DIEL FORAGING BEHAVIOR OF *DENDROCYGNA AUTUMNALIS* AND *JACANA SPINOSA*

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Abstract: Diel foraging behavior plays an important role in the community structure of wetland habitats. Specifically, foraging patterns may help explain niche differentiation between Northern jacanas, *Jacana spinosa*, and Black-bellied whistling ducks, *Dendrocygna autumnalis*, both of which are found in the wetlands of Palo Verde National Park, Costa Rica. We aimed to quantify the differences in diel behaviors between jacanas and ducks. We focused on foraging behavior, predicting that the jacanas would spend more time foraging than the ducks, except at night, because ducks are mainly nocturnal feeders. We observed the two bird species throughout the day and night, noting their foraging behavior during five different time periods. Northern jacanas fed significantly more often during the day than ducks, with a peak of foraging activity midday. Black-bellied whistling duck foraging remained constant throughout the study period and at an overall lower level than jacanas. These foraging patterns may help to explain the bird community structure of the marsh.

Key Words: jacana, black-bellied whistling duck, foraging behavior, diel activity

INTRODUCTION

Diel behaviors of foraging animals have important implications for inter-specific interactions and food-web dynamics (Armbruster and McCormick 1990, De Meester *et al.* 1995, Koperski 1997). Marsh avian communities consist of a diversity of coexisting species with many different life-history traits and a variety of prey items and foraging behaviors (Kemp *et al.* 2004). The goal of our study was to characterize and compare the diel feeding patterns of two coexisting species, *Jacana spinosa* (hereafter referred to as jacanas) and *Dendrocygna autumnalis* (hereafter referred to as ducks).

Northern jacanas' main food source is surface insects, but they also feed on the ovules of water lilies (Jenni 1983). Jacanas have two different methods of foraging. They either skim insects off the surface while moving (known as gleaning) or remain stationary and peck at the water (Bourne and Osborne 1977). Jacanas may spend up to 80% of daylight hours foraging, unless they are protecting eggs or chicks (Jenni and Mace 1999). In contrast, black-bellied whistling ducks are mostly nocturnal feeders, and fly from roosting waters to foraging waters at

sunset (James and Thompson 2001). They feed mainly on wetland seeds, leaves, and shoots, and can be a nuisance to rice farmers (Stiles and Skutch 1989). Based on these differences in the birds' natural histories, we predicted that jacanas would spend more time feeding than ducks, except during the night, when we expected ducks to be feeding more.

METHODS

This study took place in the wetlands in front of the Organization for Tropical Studies (OTS) field station in Palo Verde National Park, located in the Guanacaste province of Costa Rica.

We observed mature jacanas and ducks at five times during the day on 9-10 January, 2007: early morning (0530-0630; n=10 birds/species), morning (0830-0930; n=25 birds/species), midday (1030-1130; n=20 birds/species), afternoon (1630-1730; n=10 birds/species), and night (2130-2230; n=5 birds/species). Unequal bird sample sizes among observation periods were due to study time constraints; we were only able to observe jacanas and ducks once during the afternoon, evening and early morning, while we had two days of observation for the morning and mid-morning time frames. We monitored individual birds for 2 min periods, during which we recorded their behavior at 10 sec intervals. During night observations, we used night vision binoculars to view jacanas and ducks. We divided behaviors into foraging (eating or looking for food) or not foraging. To avoid sampling the same individuals repeatedly, we observed birds at three locations that were approximately 50 m apart: the boardwalk, the bird tower area, and the main marsh area immediately in front of the OTS site. Night observations were only conducted at the boardwalk.

We tested the effects of bird species and time of day on the percent of time spent foraging with two separate analyses. Because mean percent time spent foraging was binomially distributed, we arcsine square-root-transformed our data. To compare foraging rate in ducks versus jacanas, we used a t-test assuming unequal variance because duck foraging was more variable than jacana foraging. To test for species effects, we analyzed only the day-time data because of the difficulty inherent in identifying birds at night. We tested the effect of time of day on foraging rates with separate ANOVAs for each species. We used the Tukey-Kramer Honestly Significant Difference (HSD) test to compare mean foraging time between each time category if the ANOVA was significant. Finally, we tested for a time of day*species interaction with a two-way ANOVA to test whether

time of day affected the degree to which species differed in time spent foraging. Data were analyzed using JMP 6.0.

RESULTS

Jacanas fed significantly more than ducks during the day ($t_{127.11}$=9.20, P<0.0001). On average, jacanas spent 53% more of their daytime foraging than ducks (means ± SE, jacanas: 76 ± 34%, ducks: 22 ± 32%,). In addition, there was a significant interaction between time of day and species ($F_{4,131}$=5.30, P=0.0006). In the morning, ducks and jacanas have more similar feeding behaviors than at midday.

Jacana feeding ranged from 0 ± 0% at night to 95 ± 8% at midday (means per time period ± 1 SE; Fig. 1). Additionally, during daytime observations, time of day had a significant effect on the percent of time jacanas spent foraging ($F_{4,66}$=16.14, P < 0.0001). Jacana feeding was moderate early in the morning (43 ± 43%), peaked midday (95 ± 8%), and declined to 72 ± 39% late in the afternoon. The two lowest feeding times (early morning and night) were each significantly different from all other times at α=0.05, while feeding did not vary significantly from morning through afternoon. Although the absolute maximum foraging at midday was not significantly different from either morning or afternoon, it showed lower variance (SD=8%) relative to early morning (SD=43%), morning (SD=32%), and afternoon (SD=39%; Fig. 1).

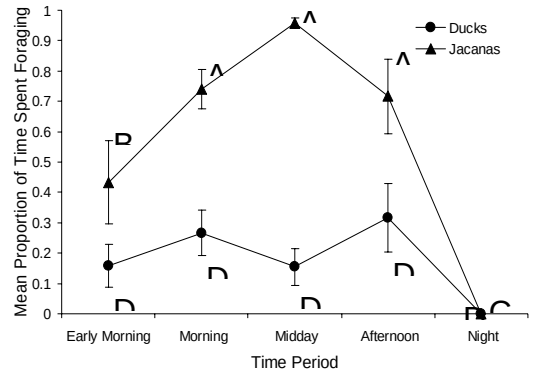

Figure 1. The mean proportion of time that northern jacanas and ducks spent foraging for each of five time periods ranging from early morning (0530) to night (2200). Error bars represent ± 1 SE. For each species, means with the same letters are not significantly different from each other.

The mean percent time spent foraging for the ducks ranged from 0% during the night to 31% in the afternoon (Fig. 1). However, because duck foraging was so variable within each time period, there was no significant effect of time of day on duck foraging ($F_{4, 65}$=1.34, P=0.26).

DISCUSSION

We found that Northern jacanas spent more time feeding during the day than black-bellied whistling ducks. This pattern may have been slightly biased toward finding a difference between species because we lumped all of our samples in the analysis and more of

our individual bird observations occurred midday, where the difference between bird feeding patterns was greatest (Fig. 1). The variation in feeding throughout the day occurred for jacanas but not for ducks. Specifically, jacana foraging peaked mid-day, compared to early morning and at night. In addition, variance was much lower at mid-day for jacanas than at any other time, suggesting that this is a biologically significant maximum in foraging. However, it is unclear whether behaviors were actually more constant mid-day or whether the lower variance was a result of unequal sampling effort throughout the day. Duck foraging behavior varied greatly within each time period, but average duck foraging fluctuated minimally throughout the day. Taken together, theses results suggest that there are species-specific differences in both the magnitude and consistency of diel foraging behaviors in Northern jacanas and black-bellied whistling ducks.

In contrast to past studies, which observed nocturnal feeding patterns in ducks (James and Thompson 2001), we did not find evidence that ducks were nocturnal feeders. We attribute this discrepancy to our night-time sampling protocol, which occurred in the same locations as our day-time sampling. Because ducks forage in different locations within the marsh than where they roost, we may not have been observing them at their nocturnal foraging site. With only night vision binoculars to observe feeding, our observations may also have been less accurate than during the day. We also had difficulty locating birds at night, thereby constraining our sample size. Finally, we also noticed a crocodile near the birds at night, which may have altered their foraging behaviors. Following ducks and jacanas to their respective nocturnal habitats could further help understand inter-specific variation in nighttime behaviors.

Finally, comparisons of diel behavior of the migratory versus resident duck individuals may help explain some of the large variation in foraging and resting patterns. Resident and migratory individuals of the same species are known to have different territorial behaviors that may also affect foraging behaviors (Forsyth and Miyata 1984). Lastly, jacana adults could be categorized by sex and current nesting status. These factors would help explain the variation seen in feeding behavior because different sizes and sexes may require different amounts of food and may have different responsibilities. The observed diel foraging behavior patterns in this study help demonstrate how different community members utilize resources throughout the day.

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