INTERSPECIFIC AGGRESSIVE BEHAVIOR OF THE POLYANDROUS NORTHERN JACANA (*JACANA SPINOSA*)

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ABSTRACT.—Adults of the polyandrous Northern Jacana (*Jacana spinosa*) defend their offspring against avian territorial intruders that are potential offspring predators. I investigated this defensive behavior in Costa Rica during 1980 and 1981. Jacanas attacked 15 species; most attacks were against Purple Gallinules (*Porphyrula martinica*), which are known predators of jacana eggs and offspring. Three factors influenced the probability of attacks: (1) spatial proximity of intruders to jacana offspring, (2) species identity of intruders, and (3) stage of breeding (jacanas were most responsive to intruders when young offspring were present). Attacks prevented intruders from reaching jacana offspring, and limited evidence suggests that attacks also reduced the density of intruders near jacana nests. The female's role in offspring defense was substantial. Females participated in the defense of eggs and small young at levels comparable to those of males. This participation included: (1) joining ongoing attacks when their mates solicited aid, (2) continuing attacks while their mates led offspring away from intruders, and (3) launching attacks in the absence of their mates, especially during incubation. *Received 8 November 1982; resubmitted 19 September 1983, accepted 12 January 1984.*

NORTHERN Jacanas (*Jacana spinosa*) have one of the rarest breeding systems known among birds: resource-defense polyandry (Jenni 1974, Emlen and Oring 1977, Graul et al. 1977). Female Northern Jacanas defend territories that include the smaller territories of their one to four mates. Females are nearly 70% heavier than males and do virtually no incubating, brooding, or escorting of the precocial young (Jenni and Collier 1972, Jenni and Betts 1978). Females do aid males in defending offspring from predators, however: males and females both attack birds of other species that are potential predators of jacana eggs and chicks. Jenni and Betts (1978) describe the behaviors that jacanas employ in this interspecific aggression, document the time that males and females spend in attacking offspring predators, and comment on other aspects of this behavior. In this paper, I confirm and extend the observations of Jenni and Betts and place emphasis on: (1) the proximate causes of interspecific attacks, (2) the consequences of such attacks, and (3) the role that females play in this form of parental care.

METHODS

I studied Northern Jacanas from June to November 1980 and May to December 1981 in the Dr. Rafael Rodriguez National Wildlife Refuge, formerly known as Hacienda Palo Verde, in Guanacaste Province, Costa Rica. The study site is part of a marsh near the Tempisque River. The marsh is an expanse of emergent vegetation interrupted by open water and floating vegetation. Scattered "Palo Verde" trees (*Parkinsonia* sp.) give the marsh a savannah-like appearance. Hundreds of jacanas arrive for breeding at the marsh when it is inundated during the rainy season (May–November; Slud 1980). The study site was covered by floating vegetation (primarily *Nymphaea*, *Eichornia*, and *Neptunia*) and bordered by emergents (primarily *Typha*, *Panicum*, *Paspalum*, and *Eleocharis*). Small patches of emergents dotted the zone of floating vegetation.

I conducted observations from towers 3–6 m tall that were within the territories of focal animals. I draped a blind over the tower before beginning systematic observations. My approach to and ascent of the tower sometimes caused nonfocal birds to flee, including species that jacanas attack. In order to reduce any effects this might have had on the data, I waited in the blind at least 5 min, and often at least 20 min, before beginning to sample.

During 1981, observation periods were 2 h long. During each period I simultaneously observed one female and one of her mates, regardless of the number of mates the female had. I observed the same mate during the entire period over which a particular female was observed, except when events such as clutch loss made it profitable for me to initiate observations of a different mate and discontinue observations of the first. The focal male and female are referred to as the "focal pair," even though some focal females were polyandrous.

During 1980, observation periods were 80 min long. During each sample I simultaneously observed one female and one of her mates for 60 min; then, after a 5-min pause, I observed the same female but a different mate for the remaining 15 min. Males of monogamous females were observed for the entire period. The same male was observed during all 60-min segments of the period spent observing a particular female, and these are the males in the male/female comparisons reported below.

Three types of sampling were conducted concurrently during each observation period. Throughout a period I recorded the details of all attacks by the focal pair, including time and position of attack, identity and behavior of attacker, species of victim, and distance moved by victim during or within 5 s after attack (= Aggression Sampling). Successive attacks against an individual were scored as separate attacks if the attacker engaged in nonaggressive behavior for at least 30 s between attacks. Second, I recorded the behavior and position of focal pairs and their offspring every 5 min (1980) or 10 min (1981) by scan sampling (Altmann 1974) (= Behavior and Position Sampling). Finally, I plotted the positions of all avian intruders on the focal female's territory every 20 min (1980) or 30 min (1981) by scan sampling (= Species Scan Sampling). Positions were plotted on vegetation maps of territories. Species Scan Sampling was momentarily interrupted to record details of any ongoing attacks, whereas Behavior and Position Sampling was completed before recording attack data.

Observation periods began at 0600, 0750, 0940, 1230, 1350, and 1440 during 1980 and at 0600, 0900, 1200, and 1500 during 1981. Observation periods were rotated randomly among male/female pairs such that approximately equal numbers of samples were accumulated at each time of day for each focal pair. A total of 16 pairs was observed, but observations were concentrated on 12 pairs. Of the latter, only one individual was observed in both years of the study. All but two focal animals were captured in mist-nets and color-banded for individual recognition.

Components of the above methodology, such as observation-period length, varied somewhat during early 1980, but these changes did not bias the results.

To examine temporal patterns, I divided the reproductive period of male jacanas into four stages: Preincubation (the period before or between nesting attempts, when no eggs or offspring are present), Incubation (the first day of egg-laying to the last full day of incubation), Downy (day 1, the day of hatching, to day 28 post-hatching, during which chicks have downy plumage), and Juvenile (day 29 to dispersal or renesting, during which offspring have juvenal plumage). The transition date between the downy and juvenile stages is somewhat arbitrary because of the gradual transition from downy to juvenal plumage.

Nonparametric statistical tests employed below are described by Siegel (1956). When means are strongly affected by outliers, medians are reported. An assumption of many of the statistical tests that follow is that attacks are temporally independent of one another. I determined that this was indeed the case by plotting interattack intervals as a log survivorship function for each species that was attacked and by comparing this distribution to the one that would be expected (the negative exponential) if attacks were to occur at random with respect to one another (see Slater 1974). Sample size was adequate for this comparison for only the most frequently attacked species (Purple Gallinule, *Porphyrula martinica*). The observed and expected distributions were not significantly different (Kolmogorov-Smirnov test, $n = 35$, $P > 0.20$), indicating that attacks against this species did not tend to occur in bouts.

RESULTS

Behavior during attacks.—Jacanas attack other birds with a combination of primarily two behaviors described by Jenni and Betts (1978). I labeled these behaviors "swoops" and "threats." In the "swoop," a jacana flies toward an intruder and strikes it with its feet, simultaneously uttering a sharp call. Jacanas sometimes feign the strike by thrusting the feet toward the intruder while flying past it or by veering away from the intruder just before reaching it (pers. obs.).

In the "threat," a jacana crouches in front of an intruder and displays its carpal spurs, simultaneously uttering a long, shrill vocalization that Jenni et al. (1975) labeled the "scream." The exposed yellow spurs are highlighted against the maroon forewings. Jacanas were never seen striking birds of other species with their spurs. See Jenni and Betts (1978) for a full description of threats.

On rare occasions, other attack behaviors such as charges or pecks were employed. Pecks occurred as an intruder turned to flee from an attacking jacana. True fights were also rare. Fights, which were seen in attacks upon Purple Gallinules only, consisted of both participants jumping up simultaneously and appearing to hit each other with their feet in a brief flurry of activity.

An attack comprised a variable number of these attack behaviors. To represent this variability, an intensity score for individual attacks

TABLE 1. Percentages of attacks of various intensities as a function of attack type (data from 1980).

Type of attack	Intensity[a] 1	2	3	4	5	6	7	>7	n	Mean intensity
Solo	11	58	9	17	1	3	1	0	103	2.52
Joint	—	8	0	30	30	11	5	16[b]	37	5.84
Either	8	45	6	21	9	5	2	4	140	3.40

[a] See text for definition.

[b] Includes 3 attacks with intensities of 8, and 3 attacks with intensities of 14, 17, and 18.

was computed. Threats were assigned a score of 1 and swoops a score of 2. Swoops were considered more intense than threats, because they often involved striking the victim, whereas threats did not. The rare attack behaviors were assigned a score of 2. Although individuals occasionally performed more than one threat during an attack, multiple threats by a single individual were difficult to distinguish from a single threat interrupted by short pauses. Individuals were therefore assigned a maximum of one threat per attack.

Nearly 90% of attacks had intensities of less than 6 (Table 1), indicating that most attacks consisted of only a few attack behaviors. Not surprisingly, solo attacks by a male or female were roughly half as intense as joint attacks by a male and female.

Certain nonaggressive behaviors performed during attacks are noteworthy: (1) jacanas nearly always interposed themselves between their offspring and intruders; (2) during joint attacks, males often led their offspring from intruders while females continued to confront the intruders; (3) during or just before attacks, jacanas occasionally gave alarm calls or distraction displays in response to intruders; and (4) jacana chicks hid themselves in the water during a few attacks. These observations reinforce direct evidence (see below) that jacana offspring are subject to predation by some species of territorial intruders and that interspecific attacks are a means of reducing such predation.

One of the most striking sexual differences in interspecific aggressive behavior was the differential use of threats. During 1980, males used threats in 49% ($n = 82$) and females in only 12% ($n = 101$) of their attacks. Threats appear to have two functions (Jenni et al. 1975, Mace 1981): (1) aggression directed against intruders and (2) communication directed toward mates, i.e. the scream uttered during threats summons the mate during ongoing attacks. The communicative function is exploited primarily by males (Mace 1981). Males initiated most joint attacks (83% during 1980) and were thus in situations in which they could recruit their mate's aid. Females were often far from attacks initiated by males but responded to their mate's scream by flying to him and joining the attack.

There was no difference between males and females in their tendency to perform single versus multiple swoops during attacks; this was the case regardless of whether solo attacks, joint attacks, or all attacks were examined (Chi-squared tests, $P > 0.05$). Little can be said concerning sexual differences in uncommon attack behaviors because of their rarity, but fights were restricted to interactions between female jacanas and Purple Gallinules.

Species attacked.—Jacanas attacked 15 species of birds (excluding conspecifics) during Aggression Sampling (Table 2). Purple Gallinules alone accounted for 79% of all attacks. This species opportunistically preys on jacana eggs and chicks (Jenni and Betts 1978; see also Bailey 1927, McIlhenny 1936, Beadel 1946). An additional eight species were recorded on focal territories at least once but were never attacked during sampling (Table 2). Not all of these species are "tolerated" (Walters 1979) by jacanas, however. Two species [Bare-throated Tiger-Heron (*Tigrasoma mexicanum*) and Limpkin (*Aramus guarauna*)] were attacked by jacanas during casual observations. Also, four species were rare (Table 2) and, therefore, provided few opportunities for attacks.

The relationship between the attack rate against each species and that species' abundance on jacana territories was examined by letting "responsiveness" (Walters 1980) equal attack rate (here calculated as attacks per 10 h) divided by the mean number of individuals of that species recorded in Species Scan Samples.

TABLE 2. Number of jacana attacks on each species of territorial intruder, abundance of each species on jacana territories, and responsiveness of jacanas to each species.

Species	Number of attacks (%)[a]	Number of intruders[b]	Responsiveness[c]
Purple Gallinule (*Porphyrula martinica*)	396 (79.0)	460	5.04
Pied-billed Grebe (*Podilymbus podiceps*)	26 (5.2)[d]	141	0.76
Least Grebe (*Tachybaptus dominicus*)		60	
Common Moorhen (*Gallinula chloropus*)	23 (4.6)	161	0.84
Green-backed Heron (*Butorides striatus*)	15 (3.0)	69	1.27
Sora (*Porzana carolina*)	12 (2.4)	2	36.33
Great Egret (*Casmerodius albus*)	9 (1.8)	25	2.10
Red-winged Blackbird (*Agelaius phoeniceus*)	8 (1.6)	4	12.17
Tropical Kingbird (*Tyrannus melancholicus*)	3 (0.6)	82	0.21
Great Kiskadee (*Pitangus sulphuratus*)	2 (0.4)	12	0.95
Snail Kite (*Rostrhamus sociabilis*)	2 (0.4)	9	1.29
Least Bittern (*Ixobrychus exilis*)	2 (0.4)	3	3.06
Groove-billed Ani (*Crotophaga sulcirostris*)	1 (0.2)	24	0.25
Black-bellied Whistling-Duck (*Dendrocygna autumnalis*)	1 (0.2)	85	0.07
Little Blue Heron (*Egretta caerulea*)	1 (0.2)	0	5.80[e]
Bare-throated Tiger-Heron (*Tigrisoma mexicanum*)	0	9	0.00
Anhinga (*Anhinga anhinga*)	0	19	0.00
Limpkin (*Aramus guarauna*)	0	3	0.00
Black-crowned Night-Heron (*Nycticorax nycticorax*)	0	1	0.00
Cattle Egret (*Bubulcus ibis*)	0	1	0.00
Fulvous Whistling-Duck (*Dendrocygna bicolor*)	0	3	0.00
Mangrove Swallow (*Tachycineta albilinea*)	0	1	0.00
White-collared Seedeater (*Sporophila torqueola*)	0	16	0.00

[a] Based on 1,100 h of Aggression Sampling.

[b] Number of individuals recorded on jacana territories during 644 Species Scan Samples; each such sample was taken midway into each observation period.

[c] Responsiveness = (number of attacks per 10 h)/(mean number of individuals recorded during Species Scan Samples).

[d] These species are combined, because I sometimes could not discern which of the two was attacked.

[e] To avoid division by zero in calculating this, I set the number of intruders equal to one.

Before considering these scores, one should note that they are inflated for any inconspicuous species that was underrecorded in Species Scan Samples. Although the magnitude of this effect is unknown, I suspect that it is small.

Responsiveness varied considerably among species (Table 2). Soras (*Porzana carolina*) elicited the highest responsiveness by far, and Purple Gallinules, the most frequently attacked species, elicited the fourth highest.

Males and females differed in the extent to which they initiated attacks against particular species (Table 3). The main difference was the males' larger proportion of initiations against grebes, which females did not attack at all. Least Grebes (*Tachybaptus dominicus*) and Pied-billed Grebes (*Podilymbus podiceps*) were attacked only when they surfaced near jacana broods. Be-

TABLE 3. Percentages of attacks initiated by males and females against different species.

	Initiator[a]	
Species attacked	Females	Males
Purple Gallinule	81.3	78.2
Red-winged Blackbird	3.6	0.9
Least and Pied-billed grebes	0.0	7.2
Green-backed Heron	2.9	2.1
Common Moorhen	4.3	5.4
Great Egret	3.6	1.2
Sora	1.4	3.0
Others[b]	2.9	2.1
Number of attacks	139	335

[a] Attack initiations among species are not independent of initiator ($\chi^2 = 19.0$, df = 7, $P < 0.01$, frequencies analyzed).

[b] These include Least Bittern, Little Blue Heron, Snail Kite, Groove-billed Ani, Tropical Kingbird, and Great Kiskadee.

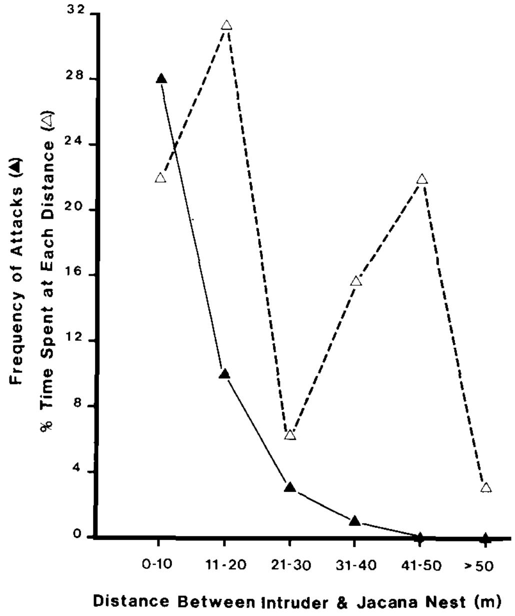

Fig. 1. Frequency distribution of attacks during incubation, as a function of distance to jacana nests, compared with the percentages of time that intruders spent at those distances (Kolmogorov-Smirnov test, $P < 0.01$, raw frequencies of intruder numbers analyzed). Purple Gallinules accounted for 90% of these attacks; therefore, the curve of time spent at different distances was restricted to Purple Gallinules. These percentages were derived from 32 Species Scan Samples. Data are from five territories sampled during 1980.

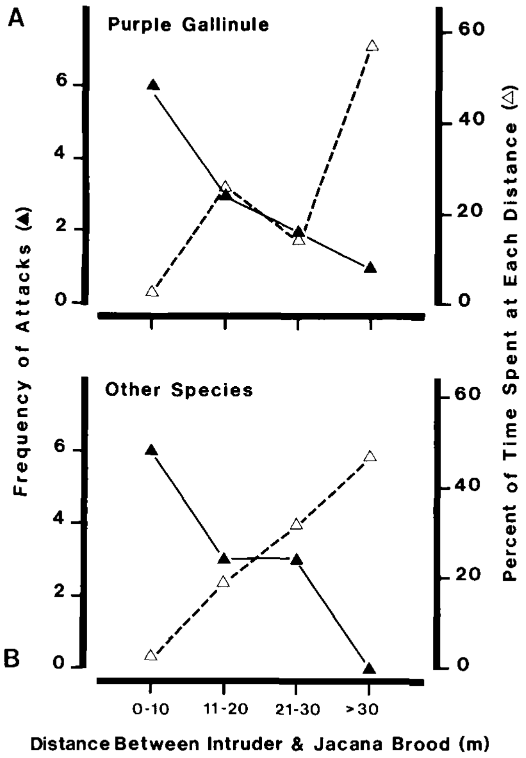

Fig. 2. Frequency distribution of attacks against (A) Purple Gallinules and (B) other species, as a function of distance to jacana brood, compared with the percentages of time that these species spent at those distances (In A and B, Kolmogorov-Smirnov test, $P < 0.01$, raw frequencies of intruder numbers analyzed). "Other species" include Pied-billed Grebes, Green-backed Herons, Great Egrets, and Common Moorhens. The percentages of time were derived from 32 Species Scan Samples in both A and B. Data are from one male jacana's territory.

cause females rarely escort broods (Jenni and Betts 1978), females were rarely in a better position to respond to grebes near broods than were males.

Spatial distribution of attacks.—Jacanas attacked heterospecifics only when the latter were close to the jacanas' offspring. This spatial specificity of attacks occurred whether jacanas had eggs or mobile offspring and was not a byproduct of similar microhabitat preferences of intruders and jacana offspring (Fig. 1 and 2). Attacks during pre-incubation clustered about the jacanas' empty nest. Thus, the Northern Jacanas that I observed defended a small area around their nest or offspring against potential predators. Those observed by Jenni and Collier (1972) at times defended their entire territory against such predators.

Attacks upon Soras were the only exception to this pattern of spatial specificity. This species arrived at the study site in small numbers toward the end of the study. Apparently, jacanas attacked them wherever they were encountered on jacana territories, regardless of their proximity to jacana offspring. This pattern was responsible for the very high responsiveness to Soras (Table 2).

One factor that influenced whether the male or the female initiated an attack was their relative proximity to the intruder. Data from Behavior and Position Sampling were used to estimate the distances of one focal male and

TABLE 4. Frequency distribution of the distances that different species moved when attacked by jacanas.

Species attacked[a]	Distance moved <6 m	 6–10 m	 >10 m
Purple Gallinule	356	41	48
Common Moorhen	17	3	3
Sora	1	1	6
Green-backed Heron	14	2	7
Great Egret	10	0	0
Grebe spp.	24[b]	0	0
Red-winged Blackbird	3	2	3

[a] Only species attacked at least four times are considered.

[b] Pied-billed and Least grebes invariably submerged when attacked.

TABLE 5. Frequency distribution (expressed as percentages) of distances moved by Purple Gallinules during attacks by lone males, lone females, and male/female pairs.

Attacker[a]	Distance moved <6 m	 6–10 m	 >10 m	*n*
Males	88	6	6	156
Females	79	10	10	154
Pairs	72	12	16	135

[a] Distances were not independent of attacker ($\chi^2 = 12.18$, df = 4, $P < 0.05$, frequencies analyzed).

female to intruders immediately before attacks. The male tended to initiate attacks only when he was closer to the intruder than the female was. The female initiated attacks regardless of her mate's proximity to the intruder, however ($\chi^2 = 6.89$, $df = 1$, $P < 0.01$).

Response to attack.—Intruders generally ducked to avoid blows from aerial attacks, and certain species, especially the larger ones, counterattacked, as noted by Jenni and Collier (1972). Purple Gallinules and Common Moorhens (*Gallinula chloropus*) counterattacked by charging their attackers, Great Egrets (*Casmerodius albus*) and Green-backed Herons (*Butorides striatus*) by thrusting their bills toward their attackers.

Most intruders moved short distances when attacked (Table 4). The exceptions are Red-winged Blackbirds (*Agelaius phoeniceus*) and, especially, Soras, the two smallest species listed.

Purple Gallinules moved farthest when attacked by pairs, less far when attacked by females, and least far when attacked by males (Table 5). Females appeared to be more formidable attackers than males; their strikes during swoops were sometimes strong enough to displace Purple Gallinules a full meter. Note, however, that the commonest response of Purple Gallinules was to move less than 6 m, even when attacked by pairs. Sample sizes from species other than Purple Gallinules are too small for separate analyses and their distance-moved distributions are too heterogeneous for pooling (Table 4).

Intruders apparently avoided areas where they were being consistently attacked. To investigate this, I analyzed the only situation in which intruders were attacked during one breeding stage but not in the preceding or following stages. This occurred on a focal territory where the breeding pair defended a nest that was eventually lost. Following nest loss, the male deserted his territory, and the area was soon incorporated into the territory of the female's other mate; the male and female did not defend the incorporated area from heterospecifics, however. I further restricted the analysis to attacks upon Purple Gallinules, because they accounted for nearly all of the interactions.

I tallied the number of Purple Gallinules recorded in a 20-m × 20-m plot, centered at the nest, during the incubation and post-egg-loss periods. The records spanned a 30-day interval in both periods. To control for a seasonal increase in Purple Gallinules present at the study site, I compared these counts to counts within the deserting male's entire territory. The proportion of Purple Gallinules present within the plot was 31% lower during incubation than during the following period ($\chi^2 = 4.09$, df = 1, $n = 261$, $P < 0.05$). This suggests that jacana attacks reduce the density of intruders near their nests. A similar density reduction may occur during the posthatching stages but would be more difficult to detect, because attacks during these stages are not restricted to the nest area; they occur wherever the nidifugous offspring happen to be at the time.

Timing of aggression.—The median attack rates of male/female pairs were fairly low, the highest rate being 4.6 attacks per 10 h (Fig. 3, "total" curve). The true rates are undoubtedly higher, as my arrival sometimes caused intruders to flee and remain off the focal territory for varying lengths of time (see Methods). The pairs' total attack rates were highest during the downy and

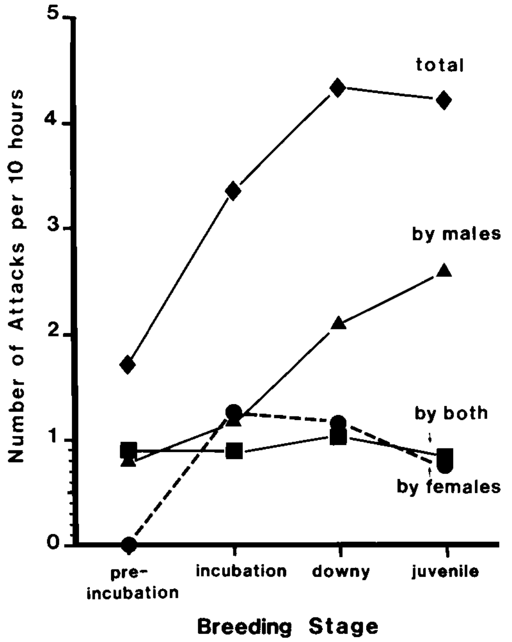

Fig. 3. Median rates of solo male attacks, solo female attacks, and joint attacks during each stage of breeding; "total" indicates the sum of the median rates of all three attack types. Data are from 5 pairs during pre-incubation, 10 during incubation, 11 during the downy stage, and 8 during the juvenile stage. Data from polyandrous females include only those attacks that occurred on the focal male's territory. Sample sizes, in terms of hours of sampling, range from 8.8 to 88.0, with the interquartile range being 20.0–42.0.

TABLE 6. Percentage contribution of solo male attacks (M), solo female attacks (F), and joint attacks (MF) to total attack rates during each stage of breeding (data from Fig. 3).

	Attacker			Males' total		Females' total
Stage	M	F	MF	(M + MF)[a]		(F + MF)
Pre-incubation	47	0	53	100		53
Incubation	36	37	27	63		64
Downy	49	27	24	73		51
Juvenile	62	18	20	82	*	38

[a] Significant differences between male and female totals (Wilcoxon Signed Ranks test, $P < 0.05$) are indicated by an asterisk (raw attack rates analyzed). See legend of Fig. 3 for sample sizes.

juvenile stages, and the same was true for solo male attacks. The median rate of solo female attacks was highest during the incubation and downy stages. Note that the rates of solo male attacks exceeded those of females during all stages except incubation. Finally, the rate of joint attacks was uniform across stages.

These data are recast as percentages in Table 6 in order to identify the contribution of solo male attacks, solo female attacks, and joint attacks to the total attack rate during each stage of breeding. These percentages approximate the percentages of all attacks that consisted of each type. Males and females had equal solo contributions during incubation, but, as the nesting cycle progressed, the males' contributions became increasingly greater than the females'. The total contributions (solo plus joint attacks) of males and females were similar during all but the juvenile stage, although more data from pre-incubation are needed.

Raw attack rates do not reveal the true effect of the breeding stage upon aggressive behavior, because intruder abundances were not independent of stage (Stephens unpubl. data). I therefore calculated responsiveness scores as a function of stage. Many pairs were sampled in more than one stage, causing samples in different stages to be statistically dependent. A subset of the data from the incubation, downy, and juvenile stages was used to determine whether or not there was an effect of subjects (pairs) on responsiveness. No effect on responsiveness to Purple Gallinules or to all other species combined was found (Friedman 2-way ANOVA by ranks, $P > 0.05$). I therefore considered data from the same pair sampled in different stages to be independent and combined these data with data from pairs sampled in only one stage in order to test for a stage effect.

Responsiveness of males, females, and male/female pairs to Purple Gallinules was highest during the downy stage (Table 7). The peak for females is especially pronounced. The males' fairly high responsiveness during pre-incubation, when no eggs or offspring were present to defend, is noteworthy.

Males and females had roughly similar responsiveness to Purple Gallinules during the incubation and downy stages, whereas males were more responsive than females during the juvenile stage (Table 7). The available data from the pre-incubation stage suggests that males were more responsive than females. Across

TABLE 7. Responsiveness[a] of males, females, and male/female pairs of jacanas to Purple Gallinules during each stage of breeding.

Median responsiveness	Males[b]		Females	Pairs	n[c]
Stage[d]					
Pre-incubation	5.56		1.79	6.33	5
Incubation	2.08		2.11	3.75	9
Downy	6.49		8.65	11.57	10
Juvenile	4.44	*	1.25	4.93	7
Overall	4.69		2.68	6.33	31

[a] See text for definition.

[b] Significant differences between males and females (Wilcoxon Signed Rank test, $P < 0.05$) are indicated by asterisks.

[c] n = number of males, females, or pairs during each stage, and the sum of these for overall.

[d] Responsiveness scores of males, females, and pairs are not independent of stage (Kruskal-Wallis tests, $P < 0.05$).

TABLE 8. Responsiveness of males, females, and male/female pairs of jacanas to species other than Purple Gallinules.[a]

Median responsiveness	Males[b]		Females	Pairs	n[c]
Stage[d]					
Pre-incubation	0.00		0.00	0.00	5
Incubation	0.31		0.27	0.53	9
Downy	0.84		0.35	1.12	11
Juvenile	0.68	*	0.00	0.97	8
Overall	0.75	*	0.15	0.88	33

[a] These include all attacked species listed in Table 2 except Purple Gallinules.

[b] Significant differences between males and females (Wilcoxon Signed Ranks test, $P < 0.05$, except for juvenile stage, where $P = 0.062$) are indicated by asterisks.

[c] As in Table 7.

[d] Responsiveness scores of males, females, and pairs do not differ significantly among stages (Kruskal-Wallis tests, $P > 0.05$). The apparent difference in responsiveness of males and pairs during pre-incubation and other stages combined is not significant [Dunn's test (Dunn 1964), $P > 0.05$ in both cases].

stages, the sexual difference in responsiveness to Purple Gallinules is not statistically significant (Table 7).

Too few data were available from other species to consider responsiveness to them individually; I therefore combined data from this heterogenous group. This failed to reveal any significant differences in the timing of responsiveness of males, females, or pairs (Table 8). However, males, females, and pairs were most responsive to other species during the downy stage, as they were to Purple Gallinules. If data from other species are reliable, then the pattern of responsiveness to these species differs in two important ways from responsiveness to Purple Gallinules: (1) relatively low responsiveness during pre-incubation and (2) similar responsiveness of pairs during the downy and juvenile stages. Males and females differed significantly in responsiveness during the juvenile stage and overall.

DISCUSSION

The discussion focuses on the proximate causes of interspecific attacks, the consequences of these attacks, and the role of females in offspring defense. Jenni and Betts (1978) discuss related topics.

PROXIMATE CAUSES OF ATTACKS

At least three factors influenced the probability of attacks by Northern Jacanas: (1) species identity of territorial intruders, (2) spatial proximity of intruders to jacana nests or offspring, and (3) stage of breeding.

Species attacked.—Of the species that were not rare at the study site, Purple Gallinules elicited the highest responsiveness and accounted for most attacks (Table 2). Purple Gallinules are known predators of jacana eggs and chicks. Some of the other attacked species, or at least their close relatives, are also predators of avian eggs and chicks at times (Hunter and Morris 1976; Skutch 1976: 444; Repenning 1977; Terres 1980: 498; Welty 1982: 110).

Species identity was less important when intruders moved rapidly toward jacana offspring or suddenly appeared near the offspring. In these contexts, jacanas seemed to attack virtually any species. These contexts account for many of the attacks on species that probably pose little danger to jacana offspring [Least Grebe, Pied-billed Grebe, Red-winged Blackbird, Groove-billed Ani (*Crotophaga sulcirostris*), Tropical Kingbird (*Tyrannus melancholicus*) and Great Kiskadee (*Pitangus sulphuratus*)].

Spatial context of attacks.—Jacanas attack heterospecifics only when the latter are near jacana nests or offspring (Fig. 1 and 2). Because of this spatial specificity, no birds of other species were fully excluded from jacana territories by aggression. This spatial specificity probably introduced some bias into responsiveness scores. For example, species that preferentially inhabited the same vegetation zones that harbored jacana offspring probably would have inflated responsiveness scores.

Stage of breeding.—Responsiveness to birds of other species was highest during the downy stage (Tables 7 and 8). This is when the jacanas studied by Jenni and Betts (1978: 215) spent most time in "overt anti-predator behaviour." The vulnerability of offspring to predators such as Purple Gallinules undoubtedly decreases as the offspring mature, and this probably accounts for the decline in responsiveness from the downy to the juvenile stages. It is less clear why responsiveness to Purple Gallinules is lower during incubation than during the downy stage, but this could be due to (1) the greater conspicuousness of the mobile chicks compared to eggs, and/or (2) the fact that eggs are incubated for a large portion of the day (Jenni and Betts 1978) and are presumably safe during this time, whereas chicks are brooded for a smaller portion of the day, especially after the first few days of chick life (Jenni and Betts 1978, Stephens unpubl. data).

The high responsiveness of males to Purple Gallinules during pre-incubation, when no eggs or offspring were present to defend, suggests that males were trying to discourage Purple Gallinules from inhabiting the area near the males' future nest.

Much theoretical and empirical work on the temporal pattern of offspring defense concerns the severity of attacks (e.g. Andersson et al. 1980 and references therein, Bierman and Robertson 1981) and not responsiveness to intruders. Temporal changes in offspring defense probably are best indicated by the severity of attacks, rather than responsiveness to intruders, when aggression is directed against moderately to highly dangerous predators of eggs and young, such as gulls and foxes, which tend to elicit attacks whenever they are near nests (e.g. Kruuk 1964). The present study primarily concerns less dangerous species that commonly search for a variety of foods within jacana territories but are also potential predators of jacana eggs or offspring. The severity of attacks against these species did not vary much from attack to attack (see above), at least according to my measure of severity.

The proximate causes of attacks and direct evidence of predation on jacana eggs and chicks by Purple Gallinules (see above) provide convincing evidence of the antipredator function of attacks against most species. Attacks against Soras were exceptional, however, in location and timing. Jacanas apparently attempted to exclude this species from their territories and were somewhat successful at this (Table 4). The habitat use and diet of Soras are similar to those of Northern Jacanas (Terres 1980). I therefore suspect that the function of attacks on this species is to defend resources, not offspring.

CONSEQUENCES OF ATTACKS

Jacana attacks appeared to have both immediate and long-term consequences for offspring protection. The immediate consequence was that intruders were prevented from getting nearer to jacana offspring. In fact, the only known cases of predation by Purple Gallinules on jacana eggs and chicks occurred while the latter were temporarily unattended by their parents (Jenni pers. comm.). The long-term consequence of attacks was a reduction in the density of Purple Gallinules (and perhaps other intruders) near jacana nests (and perhaps near the mobile offspring as well). This conclusion needs confirmation, however, as the supporting data come from only one nest. Confirmation is needed for an additional reason: the period of higher density included a higher proportion of immature Purple Gallinules than did the period of lower density and it is thus possible that the change in density was a byproduct of differences in microhabitat use between adult and immature Purple Gallinules and had nothing to do with jacana aggression. Some evidence suggests that aggression by other avian species reduces the density of potential predators near nests or offspring (Gorransson et al. 1975, Walters 1980).

THE ROLE OF FEMALES IN OFFSPRING DEFENSE

Female Northern Jacanas are highly unusual among female birds in being under intense selection to acquire multiple mates (Jenni and Betts 1978, Stephens 1982) and to retain them over a long breeding season. This requires that female jacanas be free of the major time constraints involved in incubating, brooding, and escorting the young (Jenni and Betts 1978). On the other hand, participation in offspring defense is compatible with simultaneous polyandry. Jacanas spend little time attacking offspring predators (Jenni and Betts 1978).

Moreover, because females are much larger than males, they probably are more effective than males in preventing predation against offspring. There is some support for this suggestion. Female jacanas are known to attack conspecific offspring despite vigorous attacks by males (Stephens 1982, 1984); yet they are easily repelled by other females (Jenni and Collier 1972, Stephens 1984).

I suggest that females, because of their larger size, are ultimately responsible for the fact that opportunistic predators such as Purple Gallinules do not attack jacana eggs or offspring in the presence of the parents. I therefore also suggest that, while it is often concluded that female Northern Jacanas provide little or no parental care (e.g. Wittenberger 1981, Halliday 1982, Knowlton 1982, Erckmann 1983), the females' role in offspring defense is important in the life history of jacanas, even though this activity is not time consuming. Although data are limited, females in other species of jacanas appear to have a similar role in offspring defense (Hoffmann 1949, Cunningham-van Someran and Robinson 1962, Mathew 1964).

Offspring defense through direct attack is common among birds (Skutch 1976). This study suggests that offspring defense by polyandrous females or polygynous males is compatible with polygamous breeding, when birds can become polygamous without deserting mates. In some nidifugous species, territories break down after broods hatch, and the families of a polygynous male or polyandrous female may then move apart in search of food. In such species, polygamous individuals may opt to follow and defend only one family (Hannon 1984). Even in these species, however, if mates remain within hearing range, as do Northern Jacanas, individuals can recruit distant mates to ongoing attacks. Few data are available on the role that polyandrous females or polygynous males play in offspring defense (Jenni and Betts 1978, Picman 1983). A likely contrast to emerge from such studies is that polyandrous females invest less than polygynous males in offspring defense during the pre-incubation period, when females are forming eggs.

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