

DEFENSIVE RESPONSE OF MUTUALISTIC ANTS TO SIMULATED MAMMALIAN HERBIVORY ON *ACACIA COLLINSII* AND *A. CORNIGERA*

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Abstract: Differences in the ant-acacia mutualisms between *Acacia collinsii* and *A. cornigera* have not been compared directly, but a previous study in the Palo Verde National Park suggested that the mutualism was dysfunctional in *A. cornigera*. We compared the response of ant colonies between *A. collinsii* and *A. cornigera* after simulated mammalian herbivory. As predicted, ants attacked more frequently on *A. collinsii* than on *A. cornigera*, a trend that was marginally significant in spite of low sample size dictated by the rarity of *A. cornigera*. Hybridization of these acacia species may have occurred in the study area, reducing observed differences in ant behavior.

Key Words: palatability, hybridization, Beltian bodies

INTRODUCTION

Aggressive ants occupy two species of acacia trees: *Acacia collinsii* and *A. cornigera*. Both species occur in Palo Verde, Costa Rica, but *A. cornigera* is much less common. Resources provided to the ants include carbohydrates in extrafloral nectaries, lipids in Beltian bodies, and shelter for the colony to live and rear larvae in hollowed thorns (Janzen, 1974). Several species of aggressive ants inhabit acacias in Palo Verde (*Pseudomyrmex flavicornis*, *P. spinicola*, and *P. nigrocincta*), and ant colonies aggressively defend their host trees both from herbivores and other ants.

A previous study suggested that the mutualism between *A. cornigera* and its resident ants has failed, resulting in trees that

continue to provide habitat and nutrients to the ants without receiving the benefit of ant defense (Bates et al. 2006). However, that study did not include comparative sampling of *A. collinsii* with *A. cornigera*.

We hypothesized that aggressive ant colonies would defend *A. collinsii* more effectively than *A. cornigera*, and we tested this by simulating mammalian herbivore attack on both species on the same day in the same habitats.

METHODS

Our experiment was conducted from 0725-1030 on January 12, 2008, within ca. 200m of the OTS field station at Palo Verde, on both sides of the main access road. We used every available *A.*

cornigera within the study area, but their rarity limited our sample size to five. We chose five *A. collinsii* that were of comparable size to the *A. cornigera* sampled, and nearest to them.

Branches within the approximate height range accessible to cattle were selected at random, and cattle herbivory was simulated by tearing off leaves with gloves, a modification of the technique used by Barger et al. (2005). One compound leaf was removed every 10 seconds for up to 60 seconds (6 leaves removed). We recorded the time to first arrival of an ant to the glove, and the time to first bite or sting. At time of first bite or sting, leaf removals were stopped, and if no ants had arrived, we waited up to 30 seconds more (90 seconds total) for ants to respond. We scanned each tree for one minute and recorded the number of leaves with mature Beltian bodies. We measured each tree's height, the long axis of the projected crown area, and the width perpendicular to the long axis. An index of projected canopy area was calculated as the product of these two measures. Ant species from each tree were then collected and identified.

RESULTS

TABLE 1: Attack frequencies of resident ants on *A. collinsii* and *A. cornigera* at Palo Verde National Park, Costa Rica

	No. Attacks	No. failures to attack	Total No. Ant Species Sampled
<i>A. cornigera</i>	2	3	5
<i>A. collinsii</i>	5	0	5
Total # of outcomes	7	3	10

Every herbivore simulation on *A. collinsii* generated an attack, compared to only 40% for *A. cornigera*. Each tree was inhabited by a single ant species, suggesting that these ant colonies defend against other ant colonies, if not against herbivores.

Time to first attack was not linearly related to projected canopy area ($F=0.77$, $df = 1, 10$, $p=0.42$) or height ($F=0.475$, $df=1, 10$, $p=0.52$). Of the trees sampled, 80% had one or fewer Beltian bodies, and the number of bodies was not linearly related to time to first attack ($F=0.16$, $df = 1, 6$, $p=0.71$).

The probability of attack in *A. collinsii* may be greater than in *A. cornigera* (Table 1, Fisher's exact test, $p=.083$). More replication would be necessary to confirm this difference.

TABLE 2: Ant species occupying *A. collinsii* and *A. cornigera* at Palo Verde, Costa Rica

Ant species	Acacia species	
	<i>A. collinsii</i>	<i>A. cornigera</i>
<i>P. flavicornis</i>	1	3
<i>P. nigrocincta</i>	2	0
<i>P. spinicola</i>	2	2

DISCUSSION

The mutualism between ants and *A. cornigera* did not appear as functional as that with *A. collinsii*. Two of the aggressive ant species that occur in *A. cornigera* (*P. flavicornis*, *P. spinicola*) also frequently occupy *A. collinsii* trees (Table 2). Bates et al. (2006) showed that *P. flavicornis* was far less aggressive when inhabiting *A. cornigera*. Our data support that inference, with 60% of our *A. cornigera* trees showing no aggressive response to herbivory.

The absence of aggressive response in *A. cornigera* for ant species that aggressively defend *A. collinsii* is puzzling, and further suggestive of a dysfunctional mutualism in *A. cornigera*.

In contrast to these findings, ants residing on both tree species had similar response times when ants defended aggressively. These apparently inconsistent results may be reconciled by future studies with larger sample sizes.

It is possible that *A. cornigera* is not an obligate mutualist with ants. If so, it may be less palatable to mammalian herbivores than *A. collinsii*. *A. collinsii* lacks secondary compounds (Janzen, 1977), but the palatability of *A. cornigera* has not been evaluated.

Ant acacias occasionally hybridize (Ebinger and Seigler 1992, Janzen 1974). In our samples near the

road, there appeared to be a continuum of morphological traits in the ant acacias, rather than the distinct species characteristics of *A. collinsii* and *A. cornigera* that were apparent in trees near the marsh. Hybridization between the species could have resulted in intermediate ant behaviors in some of our samples, reducing differences between the acacia species in our experiment.

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RETENTION AND MORPHOLOGY OF LEAVES OVER AN ENVIRONMENTAL GRADIENT AT PALO VERDE, COSTA RICA

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Abstract: Moisture and nutrient levels decrease with elevation on limestone ridges in tropical dry forests in Guanacaste, Costa Rica. We hypothesized that leaf area and retention would decrease, while leaf toughness would increase with elevation, in response to presumed physiological stresses over the elevational gradient. Evergreens were heavily concentrated at lower elevations, as predicted. Among deciduous woody plants, leaf traits did not change with elevation, probably because these plants escape water stress by early leaf loss in the dry season.

Keywords: Leaf morphology, elevation gradient, tropical dry forest, Palo Verde, land adaptation

INTRODUCTION

In tropical dry forests, the ridges and upper slopes generally lack soil; therefore, moisture and nutrients decrease with elevation as soil depth decreases (Janzen 1983).

We examined leaf morphology of woody species along a 100 m elevation transect running up to a limestone ridge, in a tropical dry forest in Palo Verde National Park. We predicted three trends: first, we expected leaf area to decrease with elevation due to increased mechanical and desiccation stress from wind and solar insolation; second, we predicted that leaf toughness would increase with elevation, conserving nutrients and acting as cost-effective means to deter herbivory; finally, we expected that leaf retention would decrease with elevation, because

water stress may become critical at high elevations during the dry season.

METHODS

We sampled understory and canopy woody species over a 100m elevational change from near a marsh to near the Sendero Guyacan, behind the Palo Verde Biological Station, Palo Verde National Park, Costa Rica, on January 13 and 14, 2008.

Starting near the junction of Cerros Calizos and Mirador Guayacan trails (138 m asl), we sampled at each 10 m interval (measured with GPS), down the Cerros Calizos trail. At each interval, we established a sample point 5 m off the trail, choosing the left or right side randomly, and maintaining elevation constant.

At one site (38 m) by the junction of Sendero Pizote, we encountered trailside construction that precluded sampling on one side. On the other side, we proceeded 10 m beyond the disturbance along Sendero Pizote, and a further 5 m at right angles to that trail on a randomly chosen side.

Around each sample point, we sampled the nearest three trees with diameter at breast height (DBH) > 5 cm, and the nearest three woody understory plants 1-3 m tall.

From each individual sampled, we collected a leaf that represented the mean leaf morphology of that tree, if leaves were present and within reach, and recorded genus and family where possible. We sampled 23 canopy and 29 understory plants. We defined a leaf retention index as 1 = 0% leaf cover, 2 = < 50%, 3 = > 50% leaf cover, 4 = 100% leaf cover (yellowing leaves), 5 = 100% leaf cover (green leaves), and 6 = 100% leaf cover on an evergreen species. We multiplied leaf length and maximum width to calculate a leaf area index, and computed the mean leaf area index for each elevation. We used a toughness index, giving each leaf a score of 1 (least tough), 2 (medium toughness), or 3 (most tough). We noted pubescence on the bottom of each leaf as follows: 1 (none), 2 (small) or 3 (large).

We \log_{10} -transformed mean leaf area to equalize variances and correct non-normality.

RESULTS

We observed a total of 12 families, with 20 samples from unknown genera (unknown canopy = 7, unknown understory = 13). *Erythroylon* was the most abundant family or genus sampled followed by Fabaceae and Guazuma (Table1). Leaf retention increased significantly with elevation ($r^2 = 0.83$, $df = 9$, $P = 0.0001$). This was due entirely to the presence of evergreen trees at lower elevations: when we excluded evergreens, there was no significant trend in the timing of leaf loss with elevation ($r^2 = 0.08$, $df = 9$, $P = 0.37$).

There was no trend in leaf area with elevation, for either canopy ($r^2 = 0.001$, $df = 7$, $P = 0.93$) or understory species ($r^2 = 0.23$, $df = 9$, $P = 0.13$). Mean toughness was not significantly related to elevation for canopy trees ($r^2 = 0.05$, $df = 7$, $P = 0.55$), and was marginally significant for understory plants ($r^2 = 0.32$, $df = 9$, $P = 0.07$), with a trend toward greater toughness at low elevations.

All of the evergreen leaves sampled occurred at lower elevations, starting at 38 m and ending at 88 m (Fig 2). Only deciduousness had a significant effect on toughness ($r^2 = 0.34$, $df = 53$, $P = 0.0063$), with evergreen

leaves much tougher than deciduous ones. There was no significant relationship between leaf pubescence and elevation for evergreen ($r^2 = 0.00$, $df = 10$, $P = .94$) or deciduous plants ($r^2 = 0.05$, $df = 44$, $P = 0.11$). Evergreens dominated woody plants at lower elevations ($n = 12$, Fig. 2), while they were conspicuously absent from higher elevations.

Table 1. Numbers of individuals sampled from each family/genus by understory/canopy

Family/Genus	Total Understory	Total Canopy
Apocynaceae	1	0
Burseraceae	0	1
Erythroxylon	12	1
Euphorbia	1	2
Fabaceae	2	6
Guaiacum	1	0
Guazuma	2	1
Jaquinia	0	1
Luehea	0	4
Sapotaceae	0	5
Tabebuia	1	4
Tiliceae	0	1
Unknown	13	7

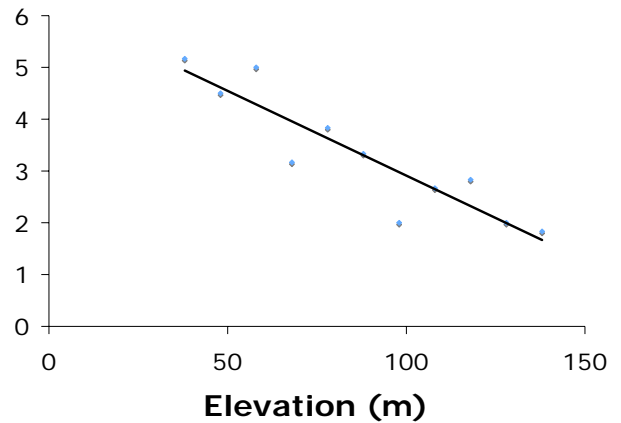


Figure 1. Trend in mean leaf retention by woody plants along an elevation gradient up a limestone ridge at Palo Verde, Costa Rica.

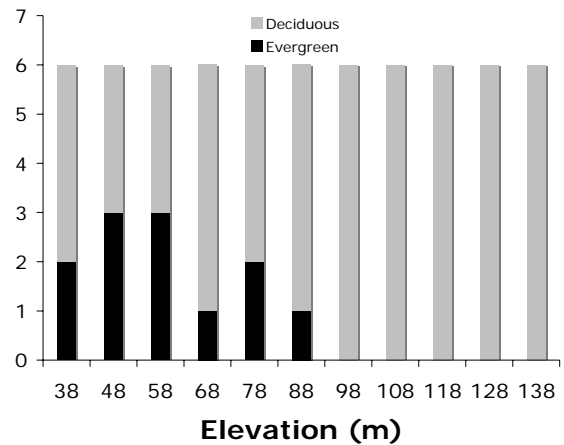


Figure 2. Proportions of evergreens sampled in woody plants along an elevation gradient up a limestone ridge, at Palo Verde, Costa Rica.

DISCUSSION

Vegetation retained fewer leaves with increasing elevation (Fig. 1), supporting our hypothesis that high elevation plants are early deciduous. Surprisingly, the trends we observed were dictated almost entirely by the concentration of evergreens at lower elevations.

Our results are consistent with the severe environmental

gradients corresponding to elevation along our transect up to the limestone ridge. This was apparent in the complete absence of evergreens between 98 and 138 m, i.e. on the higher (and steeper) slopes.

Evergreens typically have tougher leaves than deciduous species, because leaf longevity makes investment in herbivore defense cost effective (Givnish 2002). Thus explains the marginally significant trend in understory plants for greater toughness at lower elevations.

Among deciduous trees, leaf area did not change with elevation. Deciduous plants escape the water stress that would occur if they maintained leaves in the dry season, by abscising leaves at the end of the wet season. Thus, it is not surprising that early deciduous plants did not follow the predicted trend in leaf area.

Evergreens can survive the dry season lower on the elevational gradient, where the soil probably retains more moisture during the dry season. Our results suggest that the elevational trends we observed were dominated by the extreme costs of maintaining leaves in a seasonally xeric environment.

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EFFECTS OF CATTLE ON FINE ROOT DENSITY AND SOIL RESPIRATION

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Abstract: The effects of cattle on marsh plants at Palo Verde National Park have been well studied but the effects of cattle on soil biota are poorly understood. As we hypothesized, cattle reduced fine root density, but contrary to our expectation, they had no effect on soil respiration. The reduction of fine root density suggests that cattle reduce plant resource assimilation.

Keywords: Water retention, Palo Verde, Nutrients

INTRODUCTION

At Palo Verde National Park in Costa Rica, cattle are used to manage marsh vegetation. Although the effects of cattle on flora and fauna have been well studied (Burnidge 2000), effects on soil have been largely overlooked. Soil compaction by grazing cattle can negatively affect soil by damaging roots and reducing soil microbial respiration (Unger 1994). Alternatively, nutrient inputs from cattle defecations may increase soil respiration (Bilotta et al. 2007). To better understand the impacts of cattle on soil, we measured fine root density, soil compaction, and soil respiration in cattle grazed and ungrazed areas. We hypothesized that 1) fine root density is lower in cattle grazed areas and that 2) soil respiration rates differ between grazed and ungrazed areas.

METHODS

We took all field measurements on January 13, 2007 at 0700-1030 in a tropical dry secondary forest adjacent to the marsh ca. 0.4 km southeast of the OTS field station in Palo Verde National Park, Costa Rica. We randomly selected 10 *Pithecellobium dulce* trees within adjacent areas grazed or ungrazed by cattle. We took surface samples of mineral soil ranging from 30-200g, in a random direction 1m from the trunk. We assessed soil compaction immediately adjacent to where we took soil samples using an 11.3 kg drop cone penetrometer. For each soil sample, we measured the combined length of all roots > 0.5 mm diameter. To measure soil respiration, we constructed eight vial respirometers, four for each study area, each filled with 5g of soil and saturated with 2.1 ml of water (Braden et al. 2001). Respiration occurred overnight.

We calculated fine root density as total length per g of soil. We square-root transformed these data to satisfy assumptions of normality, and performed a one-tailed pooled variation t-test.

RESULTS

Fine root density was lower where cattle were present ($t = 1.82$, $df = 18$, $P = 0.04$). However, the presence of cattle did not significantly affect soil respiration ($t = 0.61$, $df = 6$, $P = 0.56$) or soil compaction ($t = 1.33$, $df = 17$, $P = 0.06$).

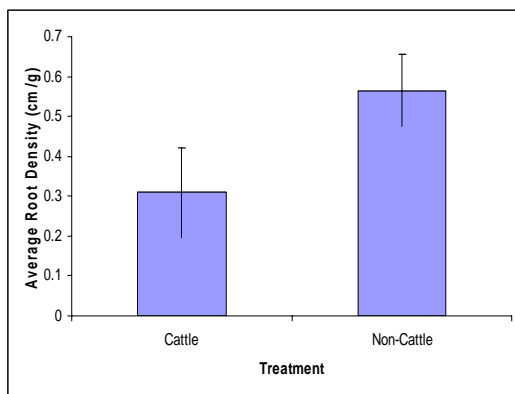


Figure 1. Mean densities of fine roots in soil (± 1 SE) in a cattle grazed area and a non-cattle grazed area in Palo Verde National Park, Costa Rica.

DISCUSSION

The lower fine root density in cattle-grazed areas may have been caused by the tearing action of cattle hooves, or by cattle grazing on the leaves of *P. dulce* and herbaceous vegetation in the cattle grazed site (Erickson et al. 2001). This lower root

density may limit plants' ability to access water and nutrients in the soil (Unger 1994).

Cattle-grazed areas contained soil that appeared comparatively drier and more cracked. The area also had less vegetative cover, as observed by Stork et al. (2006). Cattle compact soil, increasing soil density and potentially inhibiting fine root growth (Montagu, 2001).

We found no effect of cattle on soil respiration, though we may have been limited by imprecise soil incubation methods. We recommend that later studies include samples that better represent grazed and ungrazed areas, rather than sampling close to trees, where cattle may trample and graze less.

Reduced fine root density suggests that cattle reduce plant resources assimilation.

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MURDER BY NUMBERS: THE EFFICIENCY OF ARMY ANT CASTES

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Abstract: We manipulated prey availability *in situ* for the army ant *Eciton burchelli* (subspecies *parvispinum*) at Palo Verde National Park, Costa Rica. We investigated how the colony allocates the heterogeneous worker resources arising from the evolutionarily conserved caste polymorphism in army ants. We measured the frequencies at which minor and major workers attack and carry prey of different sizes. Both prey size and worker task (killing or carrying) significantly affected the numbers of major and minor workers recruited. This allocation of resources apparently contributes to the optimization of foraging strategy previously demonstrated for army ants.

Keywords: Division of labor, *Eciton burchilli parvispinum*, social insect

INTRODUCTION

Many social insects are polymorphic. Major and minor workers of the army ant *Eciton burchellii parvispinum* each have a role within the colony to maximize foraging efficiency (Franks 2001). We explored the allocation of *E. burchellii parvispinum* castes to different foraging tasks. We hypothesized that the combination of major and minor workers recruited would vary according to prey size and type of foraging behavior (killing or carrying prey). Specifically, we predicted that major workers would kill and carry larger prey more than minor workers.

METHODS

At the Palo Verde Biological Station, Costa Rica, we trapped terrestrial arthropods (grasshoppers,

katydids, crickets, spiders) and sorted them into distinct size classes: small (< 1cm), medium (1-3cm), and large (> 3cm). All insects were alive but immobilized by leg removal at the beginning of each experimental trial.

We conducted our experiment during natural foraging cycles of *E. burchellii parvispinum*, from 1650-1800 on 16 Jan 2008 and 0400-0600 on 17 Jan. We selected a random column or swarm for prey introduction, at a random distance (1-5 cm) from the column or swarm. For each trial, we measured the time from placement of prey item until the arrival of the first ant and the time to first attack (bite or sting). We also noted the caste (major, minor, soldier) of the attacking ant. For the next 5 minutes, we recorded the numbers of minor workers, major workers, and soldiers that contacted the prey, at 20 second intervals.

From 0630-1000 on 17 Jan we observed the colony returning to its underground nest site. We randomly selected a column to watch for each 10 minute period. We recorded the identity and size class (small, medium, large) of each prey item carried into the nest, as well as the numbers and castes of the ant(s) carrying each item. We classified foraging activity as killing or carrying prey.

No soldiers were seen in direct contact with prey, so they were excluded from analyses. Three experimental trials were excluded (all with small beetles) because no ant attacked. All counts of ant numbers were square-root transformed for normality in multivariate variance analysis (MANOVA). All analyses were performed in JMP 7.0.

RESULTS

As hypothesized, prey size and task type significantly affected the number and type of workers recruited (MANOVA Wilks' $\lambda = 0.378$, $df = 6, 86$, $P < 0.0001$). The numbers of major and minor workers differed significantly depending on prey size (Wilks' $\lambda_{\text{prey size}} = 0.457$, $df = 4, 86$, $P < 0.0001$) and task (Wilks' $\lambda_{\text{task}} = 0.668$, $df = 2, 43$, $P < 0.0001$). More major and minor ants attacked and carried large prey than small and medium sized prey (Figure 1 & 2). However, more minor ants attacked large prey than

major ants ($t = 3.76$, $df = 18$, $p = 0.0014$).

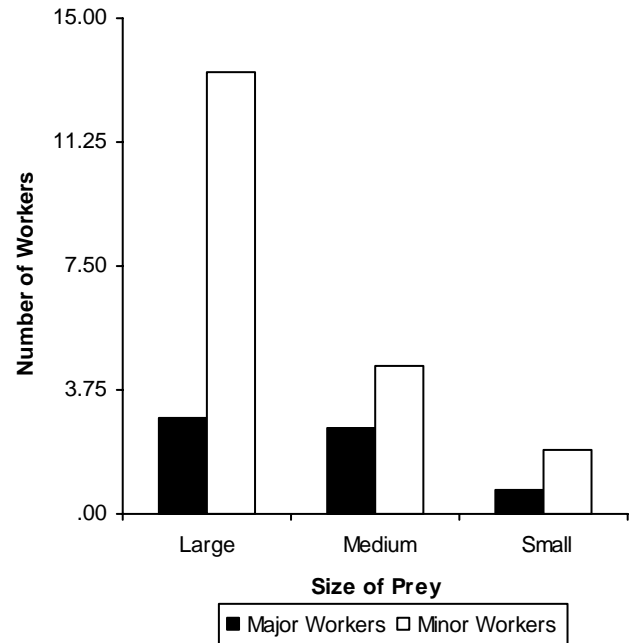


Figure 1. Number of *Eciton burchelli* workers recruited to kill different size prey at Palo Verde, Costa Rica. Mean \pm SD.

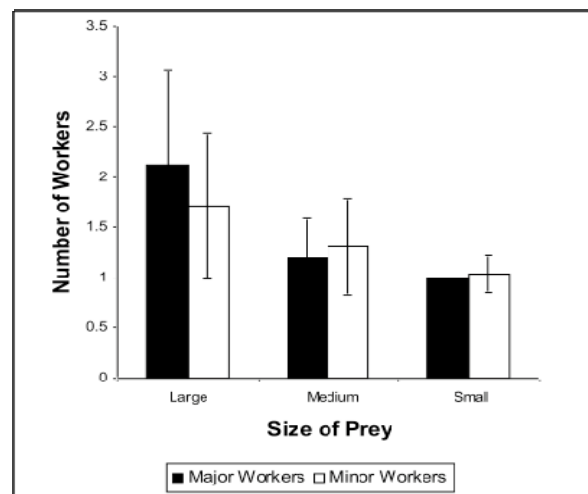


Figure 2. Number of *Eciton burchelli* workers carrying different size prey at Palo Verde, Costa Rica. Mean \pm SD.

DISCUSSION

Prey size and task affected the number of major and minor workers recruited. Contrary to our hypothesis, more minor than major workers killed large prey items. This may be simply because minor workers are most abundant. Alternatively minor workers may be specialized in killing prey, and selectively recruited for this task. This allocation of resources apparently contributes to the optimization of foraging strategy previously demonstrated for army ants (Franks 2001).

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DUCKS DECODED: GROUP BEHAVIORAL DYNAMICS IN PALO VERDE, COSTA RICA

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Abstract: At daybreak, foraging groups of Black-bellied Whistling Ducks on the Palo Verde marsh in Guanacaste, Costa Rica, settle into groups of varying size. We examined how group size and time of day influence the behavior of individual ducks within these groups. Behavior changed significantly over the course of the day, with most ducks resting at midday and becoming more active at dawn and dusk. Group size was significantly associated with individual behavior, with more aggression in larger groups and more foraging in smaller groups.

Key Words: *Dendrocygna autumnalis*, *group dynamics*, *aggregation*

INTRODUCTION

Black-bellied Whistling Ducks (*Dendrocygna autumnalis*) are abundant in the marshland of Palo Verde, Costa Rica in early January. They break into small groups to forage at night and flock together during the day (Garrigues and Dean 2007). The benefits of daytime aggregation include dilution of predation, group vigilance, and the confusion effect, which minimize an individual's chances of being preyed upon (Parrish and Edelstein-Keshet 1999). However, grouping has its costs, including intraspecific aggression and competition for food. The costs and benefits of grouping, and its effect on individual behavior, have not been adequately investigated.

We hypothesized that group size affects individual duck behavior;

in particular we predicted that larger groups would have more aggression and less vigilance per duck. Less time spent alert for predators would allow individuals more time for feeding (Caraco 1979).

We hypothesized that time of day would influence individual behavior, and specifically that ducks would feed more at dawn and dusk, and rest at midday. Finally, we hypothesized that feeding and non-feeding ducks would be found on different vegetation types.

METHODS

On 16 and 17 Jan 2008, we sampled from an open section of freshwater marsh, 0.5 km from the OTS Field Station of Palo Verde National Park, Guanacaste, Costa Rica, with a high density of *D. autumnalis*. We observed 90

individual ducks from the end of the boardwalk between 0530 and 0630 (dawn), 1030 and 1130 (midday) and 1700 and 1800 (dusk) over two days. We randomly selected a focal individual within a random group. We defined a group as a cluster of individuals within 1 m of each other, and divided the marsh area into three habitat types: water, lilies and boundary (when a group spanned both habitats). We recorded group size, habitat, and the size of the habitat patch (xs, s, m, l and xl, ranging from 1m² to 20m²). A duck's instantaneous activity was noted at 20-second intervals for a 5-minute period. Activities were divided into five categories: foraging, resting, scanning, preening, and flying/walking/swimming. The occurrence of any spar, bite, or charge within the group was recorded as aggression.

We divided the groups into four size classes of roughly equal numbers (xs, s, m, l). To compare the behavior of ducks across different times of the day and group sizes, we ran a MANOVA and computed Wilks' Λ . To test for differences in aggression levels, we used a Wilcoxon/Kruskal-Wallis test to compensate for unequal variances. We compared the habitat selection of feeding and non-feeding ducks with a contingency table and a χ^2 statistic.

RESULTS

Behavior was significantly associated with the time of day (Wilks' Λ = 0.46, df = 12, 154, P < 0.0001) but not with group size class (Wilks' Λ = 0.77, df = 18, 218, P = 0.27). There was no interaction of group size class with time of day (Wilks' Λ = 0.68, df = 36, 341, P = 0.71). Time of day did not significantly affect the mean group size (F = 0.71, df = 2, 91, P = 0.49).

We observed very little foraging during any of the observation periods (9.1% of all behaviors). The three most common behaviors were resting (39.8% of all behaviors), preening (24.9%), and scanning (20.5%). Most resting occurred at midday, and most scanning and preening at dawn (Table 1).

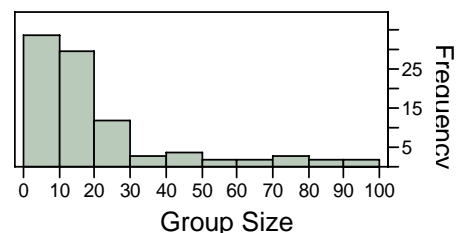


FIGURE 1. Frequency histogram of duck group sizes (16-17 Jan 2008) on the marsh at Palo Verde, Costa Rica.

Aggression level peaked in the largest groups (Table 1), and was affected by group size class (Wilcoxon/Kruskal-Wallis test, approx. χ^2 = 7.3, df = 3, P = 0.06). Most foraging occurred in the smallest groups (ANOVA, F = 4.3, df = 3, 90, P = 0.007). There was no difference in scanning (F = 0.27, df =

3, 90, $P = 0.84$) or preening ($F = 0.58$, $df = 3$, 90, $P = 0.62$) activity between group size classes.

Habitat selection depended on time of day ($\chi^2 = 11.9$, $df = 4$, $P = 0.02$). Ducks primarily rested on lilies (mostly at midday) and fed in open water. Habitat selection of feeding and non-feeding ducks was

significantly different ($\chi^2 = 10.9$, $df = 2$, $P = 0.004$).

TABLE 1. Counts of duck activity on the marsh at Palo Verde, Costa Rica, by group size classes and time of day.

Group size class	Time of day	Foraging	Resting	Preening	Walk/Swim	Scanning	Aggression
XS (2-7 ducks)	Dawn	19	8	65	2	27	3
	Dusk	37	31	37	3	27	0
	Midday	4	37	5	0	16	0
	Totals	60	76	107	5	70	3
S (8-12 ducks)	Dawn	6	0	53	3	17	2
	Dusk	11	59	18	7	28	8
	Midday	0	151	8	0	30	2
	Totals	17	210	79	10	75	12
M (13-21)	Dawn	13	22	57	2	42	10
	Dusk	6	43	22	4	18	1
	Midday	15	50	1	0	4	3
	Totals	34	115	80	6	64	14
L (22-95)	Dawn	4	20	50	3	35	10
	Dusk	10	35	28	5	29	10
	Midday	3	101	4	0	14	2
	Totals	17	156	82	8	78	22
	Overall Totals	128	557	348	29	287	51

DISCUSSION

Although time of day did not affect foraging, it influenced preening, scanning, and resting frequencies. Black-bellied Whistling Ducks spend much of the night flying in search of food, and spend time at dawn preening and scanning

for predators, after settling down to rest for the day. Future studies of *D. autumnalis* foraging should be done at night.

Duck behavior depends on group size and the time of day. Contrary to our prediction, most foraging occurred in the smallest size class, suggesting that intraspecific

competition for food might outweigh the benefits of increased protection in a large group. If predation risk is uniformly low or unrelated to group size (perhaps since an alarm call is audible to nearby groups), ducks may benefit more from being in small groups. This idea is consistent with the observed distribution of group sizes, which was skewed towards small groups throughout the day (Fig. 1).

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FORAGING AND SCANNING BEHAVIORS IN MALE AND FEMALE MANTLED HOWLER MONKEYS (*ALOUATTA PALLIATA*)

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Abstract: Grouping in social animals has costs and benefits, which typically differ by gender. We predicted that female howler monkeys (*A. palliata*) would forage more than males due to increased nutritional requirements associated with reproduction, while males would scan more than females to maintain dominance and access to mates, and to protect themselves and their kin from predators. In the early morning (0600-0900) when total troop activity was greatest, females foraged more than males and males scanned more than females, supporting our hypotheses.

Key words: primate behavior, time allocation, social groups, Palo Verde, Costa Rica

INTRODUCTION

Costs and benefits associated with group aggregation in social animals are often gender-specific. Generally, males benefit by controlling access to females, but exert energy to protect the group. Females gain protection from males, but bear the primary burden of caring for offspring.

We focused on the differential behavior of male and female mantled howler monkeys (*A. palliata*) in Palo Verde National Park, Costa Rica. Howler troops consist of 3-44 individuals of mixed age and sex (Eisenburg 1989) who spend their day foraging, resting, calling, traveling from tree to tree, and scanning for potential threats (Fierce et al. 2004). We predicted that males would scan more since their

reproductive success is linked to the protection of offspring and potential mates (Robinson 1981), while females would forage more due to greater nutritional requirements associated with reproduction, including the care and provisioning of offspring (Milton, 1980).

METHODS

Starting at sunrise on 16 and 17 January 2008, we sampled the *A. palliata* group most accessible from the OTS field station in Palo Verde National Park, Costa Rica. We determined troop composition, counting all adult males, females, and juveniles. From 0600 until 1100 we conducted two-minute observations of all visible individuals at 10 min intervals, recording time spent foraging,

traveling, grooming, resting, or scanning. An individual was considered to be resting if it was still and oriented in one direction, and scanning if it was moving its head and looking around at its surroundings.

For both foraging time and time spent scanning, we averaged data for each troop by sex, treating troops as independent samples ($n=2$). We analyzed behavioral counts for the morning (0600-0900) and for the entire observational period (0600-1100) separately based on our observation that resting strongly dominates behavior after 0900.

RESULTS

Males and females did not differ in foraging behavior across the entire sampling period ($t = 1.13$, $df = 1$, $P = 0.27$), but females spent significantly more time foraging than males from 0600-0900 ($t = 3.99$, $df = 1$, $P = 0.042$; Fig. 1). Males and females did not differ in scanning behavior across the entire sampling period ($t = 3.11$, $df = 1$, $p = 0.097$). From 0600-0900, males spent more time scanning than females, though statistical significance was marginal ($t = 5.52$, $df = 1$, $P = 0.057$; Fig. 1).

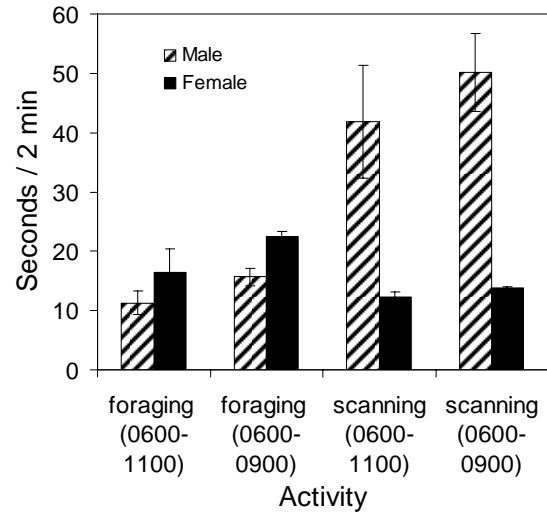


Figure 1. Mean time spent foraging and scanning (± 1 SE) for male and female howler monkeys in Palo Verde National Park, Costa Rica.

DISCUSSION

Female howler monkeys foraged more than males in the early morning, supporting our predictions. Our test of this hypothesis was conservative, as males may need to forage more than females given their typically larger size (adult males weigh 6-7 kg; females weigh 4-5 kg; Janzen 1983).

We believe that the lack of solid statistical support for our hypothesis is mainly due to small sample size and our inability to use repeated measures, which would have been possible if individuals were tracked throughout the sampling period. However, we consider our results to be biologically significant since each sample represented 20 hours of observations.

Our results do not explain why males were not more vigilant than females during the whole sampling period (0600-1100). We suggest that during the late morning, activity levels may be lower among potential predators and encroaching howler monkey troops, decreasing the need for males to scan during this time.

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TESTING MANIPULATION OF HOST TREE GEOMETRY BY TWO ACACIA ANT SPECIES, *PSEUDOMYRMEX FLAVICORNIS* AND *P. SPINICOLA*, IN NORTHWESTERN COSTA RICA

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Abstract: *Pseudomyrmex spinicola* is known to manipulate the geometry of its host plant, *Acacia collinsii*. We hypothesized that *P. flavicornis* also has this capacity, and modifies host growth in ways that reduce contact with plants occupied by the known superior competitor, *P. spinicola*. We found no significant difference in the geometry of *A. collinsii* trees inhabited by *P. flavicornis* and *P. spinicola*, indicating that the two species of acacia ants do not differ in their manipulative behavior.

Keywords: *Pseudomyrmex flavicornis*, *P. spinicola*, *Acacia collinsii*, *acacia ants*, *escape in space*, *host manipulation*

INTRODUCTION

Acacia collinsii is a host for several species of acacia ants that provide protection in return for food and shelter. *Pseudomyrmex spinicola* colonies protect host trees against arthropod herbivores and encroaching plants more vigorously than does *P. flavicornis* (Janzen p. 764, in Janzen, 1983). This, along with *P. spinicola*'s greater aggression (Janzen p. 764, in Janzen, 1983), suggests that *P. flavicornis* might avoid contact with *P. spinicola*. Growth manipulation of the host tree has been shown for *P. spinicola* in part of its range (Janzen p. 764 in Janzen, 1983). We hypothesized that *P. flavicornis* behaves similarly and would manipulate host tree

geometry to avoid contact with acacias occupied by more aggressive *P. spinicola* colonies.

METHODS

We conducted our study on both sides of La Carreta Road, ca. 6 km SE of the OTS field station in Palo Verde National Park, Costa Rica. We haphazardly chose 27 *A. collinsii* trees of base diameter 3 – 7.5 cm, inhabited by one of two acacia ant species: *S. spinicola* or *S. flavicornis*. We sampled 12 trees inhabited by the black ant *P. flavicornis* and 15 inhabited by the red ant *P. spinicola*, and randomly selected two branches on each tree. We measured the horizontal distance from the tip of the branch to

the base of the trunk and the number of secondary branches > 5 cm long on each branch. We then averaged the measurements for the two branches on each tree to obtain one value per tree.

RESULTS

We found no significant difference between the average number of secondary branches > 5 cm on *A. collinsii* trees inhabited by *P. flavicornis* and *P. spinicola* ($t = 0.25$, $df = 24.97$, $P = 0.80$). Mean horizontal distance from the branch tip to the tree trunk likewise did not differ between *A. collinsii* trees occupied by the two ant species ($t = 0.44$, $df = 23.23$, $P = 0.66$).

DISCUSSION

We found no evidence of a difference between the manipulative behavior of *P. flavicornis* and that of *P. spinicola*. Both species may manipulate their host trees similarly, but we have no clear evidence of manipulation by either species. Haphazard (rather than random) sampling could have influenced the outcomes of statistical tests.

P. flavicornis could conceivably alter branch shape in response to chemical cues from *P. spinicola* on a nearby branch. Such facultative behavior could be tested by examining the morphology and growth dynamics of paired trees (a

P. spinicola colony in close proximity to a *P. flavicornis*) compared to interspecific pairs that are not in close contact.

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LOCAL AND SYSTEMIC DEFENSES OF *ACACIA COLLINSII* BY *PSEUDOMYRMEX SPINICOLA* COLONIES

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Project design: Stephen J. Taerum. Faculty editor: David R. Peart

Abstract: *P. spinicola* defends its host *A. collinsii* in return for food and shelter. We hypothesized that *P. spinicola* would intensify its response after a second disturbance made on *A. collinsii*, regardless of whether the second disturbance was applied on the same branch as the first. However, our hypothesis was not supported; there was no evidence of induction in *P. spinicola*'s defensive behavior.

Key Words: Local induction, systemic induction, mutualism

INTRODUCTION

In the mutualism between *Acacia collinsii* and *Pseudomyrmex spinicola* (Janzen 1983), *A. collinsii* provides food and protection for *P. spinicola*, which defends the acacia against herbivores (Janzen 1983).

Plant chemical defenses are often induced rather than constitutive, which can reduce costs to the plant, because defenses are produced only when needed. We hypothesized that ant defenses against herbivory in the ant-acacia mutualism may be analogous to inducible chemical defenses. This leads to the prediction that ant recruitment will be greater after a disturbance that follows a previous disturbance.

We tested for induction in two ways. First, we determined whether ant recruitment increased from a first to a second disturbance

on a single branch, measuring recruitment on that same branch. In the second test, we disturbed the first branch in the same way, but made the second disturbance (and measured consequent ant recruitment) on a different branch of the same tree.

We performed both tests to learn whether induced ant responses are localized to the area of disturbance ("local"), or generalized to cover the entire tree ("systemic").

METHODS

We conducted our study on January 12, 2007 in an early successional forest in Palo Verde National Park, Costa Rica. Twenty-eight *A. collinsii* trees were sampled, on both sides of a dirt track ca. 6 km SE of the OTS field station (4 km E along the entrance road and then 2 km down the La Carreta Rd). We

randomly selected 1/3 of *A. collinsii* trees encountered along a series of systematically placed transects.

We measured *P. spinicola* recruitment after a standardized disturbance (tapping on the center of the branch for 10 sec). We counted all ants for a 30 sec period, crossing an imaginary line placed at least 10 cm away from any branch nodes, on the disturbed branch. Recruitment was measured beginning ca. 5 sec after each of the first and second disturbances. The second disturbance was made 15 minutes after the first, on the same (local treatment) or a different branch (systemic treatment) on the same tree. Before each disturbance, we measured the rate at which ants crossed the imaginary line, so we could calculate (by difference) the increase in ant recruitment over a baseline level. Hereafter, we refer to this increase in recruitment as simply “recruitment” after a disturbance.

To compare ant recruitment between the first and the second disturbances, we used paired t-tests for each of the systemic and local treatments. All statistical analyses were in JMP 7.0.

RESULTS

Recruitment did not differ significantly between the first and second disturbances for either local (paired- $t=0.64$, $df=13$, $P=0.27$) or

systemic treatments (paired- $t=1.33$, $df=13$, $P=0.10$). However, there was a non-significant trend for recruitment to be higher for the second disturbance, in both treatments (Fig. 1). Recruitment on the same branch was 18.9 ± 4.4 after the first disturbance and 21.1 ± 5.5 after the second disturbance. Recruitment measured on different branches was 25.7 ± 6.3 after the first disturbance and 33 ± 6.8 after the second disturbance.

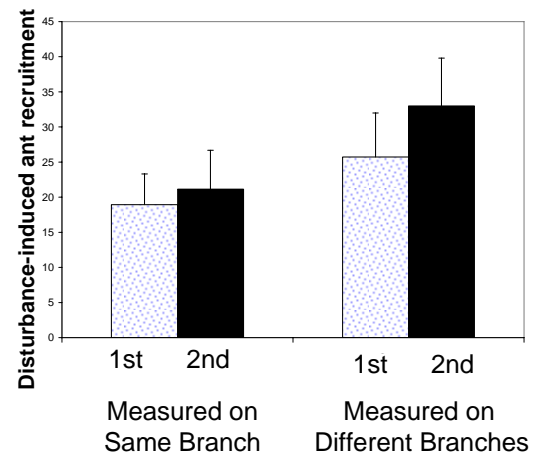


Figure 1. *P. spinicola* recruitment following standardized disturbances (see text for details) on *Acacia collinsii* at Palo Verde, Costa Rica (means ± 1 SE). Recruitment was measured after each of two disturbances, separated by 15 min, in each of two treatments (recruitment measured either on the same branch as the disturbance, or on a different branch). 1st and 2nd refer to recruitment measured after the first or second disturbance, respectively.

DISCUSSION

Contrary to our prediction, there was no evidence of local or systemic induction in the response of *P. spinicola* to repeated disturbances.

Induction may have occurred, yet we could have failed to detect it, if the effects of induction dissipated before the second disturbance was applied. Another possibility is that the duration, rather than the rate of recruitment, may increase with subsequent disturbances. Prolonged responses in acacia ants have been reported by Schwartz et al. (2006); such an induced response would not have been detected with our sampling methods.

In future work, it would be useful to evaluate duration of ant responses, as well as rates of recruitment, and to test responses to successive disturbances over a range of time intervals.

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CRUSH THOSE CATTAILS!
ASSOCIATIONS BETWEEN AVIAN FEEDING GUILDS
AND HABITATS ON A COSTA RICAN MARSH

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Abstract: The marsh at Palo Verde National Park contains three main habitats: open water; low, floating plants (water hyacinth and water fern); and sedges with cattails. We tested whether marsh birds partition feeding territory based on their preferred diet and method of feeding, hypothesizing that bird species would be distributed across these habitats according to their feeding guilds. We found very strong support for a non-random distribution of bird species and feeding guilds across the three habitats. Diving carnivores were found in areas of open water and surface-foraging carnivores were found on floating plants. Our findings suggest that maintenance of varied habitats is essential for conservation of bird diversity on the Palo Verde marsh.

Keywords: habitat heterogeneity, marsh management, conservation, marsh birds, feeding guilds, Palo Verde

INTRODUCTION

The distribution of aquatic bird species across marsh habitats may reflect partitioning of resources among coexisting species. Aquatic birds use different methods to feed, e.g. skimming, filtering or visual hunting. Different habitats may provide opportunities for effective use of these feeding methods. Marsh management can be improved with better understanding of whether and how habitat heterogeneity promotes biodiversity (e.g. Therriault and Kolas 2000; Brauns *et al.* 2007).

The habitable area in the marsh at Palo Verde, Costa Rica, was drastically reduced with the establishment of the reserve in the 1970s. The cattail *Typha domingensis*

became dominant, homogenizing the marshland. Active management maintains a few small open areas of the marsh. Cattle grazing and the use of tractors remove or crush marsh vegetation and prevent any species from dominating. This keeps the vegetation of the marsh in an early successional stage (Mitchell *et al.* 2006) and preserves heterogeneity. We focused on open water, low aquatic vegetation, and tall cattail habitats.

Since these three habitats vary considerably in physical structure, we hypothesized that each would sustain bird species with different feeding strategies. Based on known diet as described in Stiles and Skutch (1989), we also hypothesized that any given feeding guild would show a clear preference for a specific habitat and

that guilds would not share habitats. This leads to the prediction that the birds of any guild will be concentrated in one habitat type. Finally, we hypothesized that birds of the same guild should have the same distribution regardless of activity.

METHODS

We performed the study from the bird observation tower on the marsh, 0.5 km from the Palo Verde Biological Station in Guanacaste, Costa Rica. We worked in two teams, each studying two patches from each of three habitats: sedges and cattails ("cattails"), water hyacinth and water fern ("lilies"), and open water ("water"). Each team chose its six patches at random, then continued to observe the same six patches, in randomized order, over the course of the morning. Teams alternated time in the tower every hour from 0920 to 1120 on 13 Jan 2008, and 0720 to 1120 on 14 Jan, so that each patch was observed for one 5-minute period every 2 hours, totaling between 3 and 4 observation periods of each patch over 2 days. We recorded the species of every bird in the patch and noted its activity. Birds were identified using Garrigues and Dean (2007).

We divided bird species into three feeding guilds according to their diets (Stiles and Skutch 1989), and used Paszkowski and Tonn (2006) as a guide for the categories: diving

carnivores; surface-foraging carnivores; and surface-foraging omnivores (Table 1). Since feeding guilds describe only the feeding behavior of birds, we excluded observations from all non-feeding birds in our guild data analysis. We compared feeding and non-feeding birds in a later analysis.

RESULTS

There was a significant association between habitat types and species (Likelihood ratio, $\chi^2 = 52.68$, $df = 26$, $P = 0.0015$), as well as feeding guilds (Likelihood ratio, $\chi^2 = 17.27$, $df = 6$, $P = 0.0084$).

Feeding guilds tended to occupy different habitats while feeding; eighty percent of the diving carnivores observed were in open water habitats while over 70% of surface-foraging carnivores observed were on lilies (Table 2).

We found that surface-foraging birds were differentially distributed across habitats depending on whether they were feeding or resting ($\chi^2 = 6.08$, $df = 2$, $P = 0.0477$ for carnivores, and $\chi^2 = 19.6$, $df = 2$, $P < 0.0001$ for omnivores). Both of these guilds showed a more even distribution across habitats when feeding, than when resting (both rested almost exclusively on lilies).

Table 1. Numbers of feeding birds observed in three habitat types on marsh near Palo Verde Biological Station, Costa Rica

Feeding Guilds	Species	Habitat			Total
		Lilies	Cattails	Water	
Diving carnivores	Anhinga	0	0	1	1
	Least Grebe	1	0	3	4
Surface-foraging carnivores	Little Blue Heron	1	0	0	1
	Cattle Egret	2	0	1	3
	Great Egret	7	0	1	8
	Green Heron	2	1	0	3
	Limpkin	2	0	2	4
	Snail Kite	0	0	1	1
	Snowy Egret	1	0	0	1
Surface-foraging omnivores	Common Moorhen	6	1	3	10
	Northern Jacana	15	6	10	31
	Purple Gallinule	5	14	1	20
	Total	43	22	23	88

Table 2. Number and percent of birds observed by habitat on Palo Verde marsh, Costa Rica

Feeding Guild	Habitat							
	Lilies		Cattails		Water		Total	
	Count	% of guild	Count	% of guild	Count	% of guild	Count	% of guild
Diving Carnivores	1	20.00	0	0.00	4	80.00	5	100.00
Surface-foraging Carnivores	15	71.43	1	4.76	5	23.81	21	100.00
Surface-foraging Omnivores	26	42.62	21	34.43	14	22.95	61	100.00

DISCUSSION

Feeding guild helped predict the distribution of diving carnivores and surface-foraging carnivores, but the more generalist feeders in the surface-foraging omnivore guild showed no clear habitat preference (e.g. the Northern Jacana was found mostly on lilies while the Purple Gallinule was mostly in cattails). This is probably because of their broad omnivorous diets. These associations

suggest that feeding guilds alone cannot reliably predict distributions of birds among habitats.

The distributions of feeding and non-feeding birds were visibly different at the feeding guild level. Finer knowledge of such behavioral nuances could help guide habitat predictions.

Our results suggest that all three feeding guilds depend on the open water and low aquatic vegetation habitats created by current

management practices. Many aquatic bird communities worldwide have already suffered from the destruction of wetlands (Snell-Rood and Cristol 2003) and habitat fragmentation. The loss of such habitat from Palo Verde appears inevitable if human management were to cease. Maintaining vegetative heterogeneity through marsh management is essential to support the great diversity and richness of bird life in Palo Verde.

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