

## DISCUSSION

Our results support the conclusion of Nowak et al. (2002) that adult males spend a higher proportion of their time scanning than other individuals. Adult male reproduction may be more limited by access to mates than that of females, so protection of the group may benefit them more.

Contrary to our predictions, individuals with close neighbors did not scan less than those with distant neighbors. It may be that neighbors more than 10 m away improve an individual's safety as much as closer neighbors. However, the safety of individuals with neighbors beyond this distance may decrease, possibly resulting in increased scanning time.

We also found that the sex of the nearest neighbor did not influence time spent scanning. Since NND does not affect scanning rate, it follows that the sex of the nearest neighbor would similarly have no effect.

Although scanning time has been found to vary inversely with troop size (Nowak et al. 2002), our findings suggest that howler monkeys living in groups do not spend less time scanning based on nearest neighbor distance or identity. On average, howler monkeys spent between 25 - 50% of their time scanning, which illustrates the importance of this behavior. As there are few extant predators of howler monkeys in Palo Verde, the exact benefit of scanning behavior is unclear. In addition to predator detection, scanning may be involved in locating new food resources or in social interactions among troop members. Further investigation of howler monkey

behavior may help clarify the value of scanning in the behavioral repertoire of this primate species.

As a caveat, we noted that it was often difficult to differentiate sub-adult males, sub-adult females, and adult females in the field. Careful planning, strict definitions of behavior categories and better identification of age and sex will be necessary in future studies of howler monkey group behavior.

## LITERATURE CITED

- Altmann, R. V. 1974. Observational study of behavior: sampling methods. *Behavior* 49. Pp. 227 - 265.
- Begon, M., J. L. Harper, and C. R. Townsend, 1990. *Ecology: Individuals, Populations and Communities*. Blackwell Scientific Publications: Cambridge, MA. Pp. 165.
- Glander, K. E. 1983. *Alouatta palliata*. in D. H. Janzen, ed. *Costa Rican Natural History*. University of Chicago Press: Chicago, IL. Pp. 448 - 449.
- Nowak, K. S., K. N. Podolak, L. V. Reynolds, B. B. Risk, R. F. Rogers, and E. R. Schoen. 2002. Group living and vigilance in howler monkeys. *Dartmouth Studies in Tropical Ecology*. Dartmouth College, Hanover, NH.
- Sokal, R. R. and F. J. Rohlf. 1981. *Biometry: The Principles and Practice of Statistics in Biological Research*. W. H. Freeman and Company: San Francisco, CA. Pp. 414.

## Age-based social dominance in the Northern Jacana

KATHLEEN A. THEOHARIDES, KATHARINE E. SIMON, CATHERINE R. CHAMBERLIN, ARTHUR J. KEHAS AND JOEL B. WICKRE

**Abstract:** In many vertebrates, adults are dominant over sub-adults and immatures. In this study, we examined the social system of the Northern Jacana (*Jacana spinosa*), a common bird species in the wetlands of Palo Verde National Park, Costa Rica. We hypothesized that age-based differences in social status influence the outcome of agonistic encounters, habitat occupancy and time spent foraging. Adults won most (95%) agonistic encounters. However, adults and immatures showed no differences in time spent foraging or in their distribution among sites. The latter may be due to the fact that the proportions of microhabitats were similar in our sample sites. We conclude that adult Jacanas are dominant over immatures, and based on our observations we propose that adults may displace immatures from preferred foraging microhabitats within sites. Further study is needed to evaluate the consequences of social dominance of adults on the local distribution and foraging success of immature jacanas in the wetland ecosystem.

**Key Words:** habitat preference, *Jacana spinosa*, marsh, social structure, subordinate-dominance patterns, tropical wetlands

## INTRODUCTION

Social dominance hierarchies in many vertebrate species are founded on age-based social stratifications. This type of dominance hierarchy influences activities of members of different age groups and may have important consequences for immature individuals, such as exclusion from preferred habitats, food limitation and higher levels of stress (Begon et al. 1990). In this study, we examined the social system of the Northern Jacana, a species exhibiting reversed sex roles with dominant, territorial females and subordinate males (Jenni 1983). Jacanas occur in greatest abundance in areas that are seasonally flooded and covered with a variety of vegetation, conditions that characterize our study area in Palo Verde National Park, Costa Rica. Previous studies at this site found that Jacanas spend a disproportionately greater amount of time in habitats dominated by water hyacinth (*Eichhornia crassipes*) and water lily (*Nymphaea ampla*), suggesting that they prefer these vegetation types (Mahar et al. 2000).

Given these findings, we hypothesized that age class differences in social status would influence habitat occupancy

and time budgets of Northern Jacanas. We predicted that if adults are socially dominant, they should win agonistic encounters with immatures more frequently than immatures win over adults. Because adult Jacanas may displace immatures from preferred habitat, we predicted that immatures would have to spend more time foraging than adults. Finally, we predicted that the spatial distribution of Jacanas would be related to age, with adults more frequently occupying habitats dominated by water lily and water hyacinth, and immatures occupying less preferred habitats such as thalia (*Thalia geniculata*), sedge (*Oxycaryum cubense*), and cattail (*Typha domingensis*).

## METHODS

We conducted our observations on 10 - 11 January 2003 in the marshlands near the OTS station, Palo Verde National Park, Guanacaste Province, Costa Rica. We chose three sites, one east of the observation tower, one west of the observation tower, and the third adjacent to the west end of the airstrip, hereafter referred to as East, West and Airstrip. We observed the Jacanas for 3 h on each morning from 07:30 - 10:30. We observed focal individuals for 8 min, recording

time spent foraging, preening, looking, flying, and the number of displacements. Displacements were defined as one Jacana forcing another Jacana to fly out of its location but did not include chases between individuals that did not involve flight. Displacements were evaluated as wins or losses with a same-aged or different-aged bird.

We counted the number of immatures and adults in different habitats once per hour at each site to determine abundance and distribution. We visually estimated the percent cover of water lily, water hyacinth, thalia, sedge, cattail, and open water within each site to describe habitat types. We used two-way ANOVA to analyze proportion of time spent foraging with respect to site and age. Data are reported as mean  $\pm$  SE.

#### RESULTS

The mixed-age agonistic encounters we observed were won almost entirely by adults. Of 44 observed mixed-age encounters of focal birds, 42 (95%) involved dis-

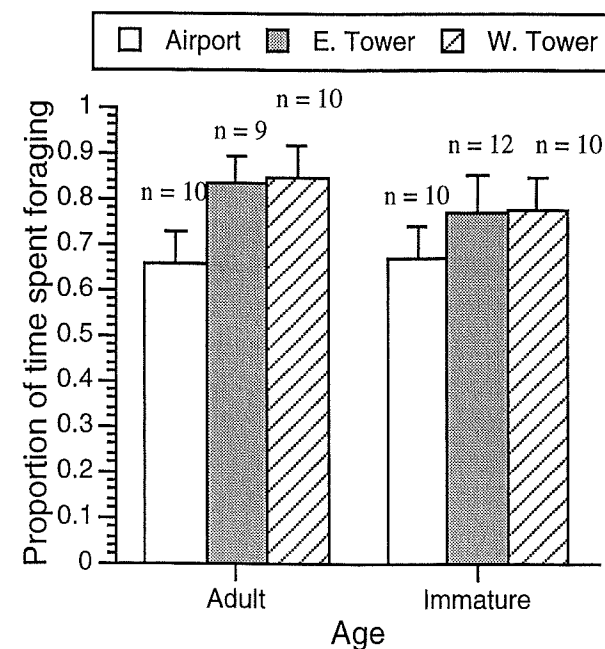


FIG 1. Proportion of time spent foraging by adult and immature Jacanas at three different sites in the marsh at Palo Verde National Park, Costa Rica. Data are presented as means  $\pm$  SE.

placements of juveniles by adults.

Time spent foraging did not differ significantly between adult and immature Jacanas (Fig. 1;  $F = 2.00$ ,  $df = 1$ ,  $61$   $P = 0.103$ ) or between sites ( $F = 1.52$ ,  $df = 2$ ,  $60$ ,  $P = 0.227$ ). The distribution of Jacanas by age also did not differ significantly among the three sites ( $F = 0.80$ ,  $df = 2$ ,  $14$ ,  $P = 0.47$ ). Immature Jacanas made up  $54.2 \pm 4.6\%$  at the airstrip,  $49.1 \pm 5.0\%$  east of the tower, and  $57.6 \pm 4.6\%$  west of the tower.

Vegetation in the three test sites was similar (Fig. 2). For example, water hyacinth and sedge were abundant in all three sites while cattails, thalia and water lily were uncommon. However, the sites did differ in percent open water and water lettuce. There was more open water to the east of the tower (31%) than to the west (5%), and water lettuce covered 30% of the area east of the tower but was not present at the airstrip.

#### DISCUSSION

As predicted, adult Jacanas won more of the different-age aggressive encounters than immatures, indicating that Jacanas exhibit an age-based social system. Despite this social dominance, we did not find differences in time spent by adults and immatures or age-based differences in distribution among sites, perhaps because the proportion of microhabitats and hence food availability was similar in all three sites. We therefore conclude that Jacanas exhibit an age based social system, but that foraging time and age distribution were not affected by this hierarchy, at least on the scale at which we examined these parameters.

Age-determined social dominance affects interactions between adult and immature Jacanas, but the ecological and behavioral consequences of adult social dominance over immatures in this species are not yet clear. We observed adults displacing immatures from certain smaller microhabitats within sites, such as water lily

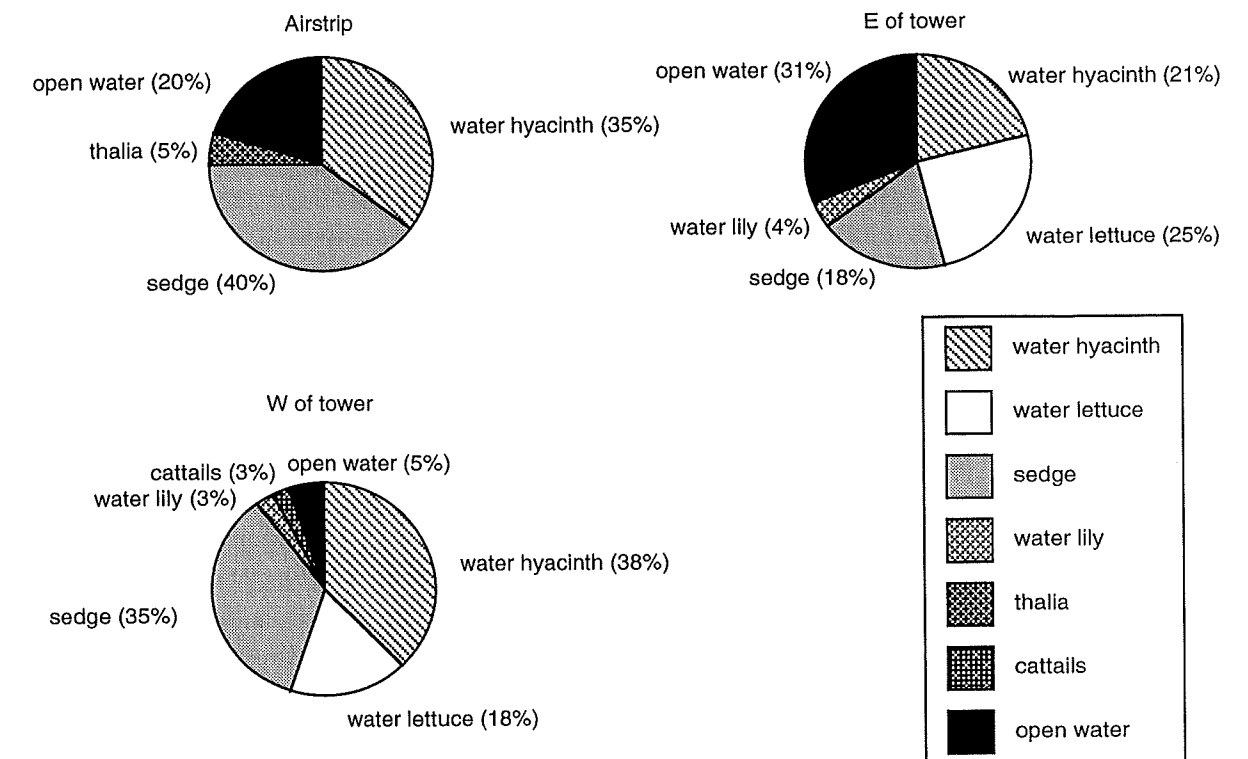


FIG. 2. Percent cover of vegetation type at each site in the marsh at Palo Verde National Park, Costa Rica.

patches. Thus, future studies might examine Jacana distribution within microhabitat patches (i.e., within sites) in order to determine the impact of adult social dominance on the local distribution and foraging activities of immatures.

#### LITERATURE CITED

- Begon, M., J. L. Harper, and C. R. Townsend. 1990. *Ecology*. Blackwell Scientific Publications: Boston, MA.
- Jackson, C. D., and S. E. Kopplin. 1996. Behavior of *Jacana spinosa* as a function of neighboring density. Dartmouth Studies in Tropical Ecology. Dartmouth College, Hanover, NH.
- Jenni, D. A. 1983. *Jacana spinosa* (Jacana Centroamericana, Mulita, Cirujano, Gallito de Agua, Northern Jacana). in D.H. Janzen, ed. Costa Rican Natural History. University of Chicago Press: Chicago, IL. Pp. 584-586.
- Mahar, E. M., L. E. Aucoin, A. K. Frank, M. K. Jennings, and M. D. Foote. 2000. Preferred foraging habitats of *Jacana Spinosa* in the Palo Verde marsh. Dartmouth Studies in Tropical Ecology. Dartmouth College, Hanover, NH.