

BREEDING BEHAVIOR AND FOOD HABITS OF THE WATTLED JACANA

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Little is known about the biology of the Wattled Jacana (*Jacana jacana*), whereas the Northern Jacana (*Jacana spinosa*), has been studied in detail (Jenni 1974, Jenni and Collier 1972, Jenni et al. 1974). The Wattled Jacana inhabits fresh-water marshes from Panama and Colombia south to Bolivia, Argentina and Uruguay (Meyer de Schauensee 1966). Because of the recent interest in polyandrous mating systems (Orians 1969, Hays 1972, Oring and Knudson 1972, Jenni 1974), and because the Wattled Jacana is believed to be polyandrous (French 1973), we investigated its breeding behavior and feeding ecology.

STUDY AREA AND METHODS

The study was conducted from 19 June to 17 August 1974 on the coastal lowlands at the Mahaicony and Abary Rice Development Scheme (MARDS), Burma, Guyana, South America (6°28'N, 57°45'W). Summer daylength is about 12 h. There are two rainy seasons and two dry seasons; mean annual rainfall is about 238 cm (Giglioli 1959). The region consists of freshwater ricefields crossed by dikes and canals. The terrain is flat and the fields are about 17 cm deep when flooded.

The study was performed on the MARDS corporation grounds. Dikes and roads divide this tract into 1.1-ha flooded lawns dominated by Bamboo Grass (*Hymenachne amplexicaulis*), Busie-busie (*Cyperus articulatus*) and Napier grass (*Echinochloa* sp.). Scattered over the lawns were a few Saman (*Samanea saman*), Flamboyant (*Delonix regia*) and Jamoon (*Syzygium cumini*) trees.

Wattled Jacanas were the only shorebirds to breed on the lawns. However, domesticated cattle (*Bos taurus*), Cattle Egrets (*Bubulcus ibis*), Striated Herons (*Butorides striatus*), Smooth-billed Anis (*Crotophaga ani*), Carib Grackles (*Quiscalus lugubris*), and Shiny Cowbirds (*Molothrus bonariensis*) foraged there each day. For a more detailed description of the flora and fauna of MARDS see Giglioli (1959) and Bourne (1976).

To determine the degree of sexual dimorphism, we took standard measurements of 31 mist-netted jacanas. We also observed the courtship and territorial behavior of 7 color-marked birds from a 3 m-high sheltered house porch. Time budgets of a pair of color-marked jacanas, female Green-Red (G/R) and male Green-Green (G/G), were obtained by continuous observation from sunrise to sunset from 20 June through 28 June. We timed each activity with a stopwatch to the nearest half-minute. Similar, but less detailed observations were

made on the other breeding pairs. We measured each egg in 9 active nests.

To study diet we collected 30 jacanas for stomach analysis. Contents of the esophagus, crop, and proventriculus were identified to the lowest taxon possible and the volume of each category was determined by water displacement.

The feeding behavior of 162 individuals was sampled for one minute each. We recorded the number of feeding attempts (pecking at different stations), time spent at different feeding habitats, and type of foraging behavior throughout the day under various weather conditions.

RESULTS

SEXUAL DIMORPHISM

Sexes of adults were easily distinguished in the field; females were bigger and had a bluish cast to the dorsal region of the frontal shield, the latter was not characteristic of males. Measurements of 31 adult jacanas (table 1) revealed females to be significantly larger than males in 7 of 9 dimensions measured. The greatest differences were in body weight, wing length and spur length.

TERRITORIALITY

Defended territories for 4 pairs averaged 1.1 ha (1.0–1.2). They were enclosed by roads or dikes and were used by both sexes for maintenance, foraging, courtship, nesting and roosting (fig. 2). A male (G/G) spent on the average 70% and a female (G/R) 53% of their time on the territory (Fig. 2A). Time off the territory was spent in adjacent fields. The territorial pair on the average spent 52% (34–99) of their time together on the territory. Thus, site and mate fidelity were strong during the breeding season.

Aerial chases were the principal manifestation of territorial defense. The frequency of aerial chases was up to 6 times greater for the female than for the male before egg laying, and the territory was not defended much during egg laying (fig. 3A). Aerial chases were generally accompanied by vocalization and were terminated when the intruder was chased over the dike or road. Hence, dikes and service roads served as territorial boundaries for breeding pairs. Males did not defend sepa-

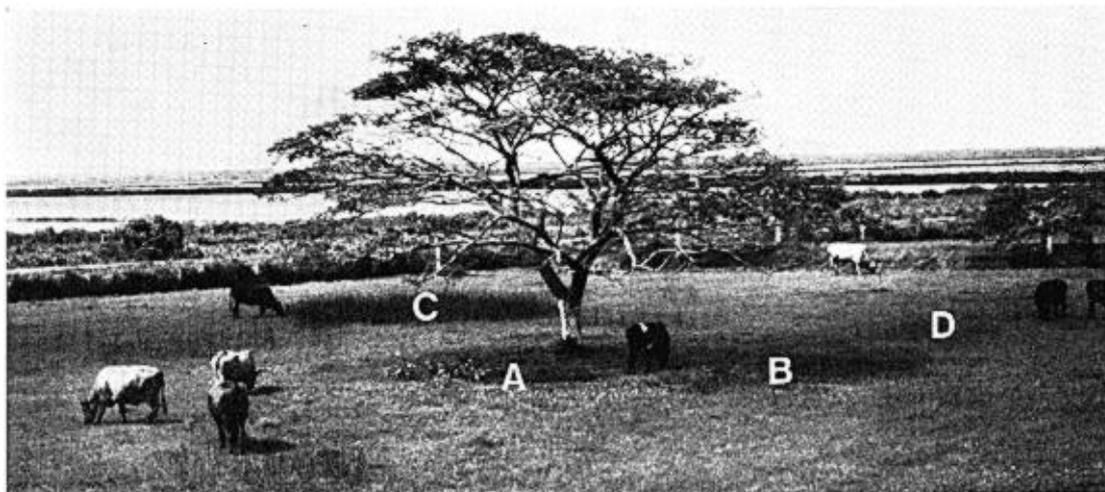


FIGURE 1. Habitat of a color-banded breeding pair of Wattled Jacanas (female—G/R; male—G/G) at MARDS, Guyana. A–D are the locations of successive active nest sites. Dikes, service roads and flooded ricefields are in the background. Dikes served as the outermost boundaries for territorial defense. Photograph taken from the southwest corner looking northeast, June 1974.

rate-sized territories and usually followed the females when they chased other jacanas out of the territory.

We noted several other responses to intruding jacanas. Jacanas infrequently defended their territory by lowering the head and holding the wings aloft with spurs and yellow underwings exposed. This behavior, which we term "Wing Posturing," was given by one or both sexes together in response to the intrusion of two or more jacanas (3 observations), by males to dogs and cattle (2 observations) when they approached the nest, but never to intrusions by single jacanas.

A more frequent behavior in which the yellow underwing linings were displayed conspicuously, occurred when jacanas moved from place to place on the territory. The role of these "Relocation Flights" is not entirely clear, but they could have a signal function. Before egg laying, when territorial defense was the greatest, jacanas on territory relocated 2 to 5 times per hour, but only once per hour during egg laying (fig. 3B).

We observed a different form of territorial defense in response to the intrusion of jacana pairs or families. A territorial female and her counterpart would stand about 30 m apart and

both "Teeter" back and forth. This mutual display, which we saw twice, lasted for about four minutes before the nonterritorial birds flew to peripheral areas of the territory.

COURTSHIP AND NEST BUILDING

Soliciting and mounting were frequent prior to egg laying, diminished after the first egg was laid (fig. 3C), and were restricted to one site on the territory. Soliciting by the female did not always elicit mounting by the male. One female solicited on the average of 4.4 times per hour, while the male mounted 1.3 times per hour; soliciting occurred about 3½ times more often than mounting. Another female was observed to solicit for over 3 min without being mounted by the male who foraged nearby.

Pair (G/G and G/R) renested 4 times in the same territory (fig. 1). Each nest had previously been a location where soliciting and mounting had occurred. Thus, it appears that the presence of a soliciting female indicates a future nest site. We did in fact use this information to predict the location of subsequent nests on the lawns and found it reliable in locating 9 of 12 nests.

Males do most of the nest building. Facing

TABLE 1. Mean weight (g) and dimensions (mm) of adult Wattled Jacanas at Burma, 1974^a.

Sex	No.	Weight	Wing (flat)	Spur	Body length	Tail	Culmen	Tarsus	Shield	Wattle
Male	16	108.3	142.6	8.1	191.5	38.9	29.2	55.4	11.7	7.7
Female	15	142.8	179.6	10.2	212.7	43.7	30.0	56.9	13.3	9.0

^a Significant differences, ANOVA ($P < 0.05$), were found between sexes in all characteristics except body length and tail.

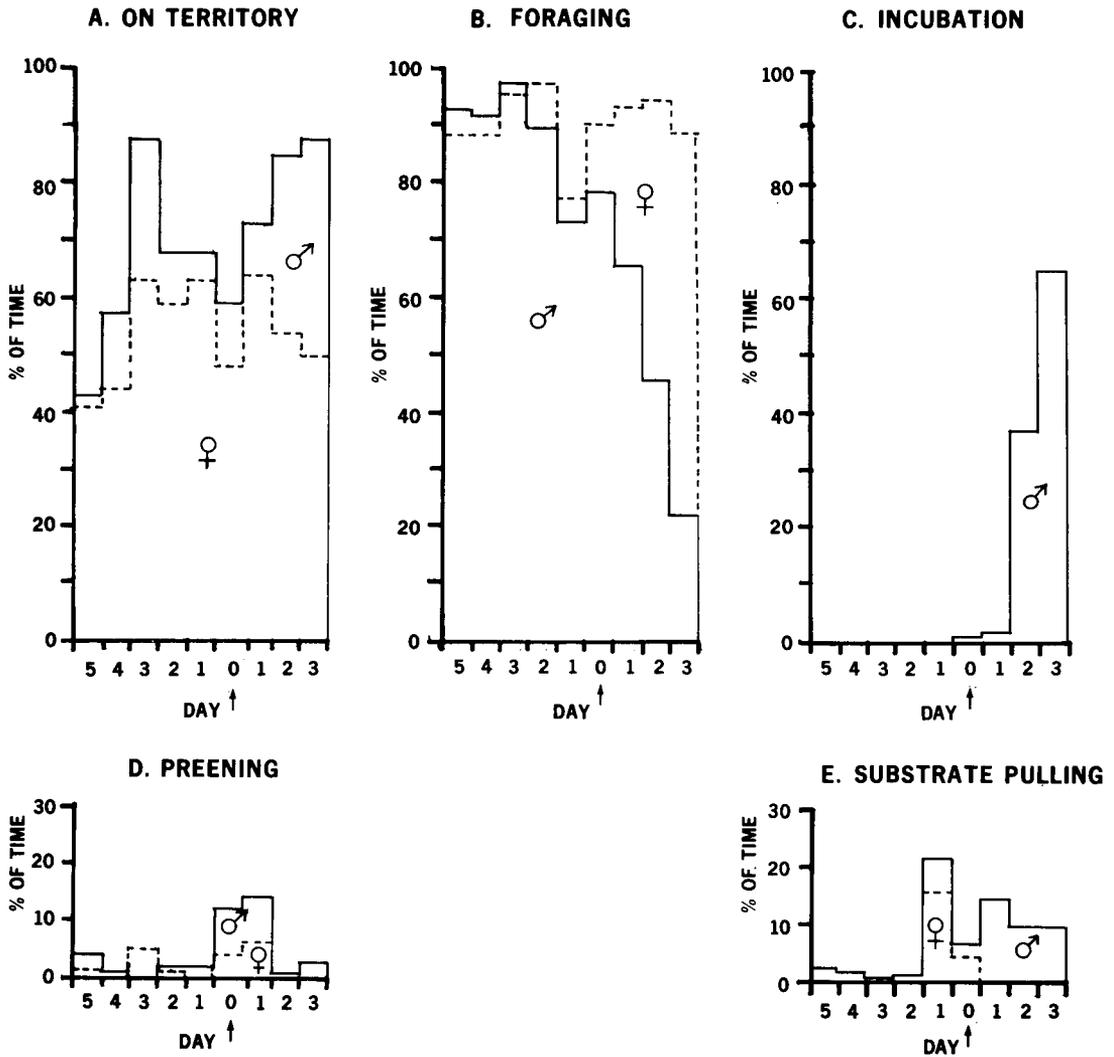


FIGURE 2. Percentage of time spent each day by a pair of Wattle Jacanas on territory (A), and in various activities while on territory (B-E), 5 days prior to and 4 days during egg laying. Male (G/G) solid line; female (G/R) dashed line. The arrow indicates the laying of the first egg on 26 June 1974 of a 4-egg clutch.

away from the nest, they gradually work their way outward from the nest site, pulling vegetation, and throwing it backwards over their shoulders. After proceeding about 15 m or more they run back to the nest and start all over again, usually in a slightly different direction. Almost 15% of their daily activity was devoted to this behavior (fig. 2E) which we call "Substrate Throwing." The result was to bring vegetation close to the nest platform, to which they add it when incubating the eggs.

Substrate Throwing, first described in jacanas by Jenni and Collier (1972), was also associated with courtship. It was restricted to within several feet of the soliciting site prior to egg laying and often occurred immediately after mounting. In 53 such instances, the male

threw substrate 22 times (41%) and the female 9 times (17%). On 14 occasions, Substrate Throwing by the male elicited soliciting in the female. Substrate Throwing peaked for both sexes on the same day but was more pronounced in the male during egg laying (fig. 2E).

Hence, it appears that in Wattle Jacanas, females select the nest site, both sexes build the initial platform, but the male plays the major role in building and adding to it, particularly after the eggs are laid.

EGG LAYING AND INCUBATION

Wattle Jacanas lay 4-egg clutches on a floating nest platform. Seven platforms averaged 313 mm × 290 mm. Successive eggs in

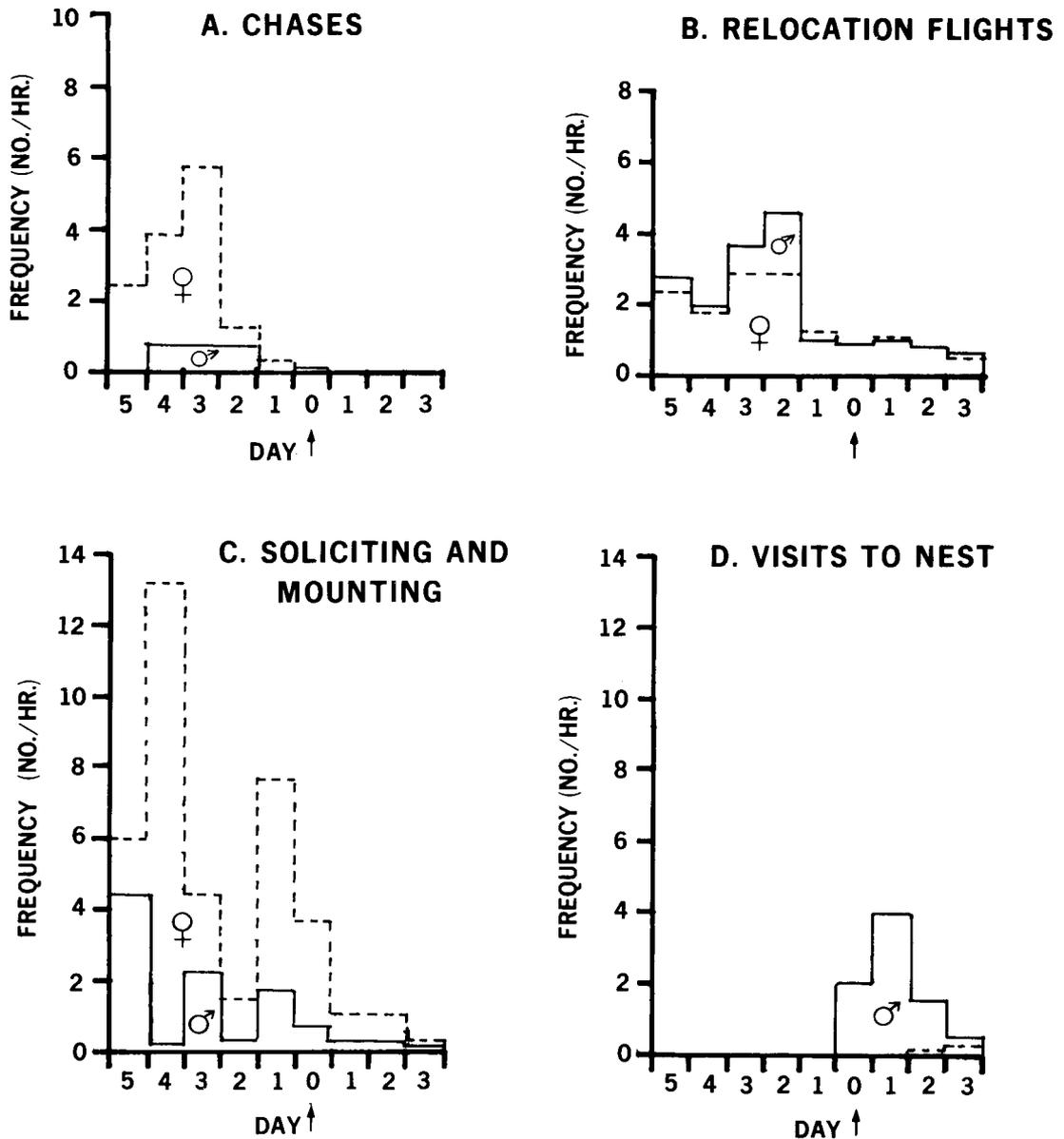


FIGURE 3. Daily frequency (no. per hour) of various activities of a pair of Wattled Jacanas on territory 5 days prior to and 4 days during egg laying. Male (G/G) solid line; female (G/R) dashed line. The arrow indicates laying of the first egg on 26 June 1974 of a 4-egg clutch.

a clutch are laid about 40 min later each day (table 2), and are grouped together by the male (fig. 4), who devotes more and more time each day to incubating them (fig. 2C). Only the male incubates, and once the eggs are laid the female rarely visits the nest (fig. 3D). Both sexes roosted together on the territory one day prior to egg laying and nocturnal incubation began when the second egg was laid.

We took standard measurements of 16 unknown and 10 known-aged eggs (5 and 4

nests, respectively). Known eggs laid sequentially in a clutch differed significantly from unknown-aged eggs in mean length ($F = 0.07$; $P < 0.01$), width ($F = 9.81$; $P < 0.01$), weight ($F = 7.89$; $P < 0.05$), but not volume ($F = 0.24$; $P = 0.64$). Comparisons of eggs within a clutch revealed that the last egg laid was significantly larger ($P < 0.05$) in length, breadth, volume and weight than the first egg (table 3). Although our sample was small, it appears that Wattled Jacanas lay successively larger eggs each day. Weights



FIGURE 4. Jacana nests showing characteristics of the eggs and nest. (upper) Nest platform of Bamboo Grass (*Hymenachne amplexicaulis*) with a newly-laid egg on the right. (lower) Nest platform of Club Rush (*Eleocharis mutata*) with a full egg clutch. The male groups the eggs together for incubation shortly after each egg is laid. MARDS, Guyana, June 1974.

TABLE 2. Time (h) of egg laying in the Wattled Jacana at Burma, June–August 1974.

Nest ^a	Egg Number			
	1	2	3	4
1	05:05(40) ^b	05:45(80)	07:05	none
2	05:00(40)	05:40(79)	06:59	none
3	unknown	05:49(73)	07:02(122)	09:04
4	unknown	05:30(80)	06:50(130)	09:00

^a Egg laying began on 20 July, nest 1; 26 July, nest 2; 8 August, nest 3; 25 June, nest 4.

^b The number in parenthesis is the delay (min) each day between successive eggs in the clutch.

TABLE 3. Mean differences in the size of jacana eggs as determined by the Duncan new multiple range test (Duncan 1955)^a.

Egg no.	N	Length (mm)	Breadth (mm)	Volume (ml)	Weight (g)
1	3	32.7A	23.7A	8.0A	9.2A
2	3	34.3B	25.3AB	8.5A	9.4A
3	3	35.7C	25.3AB	9.0AB	9.9B
4	1	37.0C	27.0B	10.0B	10.2B

^a Means not followed by a common letter differ significantly ($P < .05$) from each other.

of four newly hatched but dry chicks averaged 6.2 g (6.0–6.5).

RENESTING AND MATING

The locations of successive nests for jacanas (G/G and G/R) at Burma are shown in figure 1. Nest A, started 24 June, had a 4-egg clutch. One egg was removed by a Carib Grackle on 1 July and all eggs were missing the next day. The pair renested at site B on 4 July. This nest with its 3 eggs was destroyed by cattle on 11 July. A nest platform was found at location C, a former roosting site, on 26 July. On 1 August, the 3-egg clutch was trampled by cattle. The pair renested at site D on 8 August. The fate of this nest with its 4 eggs was unknown. The average recycling between successive nests was 8 days (2–15).

We did not observe renesting to occur in the 6 other marked pairs, nor did we observe pairing or copulation of our marked females with additional males. Also, males did not appear to outnumber females on the Burma lawns. The only evidence of a polyandrous system at Burma was based on circumstantial evidence; two active nests with completed clutches were found only 2.5 m apart in a distant fallow ricefield, thereby suggesting that the two clutches were laid by a single female. It appears that the population of jacanas breeding on the Burma lawns was strictly monogamous.

DIET

The diet of the Wattled Jacana consisted of 4 types of seeds, 5 kinds of animals; no single food item occurred in all individuals (table 4). Seeds comprised about 20% of the total diet by volume. Club Rush (*Eleocharis mutata*) seeds averaged 7.7% of the total diet volume and was the plant most frequently eaten, occurring in 13 (43%) of the 30 jacanas examined. No significant sexual dif-

TABLE 4. Mean volume, percent and frequency of food items of 14 male and 16 female Wattled Jacanas collected at Burma, 11-17 July 1974.

Food	Volume (ml)		t ^a	% of total M&F	Percentage of occurrence	
	Male	Female			Male	Female
Plant (seeds)						
<i>Eleocharis mutata</i>	0.9	1.3	0.89 NS	7.7	57.1(8) ^b	31.2(5)
<i>Echinochloa</i> spp.	0.5	1.3	1.48 NS	3.4	14.3(2)	37.5(6)
<i>Paspalum</i> spp.	0.9	1.2	0.49 NS	4.7	28.6(4)	25.0(4)
<i>Oryza sativa</i>	1.0	1.3	2.00 NS	3.8	21.4(3)	18.7(3)
Total plant	0.8	1.2	0.89 NS	19.6	100.0(14)	100.0(16)
Animal						
Invertebrates						
<i>Calandra</i> sp. (adult)	1.8	3.0	2.62 S	26.9	71.4(10)	68.7(11)
<i>Lissorhoptrus</i> spp.	2.2	2.8	1.00 NS	23.8	50.0(7)	68.7(11)
<i>Scatella stagnalis</i>	1.5	2.0	0.78 NS	10.6	35.7(5)	37.5(6)
Grylloidea	2.0	1.9	0.17 NS	4.9	7.1(1)	25.0(4)
Acridoidea	1.7	4.4	3.10 S	14.2	42.8(6)	31.2(5)
Total animal	3.8	6.6	4.50 S	80.4	100.0(14)	100.0(16)
TOTAL PLANT AND ANIMAL	4.9	8.1	5.10 S	100.0		

^a Significant differences (S), ANOVA ($P < 0.01$), between sexes in mean volume of prey items taken.

^b Numbers in parentheses indicate number of individuals in which the food item was found.

ferences were found in the average volumes of specific seeds consumed.

Invertebrates made up the bulk (80%) of the diet by volume. About 50% were beetles consisting of Rice Water Weevils, *Calandra* sp. (26.9%) and *Lissorhoptrus* sp. (23.8%). Fourteen percent were grasshoppers (*Acridoidea*), 10% were Shore Flies (*Scatella stagnalis*), and 5% were crickets (*Grylloidea*). Rice Water Weevils occurred in 21 (70%) of the jacanas and *Lissorhoptrus* sp. beetles in 18 (60%).

Females differed significantly from males in taking a greater average volume of Rice Water Weevils ($F = 6.92$; $P < 0.05$), grasshoppers ($F = 9.63$; $P < 0.05$), total animal ($F = 20.73$; $P < 0.001$), and total plant and animal ($F = 25.75$; $P < 0.001$) food.

FORAGING BEHAVIOR

Prior to egg laying, jacanas (G/G and G/R) spent over 80% of their time foraging on the territory (fig. 2B). Forty-three percent of this time was spent foraging together as a pair. During egg laying the male foraged less, devoting increasingly more time each day to incubation. Females appeared to be dominant at feeding stations, because on three occasions, we observed females pecking at males thereby displacing them from their foraging sites.

Jacanas foraged in two ways. They either pecked at food on the surface of the vegetation (gleaning) while walking at a constant pace, or they remained stationary and pecked at food in the water (feeding deep). To test whether foraging methods differed between sexes, we observed 162 birds for one minute

TABLE 5. Mean number of pecks and time (sec) spent per minute by Wattled Jacanas in various foraging behaviors during the day.

Foraging Behavior ^a	Clear mornings		Clear afternoons		Rainy mornings		Rainy afternoons	
	males (42) ^b	females (42)	males (18)	females (24)	males (4)	females (14)	males (6)	females (12)
Pecks	11	8	7	7	16	10	9	13
Stationary	10	20	8	22	0	9	17	5
Walking	50	40	52	37	60	51	42	55
Gleaning	32	27	25	16	60	47	50	35
Feeding Deep	26	32	32	44	0	13	10	25

^a No significant difference ($P > .05$) was found between sexes for each foraging behavior as determined by the paired t test.

^b Number in parenthesis is the sample size.

each as they fed throughout the day (table 5). We found no significant differences between sexes in their foraging behavior, either at different times of the day or under various weather conditions.

DISCUSSION

BREEDING SYSTEM

Jenni (1974) reviewed avian social systems in which females lay more than one clutch in rapid succession. In this study, Wattled Jacanas breeding on the Burma lawns were serially monogamous and did not exhibit serial or simultaneous polyandry like that found in the Bronze-winged Jacana (*Hydrophasianus chirurgus*, Hoffman 1949, 1950) and Northern Jacana (Jenni and Collier, 1972), respectively.

The circumstantial evidence of simultaneous polyandry observed in the Burma ricefields is substantiated by unpublished observations by Bourne on unmarked jacanas at Blairmont, Guyana during August 1955. On 3 August, a female was mounted by two different males within 15 min at two different nest sites located about 10 m apart. She completed a four-egg clutch on 7 August, and began laying in the second nest on 11 August.

Graul (1973:84) referred to these monogamous and polyandrous relationships as "rapid multi-clutch systems." Research on these systems has produced several hypotheses (Orians 1969, Jenni 1974) that might explain the adaptiveness of Wattled Jacanas' social systems. The critical questions are related to suitable breeding habitat, predation pressure, and the abundance of food.

The type of habitat required for optimal breeding success in Wattled Jacanas is not clear. We saw birds breeding on the Burma lawns, ricefields and ponds. The structurally diverse ponds in Costa Rica were optimal breeding habitats for the polyandrous Northern Jacana, while lawns were used only for foraging by a nonbreeding population (Jenni and Collier 1972).

Mating systems seem to be related to territory size and habitat diversity. Defended territories for four monogamous females breeding on the Burma lawns averaged 1.1 ha (2.6 acres). This is similar to sizes found by Jenni and Collier (1972) for Wattled Jacanas occupying swamps in Panama (2.5 acres), but larger than they found for polyandrous Northern Jacanas breeding on ponds in Mexico (1.7 acres) and in Costa Rica (0.88 acres for females; 0.37 acres for males). Males in our study did not defend separate-sized ter-

ritories. The fact that polyandrous and monogamous females on the Costa Rica pond held different-sized territories (0.80 and 0.52 acres, respectively, Jenni and Collier 1972) also supports the thesis that mating strategies may be related to territory size.

Predation pressure and nest destruction appear to be important in the adaptiveness of the Wattled Jacana breeding system. Clutch size is 3-5 eggs for Wattled Jacanas in Trinidad (French 1973) and 2-4 eggs for birds breeding in Surinam (Haverschmidt 1968). Based on our observations, four eggs constitute a full clutch; anything less indicates egg loss. There is some evidence that predator pressure limits clutch size in tropical forest birds with open nests (Lill 1974), but none we know of for jacanas. However, 12 species of polyandrous shorebirds listed by Oring and Knudson (1972:71) have reduced clutch sizes.

Based on calculations of egg and body weights, female Wattled Jacanas have the smallest egg-to-body-weight ratio (6.8) of 20 species of shorebirds reported by Graul (1973). We agree with Jenni's interpretation (Jenni 1974), that small egg size is an adaptation of females to lay additional clutches, rather than allowing females to lay a clutch under poor food conditions (Parmelee and Payne 1973).

Results from our study during the rainy season do not support a specialized diet or a fluctuating food hypothesis as has been proposed for arctic multi-clutch systems (Graul 1973, Nethersole-Thompson 1973, Parmelee and Payne 1973). Wattled Jacanas are omnivorous; those that we watched ate much the same food as those in Surinam (Haverschmidt 1968). Females take significantly more of specific food items probably because egg production requires more protein than does sperm production (King 1973). Food does not seem to be limited during the peak breeding season, since feeding rates and foraging methods do not differ according to sex, time of day, or weather conditions.

We suggest that the factors influencing the development of serial monogamy in the Wattled Jacana involve the following behavioral adjustments to ecological conditions. Burma lawns are structurally simple, resulting in large territories and wide dispersal of breeding pairs. With the increase in importance of the pair-bond, and an increase in attachment to the territory because resources are abundant, females, when subjected to high nest destruction find it advantageous to lay sequential

clutches with the same male rather than reducing clutch size or pairing with other males. Selective forces may be operating differently in the ricefields and ponds. Jacanas offer an excellent opportunity to learn about the behavioral and ecological factors acting on the development of rapid multi-clutch systems.

SUMMARY

Behavior of Wattled Jacanas associated with territoriality, courtship, nest building, incubation and feeding is described, for the first time. The usual roles of the sexes are nearly reversed. Females defend a large territory, select the nest site, and participate in the initial stages of nest building. Males do not defend territories, but do most of the nest building and all of the incubation. Mate and site fidelity are strong.

Females are sexually dimorphic in 7 of 9 physical dimensions and in diet, but not in methods of foraging.

Wattled Jacanas breeding on the lawns are serially monogamous, those on the ricefields, polyandrous. Results are discussed with respect to various selective forces operating on rapid multi-clutch breeding systems. We propose that serial monogamy may be characteristic of species breeding in simple habitats who have strong fidelity to mates, and to a large territory with abundant resources, and are subjected to heavy predation pressures.

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