matter in more frequently managed sites demands more oxygen than respiration of standing cattails. Fish abundance was greatest in the most frequently managed site, suggesting that the cattail crushing treatments can enhance fish abundance in the long term. We recommend that follow-up research include replication within sites, fish sampling by seine nets, and repeated zooplankton samples. Nevertheless, our findings suggest that long term, consistent cattail management can improve productivity of the aquatic food web, which may in turn benefit bird populations.

STILL LIFE: GREAT EGRET RESPONSE TO ENCOUNTERS WITH CONSPECIFIC AND HETEROSPECIFIC BIRDS

CATRINA A. LINDGREN AND WILLIAM F. J. STORK

Research advisors: Faculty and graduate students. Faculty editor: David R. Peart

Abstract: Because Great Egrets (*Casmerodius albus*) rely on stealth for foraging success, we hypothesized that they would respond to birds encountered while foraging by an aggressive move, or a retreat to an undisturbed area. Encounters with conspecific individuals consistently elicited an aggressive move or a retreat, in 26 of 28 encounters. But Great Egrets ignored heterospecific birds in 63 of 63 encounters, including species that are potential competitors for food.

Key Words: Casmerodius albus, Great Egret, foraging, competition

INTRODUCTION

The Great Egret (*Casmerodius albus*) is a large, piscivorous bird that relies on stealth to forage successfully. Encounters with heterospecific birds while foraging could interfere with foraging success by disturbing fish. In addition, other Great Egrets and similarly large, piscivorous birds may be perceived as direct competitors for food. Therefore, we predicted that (1) Great Egrets would respond to conspecific bird encounters by an aggressive move towards the arriving individual or retreat to an undisturbed foraging area, and (2) Great Egrets would respond to other large, piscivorous birds (Wood Storks, Snowy Egrets, Cormorants) as they do to conspecifics.

METHODS

We observed Great Egrets from the observation bridge overlooking the marsh at the OTS field station in Palo Verde National Park, Costa Rica, on 12-13 January 2006. We compiled our observations from 0545-0645, 0745-0845, and 1700-1800 on both days, a total of 12 person-hours. We observed 47 individuals, watching two Great Egrets for a maximum of an hour, choosing a new Great Egret if one flew out of sight. We recorded Great Egret response whenever there was an encounter with a bird and recorded the species and abundance (number) of the encountered birds. Encountered birds were defined as birds that entered within a 5 m radius of the Great Egret, birds that were present within 5 m of the Great Egret when it landed, and birds that flew within 5 m of the Great Egret (flybys). We recorded 4 types of Great Egret response: (1) ignoring, which meant no difference in the Great Egret's foraging behavior; (2) aggressive move, which meant the Great Egret made an antagonistic approach towards the bird(s) within the

5 m radius; (3) walking away, and (4) flying away. The 5 m radius was estimated based on the body length of the Great Egret.

RESULTS

We observed 91 bird encounters, including 15 flybys. In all 63 observations of heterospecific bird encounters, Great Egrets ignored the encountered bird(s), regardless of species or number (Table 1). Furthermore, Great Egrets ignored encounters with similarly large, piscivorous birds, as they did other heterospecifics (Table 1). However, in 26 of 28 conspecific encounters, Great Egrets responded (Table 2). The most common Great Egret response to a conspecific encounter was to fly away (13 of the 28 arrivals). The Great Egret responded to all 7 conspecific flybys by flying away.

DISCUSSION

Our finding that Great Egrets ignored all encounters with heterospecific birds suggests that the energy cost of flying to a new foraging area in response to heterospecific bird encounters (and the resulting disturbance of fish) outweighs the cost of foraging in a disturbed area. In addition, the result that Great Egrets ignore other large, piscivorous birds while foraging suggests that Great Egrets do not identify those birds as direct competitors, perhaps because they do not overlap in resource or habitat use.

TABLE 1. Heterospecific bird encounters ignored by Great Egrets at Palo Verde National Park, Costa Rica. Values indicate encounters ignored by the Great Egret out of total encounters observed. N/A indicates no observations. Great Egrets foraging behavior does not appear to be influenced by heterospecific encounters.

Arrival species	Single bird encounters, excluding flybys	Multiple bird encounters, excluding flybys	Flybys
Cormorant*	3 of 3	N/A	2 of 2
Wood Stork*	1 of 1	N/A	1 of 1
Snowy Egret*	1 of 1	3 of 3	2 of 2
White Ibis	N/A	2 of 2	N/A
Cattle Egret	1 of 1	1 of 1	1 of 1
Snail Kite	1 of 1	N/A	N/A
Northern Jicana	12 of 12	10 of 10	1 of 1
Whistling Duck	2 of 2	18 of 18	1 of 1
Total	21 of 21	34 of 34	8 of 8

* indicates large, piscivorous bird species

TABLE 2. Great Egret responses to conspecific encounters at Palo Verde National Park, Costa Rica. Great Egrets consistently respond to encounters with conspecifics, including flybys, often by retreat.

Response	Conspecific encounters, excluding flybys	Conspecific flybys
Ignore	2	0
Aggressive move	7	0
Walk away	4	0
Fly away	8	7
Total	21	7

The Great Egret's consistent response to conspecific encounters suggests that Great Egrets may recognize conspecifics as direct competitors. Most responses to conspecific encounters were to walk or fly away (22 of 28), suggesting that an intruding Great Egret is often successful in forcing the resident Great Egret out of a foraging area. However, the observation that Great Egrets flew away in response to all conspecific flybys, which do not represent an immediate threat of competition for food, may suggest that conspecific responses are not predicated upon competition for food.

EFFECTS OF LARGE-SCALE CATTAIL MANAGEMENT ON LOCAL, MICROHABITAT-SPECIFIC FORAGING BEHAVIOR OF GREAT EGRETS

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Abstract: In Palo Verde National Park in Costa Rica, cattail abundance in the marsh has been managed since 1998. The correlated increase in Great Egret (*Casmerodius albus*) abundance may be due to increased representation of preferred microhabitat types following cattail control. We focused on relatively open habitats, in both managed and unmanaged areas, to determine whether cattail management in the surrounding area influenced the local abundance and microhabitat-specific foraging behavior of Great Egrets. We hypothesized that the local abundance of Great Egrets would be greater when cattail abundance in the surrounding area had been reduced by management; this hypothesis was supported by our data. Our second hypothesis, that foraging behavior would depend upon local microhabitat, rather than the surrounding cattail abundance, was also confirmed by our results. Because local microhabitat conditions appear to be the primary influence on Great Egret foraging behavior, we suggest that the creation of suitable microhabitats should play a prominent role in strategies for cattail management.

Key Words: Casmerodius albus, *forage, habitat management, microhabitat*

INTRODUCTION

Since 1998, managers in Palo Verde National Park, Costa Rica have controlled cattail abundance in marshy areas along the Tempisque River, and the abundance of waterbirds has correspondingly increased. Reducing cattail abundance increases open water habitats, and may create gaps for other species of plants. However, little is known about how cattail management affects bird foraging behavior.

We focused on relatively open habitats, in both managed and unmanaged areas, to determine whether cattail management in the surrounding area influences the local abundance and microhabitat-specific foraging behavior of Great Egrets (*Casmerodius albus*). We hypothesized that the local abundance of Great Egrets in a particular area would depend on the suitability of habitat in the surrounding, larger area. Specifically, we predicted that local Great Egret abundance would be greater when cattail abundance in the surrounding area had been reduced by management.

In contrast, because foraging behavior should depend on a bird's immediate surroundings, we hypothesized that it would be best predicted by microhabitat (local scale), rather than whether an area had been managed or not (larger scale). Mahar et al. (2000) found that *Jacana spinosa*, a species with similar habitat preferences, spent significantly more time foraging in vegetative mats than they did on cattails. Therefore, we expected that Great Egrets would spend more total time, and more foraging time, in microhabitats dominated by low vegetative mats. We also expected the proportion of time spent foraging by Great Egrets to vary according

to the occupied microhabitat, and to be least in local areas dominated by cattails.

METHODS

We observed focal Great Egrets in Palo Verde National Park, Costa Rica on 12 January 2006 and 13 January 2006. We collected data on each day starting at approximately 5:30am, 10:30am, and 4:00pm, for one-hour intervals in two locations of roughly the same size: a marsh area where cattails had been crushed 7 times since 1998, and a naturally cattail-free marsh area. In each location, we recorded the total number of Great Egrets present and observed each bird for a 15 minute interval. We described the microhabitat occupied by each bird as mostly reed, mostly floating vegetative mat, mostly open water, half reed-half vegetative mat, half reed-half open water, half vegetative mat-half open water, or a mix of the three based on estimated percentages. We described behavior as foraging (extended neck), resting (retracted neck), or flying, and recorded the time whenever microhabitat or behavior changed.

We compared bird numbers between the managed (reduced abundance of surrounding cattails) and unmanaged areas, and the proportion of time spent foraging in each area and in each microhabitat, using ANOVA in JMP 5.0.1. We compared the fraction of total time spent in each microhabitat and the fraction of foraging time spent in each microhabitat, with ANOVA. We ran a Tukey-Kramer HSD to test for differences between microhabitat categories.

RESULTS

Great Egrets were significantly more numerous locally in areas where the surrounding cattail dominance had been reduced ($F_{1, 10}$=23.44, P=0.0007; Fig. 1). The proportion of time spent foraging (across all local microhabitats) was similar, irrespective of the surrounding cattail abundance (i.e. managed or not; $F_{1, 67}$=0.25, P=0.62; Fig. 2). In both managed and unmanaged areas, Great Egrets spent significantly more time in the mostly-vegetative-mat microhabitat than in any other microhabitat type ($F_{5, 252}$=17.88, P<0.0001). Also, Great Egrets spent by far the greatest proportion of their foraging time in the mostly-vegetative-mat microhabitat ($F_{5, 245}$=22.5, P< 0.0001; Fig 3). Proportion of total time in a microhabitat that was spent foraging also differed significantly among microhabitats ($F_{5, 63}$=6.80, P< 0.0001; Fig. 4). When we pooled all microhabitat data, we found that Great Egrets spent a significantly greater proportion of their time foraging when in mixed microhabitats (0.97) and mostly vegetative mat microhabitats (0.85) than when in half-vegetative-mat-half cattail (0.47) and mostly-cattail microhabitats (0.17; Fig. 4).

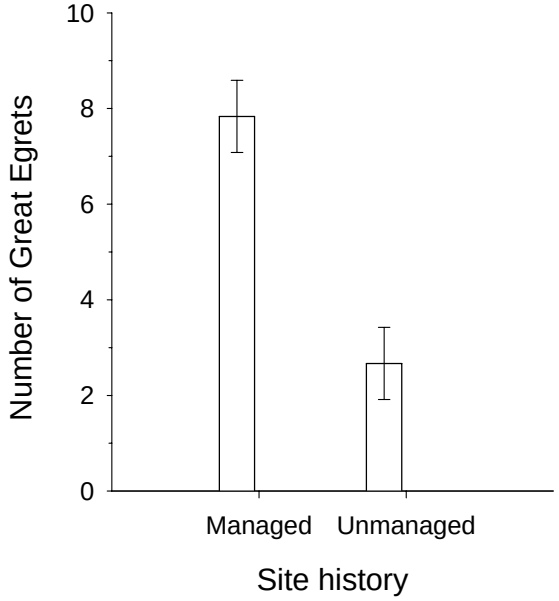

Figure 1. Number (mean ± SE) of Great Egrets observed per hour in a marsh managed for cattails and an unmanaged marsh in Palo Verde National Park, Costa Rica. In managed areas, the surrounding cattail abundance has been reduced. Data are from 6 periods of observation at each site.

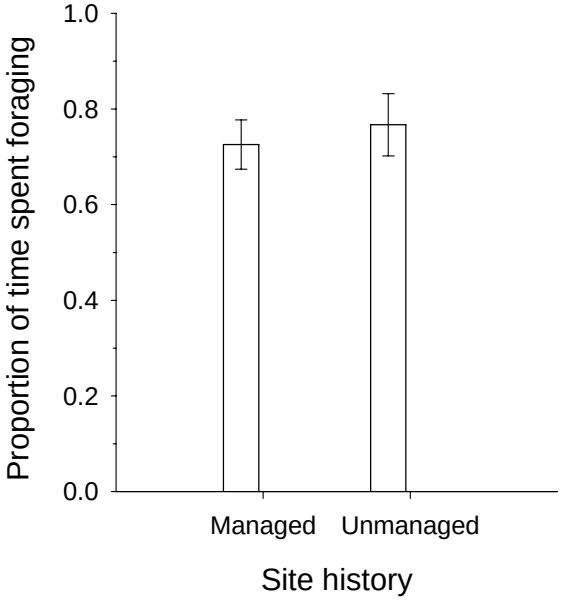

Figure 2. Proportion of time (mean ± SE) Great Egrets spent foraging in a marsh managed for cattails and an unmanaged marsh at Palo Verde National Park, Costa Rica. In managed areas, the surrounding cattail abundance has been reduced. Sample sizes of birds from left to right are 33 and 9.

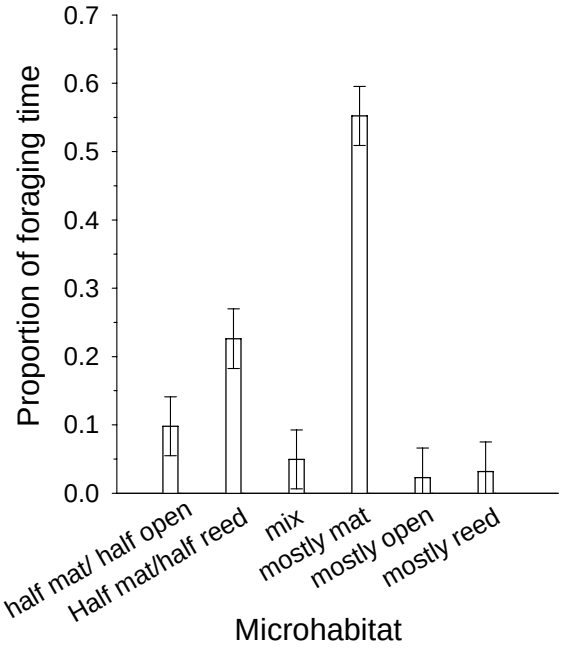

Figure 3. Proportion of foraging time (mean ± SE) Great Egrets spent in different microhabitats in the marsh at Palo Verde National Park, Costa Rica. Microhabitats not sharing the same letter are significantly different (α = 0.05). Microhabitat data are pooled across sites with different management histories. Sample size is 42 birds for each microhabitat. "Reed" refers to cattails.

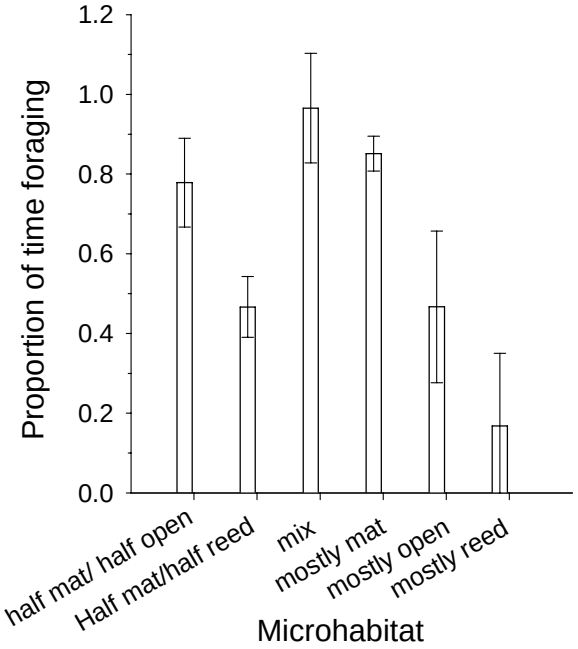

Figure 4. Proportion of time (mean ± SE) Great Egrets spent foraging, by microhabitat, in the marsh at Palo Verde National Park, Costa Rica. Values not sharing the same letter are significantly different (α = 0.05). Sample sizes from left to right are 11, 16, 6, 30, 3, and 3 birds. Microhabitat data were pooled across sites with different management histories. "Reed" refers to cattails.

DISCUSSION

Habitat suitability on a large scale, as influenced by cattail management, clearly influences the abundance of Great Egrets in local microhabitats. May et al. (in prep.), who studied the same managed and unmanaged areas, found a trend towards greater fish abundance in the managed area, which could improve Great Egret habitat quality. On a smaller scale, Great Egret foraging behavior seems to be determined by local microhabitat conditions. Because we believe our sites to be representative of managed and unmanaged areas in the Palo Verde marsh in general, we suggest that the creation of suitable microhabitats should play a prominent role in strategies for cattail management.

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