BEHAVIORAL FUNCTIONS OF VOCALIZATION DURING SHORT FLIGHTS IN *JACANA SPINOSA* AT PALO VERDE, COSTA RICA

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Abstract (JMH). We investigated the functions of three levels of *Jacana spinosa* vocalization during short flights within feeding grounds at Palo Verde National Wildlife Refuge, Costa Rica. We quantified differences in occurrence of specific behaviors (aggression, feeding, and wing-raising displays) after flights of different vocalization levels. The level of flight vocalization was positively related to aggression, duration of wing-raising, and time until feeding after alighting. The wing-raising display was associated with aggressive behavior. Silent flights appear to serve to change feeding location, while loud and intermediate level flights have territorial and aggressive functions.

INTRODUCTION (JLM)

The Northern Jacana *(Jacana spinosa)*, common in the seasonally flooded areas of the Guanacaste region of Costa Rica, is one of the few bird species with a polyandrous mating system. The male Jacana maintains a nesting and feeding territory. The female defends the territories of one to four males, for whom she provides one or more clutches of eggs during the breeding season (Jenni 1983). Intraspecific aggression is associated with this territoriality.

In this study, we examined the role of vocalization and wing-raising display behavior in the Jacana's intraspecific aggression. Preliminary field observations indicated that most vocalizations and wing-raising displays occurred during and immediately following short flights made by Jacanas. We hypothesized that aggression and wing-raising would be positively associated with intensity of flight vocalization. As a consequence of this association between aggressive behavior and flight vocalization intensity, we also hypothesized that feeding behavior following flights would be inversely correlated with intensity of flight vocalization. We therefore examined the relationships between intensity of vocalization and 1) aggressive behavior, 2) wing-raising displays, and 3) feeding behavior in adult Jacanas.

METHODS (JMH)

We studied adult Jacanas at Palo Verde National Wildlife Refuge, Costa Rica on 12-14 January 1995. We categorized the vocalization level during a Jacana flight as loud (a distinctively high-pitched and raucous call), intermediate (any other noise made during flight), or silent. For each vocalization level, we recorded: (1) presence or absence of aggressive behavior towards another Jacana, during flight or in the first 10 seconds after alighting (30 replicates); (2) duration of wing-raising display after alighting (20 replicates); and (3) time until first feeding motion after alighting (20 replicates).

We set up 100 "visual" transects radiating out from our observation point, one every 2°. The transects were assigned numbers from 1-100. We used a random number table to determine the transect number for individual flights, using some transects more than once. A total of 210 Jacana short flights were observed.

Jacana flights prompted by intraspecific aggressive encounters were not recorded. We assumed that the vocalization level on those flights was related to the activity occurring immediately before the flight.

RESULTS (JLM)

The form of aggression following short flights made by Jacanas differed

significantly between vocalization levels (G=56.89, df=2, P<0.0001, Table 1). Loud flights were followed by aggressive behaviors more often than expected, while silent flights were followed by non aggressive behaviors more often than expected.

TABLE 1: Number of aggressive and non-aggressive responses to varying flight vocalization levels of Northern Jacanas at Palo Verde, Costa Rica (n=30).

Behavior	Loud Flights	Inter-mediate Flights	Silent Flights
Aggressive	27	19	1
Non aggressive	3	11	29

Duration of wing-raising displays differed significantly among vocalization levels (F=66.1, df=2,57, P<0.001, Fig. 1). Loud flights were followed by the longest wing-raising displays, while intermediate and silent flights were followed by shorter displays .

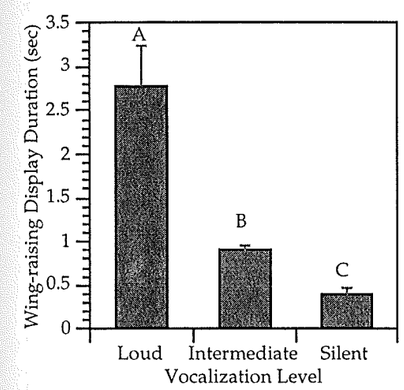

FIG. 1: Relation between vocalization level and duration of wing-raising displays for short flights of Northern Jacanas at Palo Verde, Costa Rica (means ±SE., n=20). Different letters indicate significant differences based on a Tukey means comparison test.

We also found significant differences in time to first feeding motion following the different flight vocalization levels (F=17.02, df=2,43, P<0.0001, Fig. 2). Time to first feeding motion following silent flights was significantly shorter than times following loud and intermediate flights. However, times to first feeding motion following intermediate and loud flights were not significantly different.

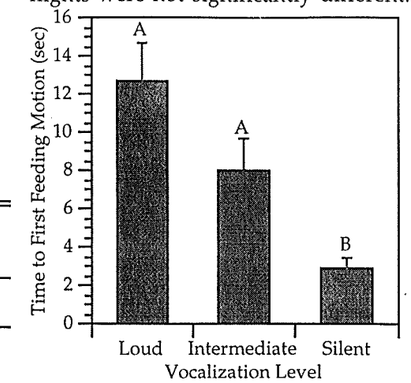

FIG. 2: Relation between vocalization level and time to first feeding motion for short flights of Northern Jacanas at Palo Verde, Costa Rica (mean ± SE., n=20). Different letters indicate significant differences based on a Tukey means comparison test.

DISCUSSION (JMH)

Silent flights were associated with the absence of aggression and with very low durations of the wing-raising behavior. Since we also found a significantly greater time to feeding after the intermediate and loud flights than after silent flights, it appears the silent flights only serve to change feeding location.

Because aggression and wing-raising duration increased with increasing flight vocalization levels, we inferred that there is a relationship between aggression and wing-raising duration. The wing-raising behavior is very conspicuous and, combined with loud or intermediate level vocalization, may serve as an effective territorial signal.

We found that loud vocalization level flights were associated with aggression (Table 1), and that loud and intermediate vocalization level flights were positively correlated to duration of wing-raising display (Fig. 1) and time until first feeding motion (Fig. 2). Thus, it appears that the

function of both loud and intermediate vocalization level flights is aggressive in nature.

We found no statistical difference between the loud and intermediate levels of flight vocalization in time until first feeding motion (Fig. 2). This indicates that we might have arbitrarily created the three levels of flight vocalization when Jacanas actually exhibit only two flight vocalization levels: e.g. flights with or without vocalization. If this were the case we would not have expected to see any differences in behavior between these two vocalization levels. However, wing-raising duration and occurrence of aggression were significantly different between loud flights and intermediate flights. We also observed a difference in the type of aggressive interaction occurring after the loud and intermediate vocalization level flights. After intermediate flights the interactions were usually comprised of landing, then chasing and attacking another Jacana on the ground, while those interactions occurring during the loud flights were most often diving air attacks. Because of these differences between intermediate flight vocalization level behavior and loud flight vocalization level behavior, we concluded that, within flights with vocalization, there are two separate levels of Jacana short-flight vocalizations.

Based on the observed differences in types of aggression occurring after loud and intermediate level flights, we believe that the intermediate level of flight vocalization may be used as a warning. We found aggression occurring after approximately half of the 30 intermediate flights sampled. This is the pattern we would expect to find if this level of call is in fact a warning. If the "warning" was heeded, no aggressive interaction would follow. As Jacanas' motives for heeding or not heeding a "warning" call are unknown, we would predict them to respond or not on a random basis. This would give us the approximately 50:50 split of aggression occurrences that we observed after intermediate level flights.

Ground vocalizations, in these same three levels of intensity, are also common. The functions of such loud and intermediate calls made from the ground should also be examined.

In our study we did not take separate data for males and females, because we were not able to sex adult Jacanas with confidence. We did observe both sexes of birds making all three levels of flight vocalization, however. An investigation into behavioral differences between males and females and between adults and juveniles could shed more light on the function of short-flight vocalizations.

In many species of birds, a primary function of vocalization is in anti-predatory behavior. However, because adult Jacanas do not exhibit anti-predator behaviors in the non-breeding season (Jenni and Betts, 1978), and because we observed no chicks or nests in the population during our study, we assumed that the observed levels of flight vocalization in our study were not related to such an anti-predator function.

Jacana short flight vocalization plays a significant part in aggressive interactions between conspecifics. Differentiated vocalization levels related to different types of behaviors should be useful and important for a species in which all adults attempt to hold overlapping territories for at least a portion of the year and where all adult females do not breed every breeding season, leading to intense intraspecific and intrasexual aggression.

LITERATURE CITED

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