INTRASPECIFIC AGGRESSION IN *JACANA SPINOSA* AS A FUNCTION OF AGE CLASS AND HABITAT TYPE

ZACHARY A. MAYER, JENNIFER N. CECH, PAMELA M. COLLINS, TINA HARRISON, AND JAMES A. MARLOW

Faculty Editor: Rebecca E. Irwin

Abstract: Aggressive behavior in foraging birds often results in dominance hierarchies based on age, territoriality, and distributions of food and reproductive resources. We examined how age-based (juvenile and adult) dominance hierarchies in foraging northern jacanas varied between two marsh habitats: floating vegetation mats (their preferred habitat) and grassy mudflats. We hypothesized that the frequencies of aggressive behaviors would vary with age class and habitat type. We predicted that adults would be more aggressive overall, and would dominate over juveniles. We also predicted that aggressive interactions would be more common in floating vegetation mats than on grassy mudflats because floating vegetation mats are their preferred habitat type. We recorded aggressive and submissive behaviors of juvenile and adult jacanas in the two habitat types. Adults were equally aggressive to adults and juveniles. In contrast, juveniles were more aggressive toward each other than to adults. Jacanas of both age classes were more aggressive on floating vegetation mats than grassy mudflats. While we observed more total interactions on the floating vegetation mats than the grassy mudflats, the frequency of interactions within and between age classes remained the same across habitats.

Key Words: Jacana spinosa, northern jacana, social aggression, habitat conditionality, dominance hierarchies

INTRODUCTION

Animals often aggressively defend limited resources, such as food and access to mates. Older and stronger individuals are often able to monopolize resources, establishing age–based hierarchies to secure these resources for themselves (Krebs and Davies 1993). Jacanas are suitable organisms to use when studying intra-specific aggression because they are conspicuous territorial birds that inhabit open marsh areas (Stiles and Skutch 1989).

Aggressive behavior may vary as a result of an individual's location with respect to available resources and other competing individuals. Different patterns of aggressive behavior in northern jacanas may be employed depending on these two factors. Aggressive jacana behaviors include ground charges, flying charges, and wing raises. These movements cause the victim of the behavior to run or fly away (Janzen and Carroll 1983). Some studies have found that aggression is correlated with jacana density (Dickinson and Poulin 1998,

Jackson and Kopplin 1996), while others have found no such correlation (Wright et al. 1998). Other studies have demonstrated that aggression is highest in floating vegetation mats, the jacanas' preferred habitat (Mahar *et al.* 2000). Further studies have shown that adults generally win aggressive encounters with juveniles (Theoharides *et al.* 2003). Finally, aggressive behaviors tend to be more common in morning and early evening when the birds congregate, and lowest in the middle of the day when the birds disperse throughout the marsh (Hourdequin *et al.* 1996, Jackson and Kopplin 1996).

While these and other studies have examined either the effects of age or habitat on intra-specific aggression in jacanas, no studies have tested the combined effects of age and habitat to understand how age-based patterns of aggression might vary across habitats. Therefore, we examined how different habitats affected age-based hierarchies of aggression in northern jacanas. We predicted that (1) aggressive interactions would be more common in the preferred floating vegetation mats than in grassy mudflats, (2) adults would dominate over juveniles in all habitat types, and (3) there would be more adult aggression than juvenile aggression in the preferred habitat.

METHODS

Study organism.

The northern jacana, *Jacana spinosa*, is a polyandrous territorial water bird ranging from southern Texas and northern Mexico, to western Panama and the Greater Antilles (Stiles and Skutch 1989). Jacanas are diurnal feeders and prefer to forage for macroinvertebrates in floating mats of aquatic vegetation (Mahar *et al.* 2000). Their breeding season coincides with the rainy season (April-November). Female jacanas are larger than males, socially dominant, and aggressively defend breeding territories on the marshes they inhabit (Goldfarb *et al.* 1991). Male-male aggressive interactions are rare (Goldfarb *et al.* 1991). While we observed both male and female adults in our study, we assumed that the majority of aggressive interactions would be initiated by territorial females (Stiles and Skutch 1989).

Field sites.

Our observations were made between 0800 and 1130 on 9 and 10 January, 2007 at four sites on the open marsh near the Organization for Tropical Studies field station in Palo Verde National Park, Costa Rica. We observed jacanas at four locations, each at least 50 m apart, in a 500 m stretch of marsh. We observed birds at two areas with

floating mat vegetation (immediately east of the bird tower and in the vicinity of the boardwalk west of the tower) and two areas with grassy mudflats (approximately 100 m east of the bird tower and at the eastward-most edge of the bird tower). We sampled two areas twice (immediately east and 100 m from the bird tower) and the remaining areas once.

Field methods.

Observation teams consisted of two observers and one recorder. An observer haphazardly selected a juvenile or an adult jacana and observed the individual for 10 min, or until the bird was lost from sight. For each individual bird, the observer noted the number of ground charges, flying charges, and wing raises, and the age class of the jacana(s) that each aggressive behavior(s) was directed against. The observer also noted the number of times individuals flew or ran away from another bird's aggressions, and the age class (juvenile or adult) of the aggressing bird. Juveniles can be differentiated from adults based on their physical characteristics; adults are red-brown, while juveniles are slightly smaller with grey and white coloration (Stiles and Skutch 1989). To prevent the observers from removing their eyes from their individuals, the recorder tallied the incidences. We minimized observer bias by shuffling group members between observation sites and by alternating observing and recording roles. Over the two-day observation period, we observed 22 adults and 17 juveniles in the floating vegetation mat habitats, and 23 adults and 19 juveniles in the grassy mudflat habitats.

Statistical analyses.

To test whether there were differences in the frequency of aggressive interactions between floating mats and grassy mudflats, we used a non-parametric van der Waerden test. We used a non-parametric chi-squared test because our data were left-skewed and no transformation would normalize our data. To understand the distribution of aggressive behavior within and between age classes, we performed a 2x2 chi-squared test with two factors: aggressor (juvenile or adult) and victim (juvenile or adult). To understand the difference in the relative rates of different interaction types between habitat types, we also performed a 2x2 chi-squared test with two factors: interaction type [aggressor-victim: adult-adult (AA), adult-juvenile (AJ), juvenile-adult (JA), and juvenile-juvenile (JJ)] and location (floating vegetation mats or grassy mud flats). After removing a single juvenile jacana that had 20 more aggressive interactions than any other juvenile, we performed the same analysis to test the strength of the observed relationship between

habitat type and the distribution of aggressive interactions.

RESULTS

On average, jacanas displayed more aggressive interactions per minute on the open mat vegetation than on the grassy mudflats (X^2_1=8.06, P=0.0032; Fig. 1).

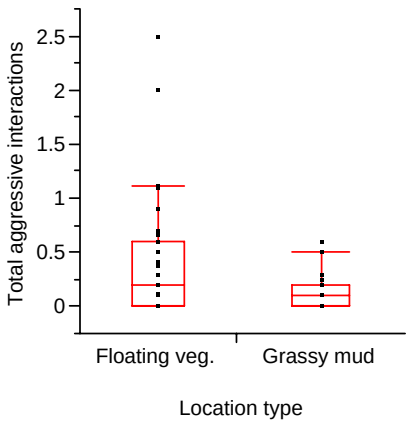

Figure 1. More aggressive interactions occur between jacanas on the floating vegetation mats (preferred habitat) than on the grassy mud flats (less preferred habitat). Each dot represents an individual jacana.

The frequency of interactions between aggressors and victims of different age classes also varied. When an adult was a victim of aggression, there was a 91% chance the aggressor was an adult and a 9% chance that the aggressor was a juvenile. When a juvenile was the victim of aggression, the aggressor was an adult 57% of the time and a juvenile 43% of the time (Fig. 2).

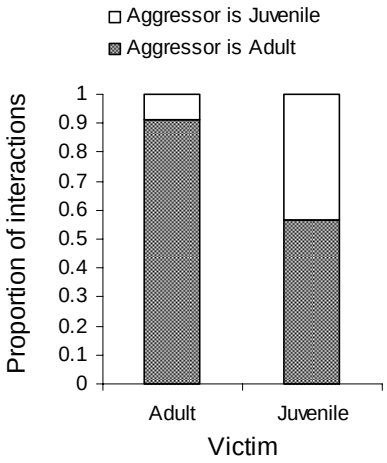

Figure 2. Aggressor age class by victim age class in northern jacanas. Adults were attacked in higher frequencies by other adults, while juveniles were attacked in higher frequencies by other juveniles.

When an adult was the aggressor, an adult was the victim 54% of the time, while a juvenile was the victim 46% of the time. When a juvenile was the aggressor, an adult was the victim 13% of the time, while a juvenile was the victim 87% of the time (X^2_1=29.45, P<.0001; Fig. 3).

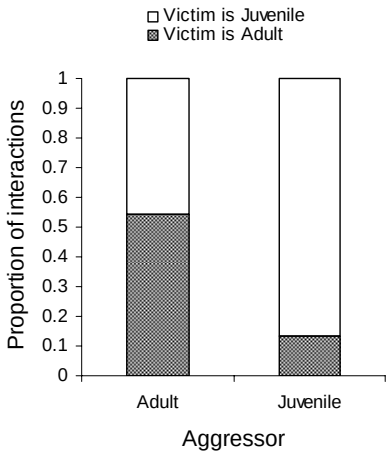

Figure 3. Victim age class by aggressor age class in northern jacanas. Adults attacked adults and

juveniles with equal frequencies, while juveniles usually attacked other juveniles.

There was a significant difference in the distribution of aggressive interactions between habitat types (X^2_1=9.76 P=0.0207; Fig. 4). However, one outlier drove this relationship. With the removal of one particularly aggressive juvenile, the distribution of aggressive interactions between habitat types was no longer statistically significant (X^2_1=3.60 P=0.31).

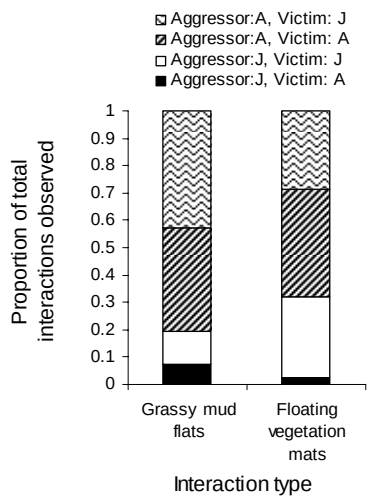

Figure 4. Interaction type by aggressor, victim, and age class in grassy mud flats and floating vegetation mats. There is a significant difference between the distributions of aggressive interactions between habitat types; however, this interaction is entirely driven by one especially aggressive juvenile.

DISCUSSION

In theory, aggressive interactions should be more common when more valuable resources are at stake (Krebs and Davies 1993). Previous studies have found that jacanas are more aggressive on their preferred habitat type and that territorial adult females are more aggressive overall (Stiles and Skutch 1986). However, no studies, to our knowledge, have looked at the interaction between adult female aggression and habitat type. We hypothesized that jacana aggression would vary with age class and that adult aggression would be greater in preferred habitat, perhaps due to female territoriality.

Our data revealed that while jacanas were more aggressive in their preferred, floating-vegetation mat habitat, adults typically dominated juveniles across both habitat types, which supports our hypothesis that jacana aggression varies across habitat types and with age class. This study adds to the growing body of literature documenting how age-based hierarchies structure marsh bird communities (Mahar *et al.* 2000).

Our results also support our prediction that adult jacanas are more likely to be aggressors than victims, complementing past studies that show that adult jacanas are more likely to win confrontations than are juveniles (Theoharides *et al.* 2003). Therefore, our study supports our hypotheses that frequencies of aggressive behavior will vary with habitat type and age class. Our work builds on previous studies of jacana aggression by identifying not only which age classes were more likely to be aggressors or victims, but also which age classes the jacanas were

more likely to be aggressive towards or victimized by. When adults were victims, their aggressor was more likely to be another adult than a juvenile (Fig. 2). When adults were aggressors, they were equally aggressive to adults and juveniles (Fig. 2). When juveniles were aggressors, they were rarely aggressive toward adults (Fig. 3).

The data do not support our prediction that adults will initiate a greater percentage of aggressive interactions. In fact, we found that a greater percentage of aggressive interactions on the preferred habitat type were initiated by juveniles (Fig. 4). However, this result was driven by one particularly aggressive juvenile, without which there would be no significant difference between the percentages of the four different interaction classes across habitat types. More observation hours are needed to understand whether this result is simply driven by one aggressive individual or whether juveniles do indeed initiate more aggressive interactions.

Finally, we noted in our field observations that larger individuals seem to be more aggressive than smaller ones. Because size is correlated with gender in jacanas, it has been hypothesized that this difference is due to the territoriality of the larger, female jacanas (Janzen and Carroll 1983). A next step in this system would be to test whether the greater number of aggressive interactions we observed on the preferred habitat could be due to a higher density of jacanas, which would create more interactions with larger, territorial females. Such a study should take into account both the age and gender of the jacanas. Further studies combining age-based hierarchies and habitat differences could prove important for understanding territoriality in birds.

LITERATURE CITED

Bergholtz, A., V. Vaswani, G. Goldfarb, T. Grabowsky, and G. Kunz. 1991. Vigilance & foraging in northern jacanas. Dartmouth Studies in Tropical Ecology 1991, pp. 25-28.

Dickinson, S.W. and D.L. Poulin. 1998. Effect of gallinule presence on jacana aggression. Dartmouth Studies in Tropical Ecology 1998, pp. 22-24.

Goldfarb, G., G. Kunz, and T. Young. 1991. Non-breeding season aggression in female *Jacana spinosa*. Dartmouth Studies in Tropical Ecology 1991, pp. 29-31.

Hourdequin, J.W., C.D.R. Jackson, S.E. Kopplin, G.M. Lief, and M.K. Little. 1996. Diurnal changes in agonistic behavior of *Jacana spinosa*. Dartmouth Studies in Tropical Ecology 1996, pp. 9-10.

Jackson, C.D.R. and S.E. Kopplin. 1996. Behavior of *Jacana spinosa* as a function of neighboring density. Dartmouth Studies in Tropical Ecology, pp. 25-27.

Janzen, D. H., and C.R. Carroll. 1983. *Jacana spinosa* (Jacana Centroamericana, Mulita, Cirujano, Gallito de Agua, Northern Jacana). Pp. 584-586 *in* D. H. Janzen, editor. Costa Rican Natural History. University of Chicago Press: Chicago, IL.

Krebs and Davies. 1993. Introduction to Behavioural Ecology. Blackwell Science: Chicago, IL.

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, pp. 10-13.

Stiles, F.G., and A.F., Skutch. 1989. A guide to the birds of Costa Rica. Cornell University Press: Ithaca, NY. p.132.

Theoharides, K.E. Simon, C.R. Chamberlin, A.J. Kehas, and J.B. Wickre. 2003. Age-based social dominance in the Northern Jacana. Dartmouth Studies in Tropical Ecology, pp. 19-21.

Wright, B.W., M.J. Ungerer, K.E. Weir, E.A. Wright, and R.C. Yale. 1998. Effect of habitat on the density and behavior of jacanas in a tropical marsh. Dartmouth Studies in Tropical Ecology, pp. 14-16.