# POLYANDRY IN THE AMERICAN JAÇANA (*JACANA SPINOSA*)

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LITTLE is known about the biology of any of the Jacanidae, a circumtropical family of shorebirds that inhabit freshwater swamps and marshes. The lack of knowledge reflects the limited field research done on tropical aquatic birds in general (Birkenholz and Jenni, 1964; Lack, 1968; Orians and Paulsen, 1969). The reversal of roles of the sexes in the American Jaçana (*Jacana spinosa*), in which males incubate eggs and rear young without help from the females has long been known (Miller, 1931). The same reversal of sex roles occurs in the Pheasant-tailed Jaçana (*Hydrophasianus chirurgus*) (Hoffmann, 1949, 1950), in the Bronze-winged Jaçana (*Metopidius indicus*) (Mathew, 1964; Collier, pers. obs.), and probably in the African Greater Jaçana (*Actophilornis africana*) (Miller, 1951). Furthermore, both Hoffmann and Mathew studied small breeding populations consisting of one female and two or three males. Although they investigated very small, unmarked populations, and almost all of Hoffmann's excellent data were gathered in Peking at the northernmost distributional limits of the Pheasant-tailed Jaçana, there is little doubt that these two species are polyandrous.

Polyandry is a rare form of social organization in birds (Lack, 1968; Orians, 1969). It is known or postulated to occur in some Tinamiformes, Charadriiformes (Rostratulidae, Jacanidae), Gruiformes (Turnicidae, Pedionomidae, Mesitornithidae, and one Rallidae). Polyandry has been suggested, but not substantiated, in a number of other orders. Although the Phalaropidae have been considered polyandrous, Höhn (1965, 1967) and Johns (1969) have recently shown that Wilson's Phalarope (*Steganopus tricolor*) is probably monogamous though it may be promiscuous. After reviewing the literature on the other two phalaropes, Höhn (1967) concludes that no real evidence of their polyandry exists.

True polyandry, defined here as one female being mated simultaneously or having simultaneous pair bonds with more than one male, is difficult to distinguish from promiscuity and successive polyandry. When polyandry is suspected, it must be verified in the field with individually marked birds. The purpose of this paper is to document polyandry and certain related phenomena in the American Jaçana. To our knowledge there are no previous accounts of polyandry based on the study of a marked population of birds. Both authors are currently working on other aspects of the biology of the American Jaçana (population dynamics and food habits, Collier; and behavior and social organization, Jenni).

 The Auk, 89: 743–765. October 1972

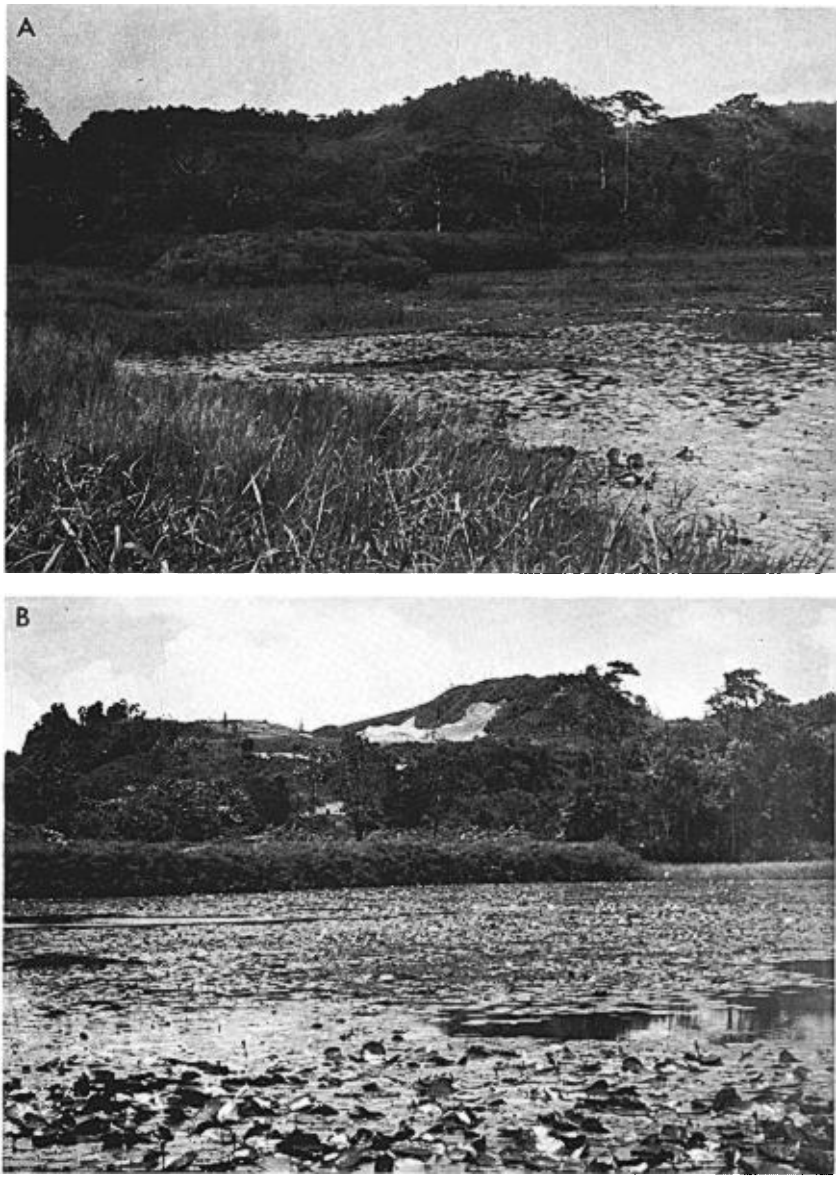


Figure 1. A, The pond at Turrialba. Photograph taken from southwest shore of pond facing northeast, August 1963. B, Same view as A, August 1970.

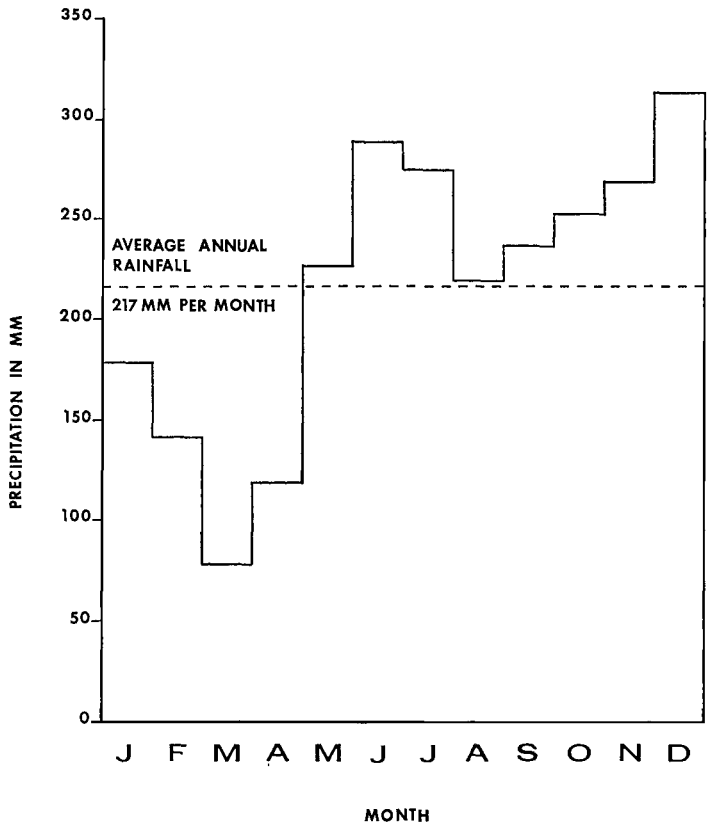


Figure 2. Mean monthly rainfall at Turrialba, Costa Rica, 1944–68 (data from IICA Climatological Laboratory).

## Study Area

This study was conducted on the grounds of the Instituto Interamericano de Ciencias Agricolas, near Turrialba, Province of Cartago, Costa Rica. The institute lies in a broad protected valley at 600 m (approximately 2,000 feet) on the Caribbean slope of the Cordillera Central, 9° 53′ N. Ecologically, the locality is near the lower limit of the premontane belt in the tropical wet forest zone (Holdridge, 1967).

The study site was a shallow 7-acre pond (Figure 1), formed as an artificial impoundment in 1947. The pond is bounded on the south and west by lawn and the main road through the institute, on the east by a broad expanse of lawn, and on the north by trees, patches of lawn, a gravel road, and coffee plantations. The east and most of the north shores are overgrown by heavy stands of papyrus (*Cyperus papyrus*) and semiaquatic

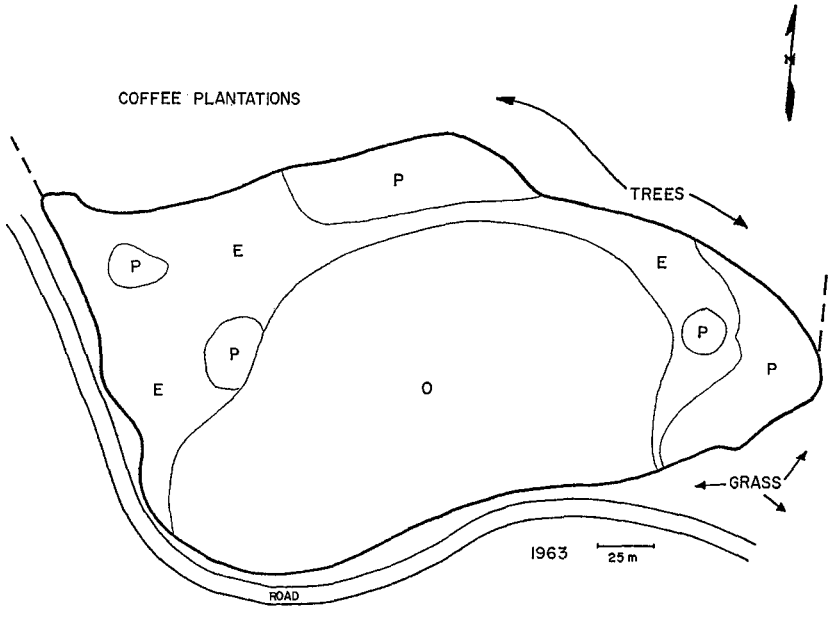


Figure 3. The distribution of vegetation at the pond at Turrialba, 1963 and 1964. P = papyrus and bamboo, E = grasses of intermediate height, O = water lilies, patches of low dense mats of vegetation, mud islands, and open water (see text for species composition).

grasses. The margin of the whole pond was demarked by a ground-level rock wall. The turf areas provided over 20 acres of open habitat within 300 m of the pond. The aquatic birds of the pond were relatively undisturbed by the presence of observers, probably as a result of habituation to heavy pedestrian and vehicular travel along the adjacent road.

Annual variations in temperature and day length at the institute are moderate (Lojan, 1967). Extreme day lengths are 11 hours 25 minutes and 12 hours 34 minutes. The average annual maximum and minimum temperatures were 27.2° and 17.3°C for the 25 years from 1944 through 1968. The mean monthly minima and maxima over this 25-year period never deviated more than 1.4°C from the annual averages. Unlike temperature, rainfall varies substantially over the year (Figure 2). The rainy season extends from May through December, and usually into January; 87 percent of the 2,610 mm mean annual precipitation falls during these 9 months. A moderate dry season of irregular onset and duration generally occurs between January and April (the Costa Rican "summer").

A diverse and abundant aquatic flora, mostly introduced, grows in the pond. During 1963–64, there were four distinct zones of vegetation, each

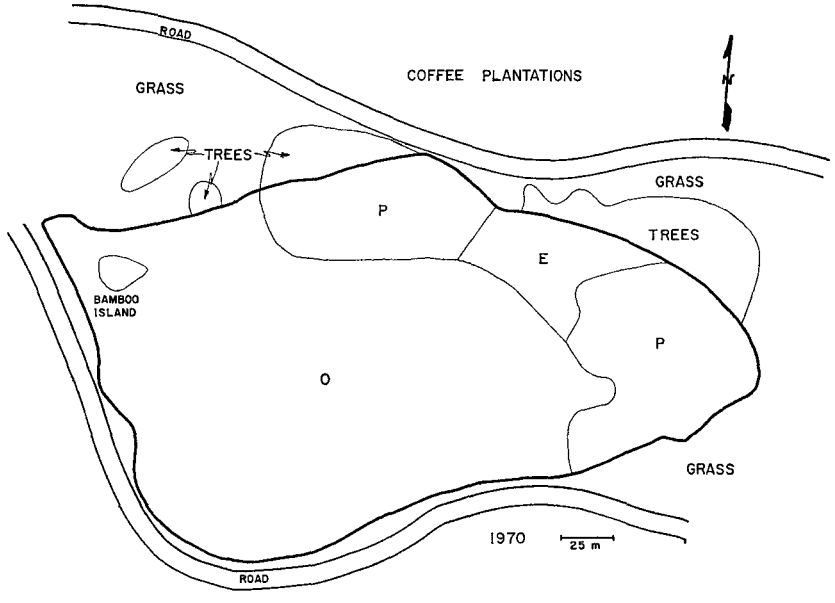


Figure 4. Distribution of vegetation in 1969 and 1970. See legend Figure 3 for explanation of symbols.

characterized by one or more conspicuous plant species (Figures 1 and 3). First, bands of papyrus and bamboo (*Bambusa* sp.) that attained heights of 3.5 and 10 m respectively, grew on the north and east sides of the pond. This association occupied about 12 percent of the pond area. The second association was a C-shaped area of semiaquatic grasses (mainly *Panicum purpurascens* and *P. maximum*) 0.3 to 2 m high. The grasses occupied about one-fourth of pond area. The third zone, dominated by broad-leaved water lilies (*Nymphaea ampla*), covered most of the central, south, and southwest parts or about one-third of the pond. The water lilies were interspersed with floating aggregations of aquatic fern or water moss (*Salvinia auriculata*), plus some submergent bushy pondweed (*Naias* sp.). This part of the pond was generally deeper, to 1.8 m, and had the lowest overall vegetation height. Small open-water areas were scattered throughout this zone, but open water comprised less than 2 percent of the pond.

The fourth zone occupied the area between the water lilies and the grass, but was so interdigitated and intermingled with the water lily association that it was not practical to distinguish them in Figure 3. Although many species grew in this association, the profile was typically low with most plants less than 0.3 m. The most abundant plants were water pennywort (*Hydrocotyle umbellata* and *H. ranunculoides*), spike rush (*Eleocharis*

*interstincta*), water knotweed (*Polygonum punctatum*), water hyssop (*Bacopa rotundifolia*), water milfoil (*Myriophyllum* sp.), mud plantain (*Heteranthera reniformis*), water moss, water primrose (*Jusseia erecta*), false loosestrife (*Ludwigia palustris*), day flower (*Commelina elegans*; most common on pond borders), and submergent pondweed. This association contained many other small herbs, none of which was abundant. Several dozen mud islands were found most commonly in this association and some were found in the water lily association. These islands were comprised of floating masses of organic debris (mainly decaying plant parts) and silt sediments. Such islands varied in size up to 5 m in diameter.

The conspicuous breeding birds on the pond during 1963 and 1964 included the Least Grebe (*Podiceps dominicus*), Common Gallinule (*Gallinula chloropus*), Purple Gallinule (*Porphyrula martinica*), and the American Jaçana. Other water birds occurring regularly included the Pied-billed Grebe (*Podilymbus podiceps*), Green Heron (*Butorides virescens*), and Masked Duck (*Oxyura dominica*). Less frequently seen were the Little Blue Heron (*Florida caerulea*), Common Egret (*Casmerodius albus*), Cattle Egret (*Bubulcus ibis*), Tri-colored Heron (*Hydranassa tricolor*), Black-crowned Night-heron (*Nycticorax nycticorax*), Least Bittern (*Ixobrychus exilis*), and Fulvous Tree Duck (*Dendrocygna bicolor*).

Between 1964 and 1969 much of the emergent vegetation was removed from the pond as part of a beautification program (Figure 1). The only part of the pond that remained undisturbed was the zone of papyrus along the north and east edges and shoreline grass on the northeast shore. The west end of the pond was affected radically (compare Figures 3 and 4), and the heterogenous zone of vegetation was completely destroyed. A reduction in avian diversity has accompanied the reduction of plant diversity. The following species were not seen at the pond in 1970: Fulvous Tree Duck, Common Gallinule, Little Blue Heron, Common Egret, Cattle Egret, and Tri-colored Heron. Visits by Masked Ducks also became rare.

## METHODS

Brief visits to the institute during July and August 1962 provided initial stimulus for this study and some preliminary observations. Observations reported here were made between the end of June and late August 1963 (Jenni), 1964 (Collier), 1969 (Collier), and 1970 (Jenni and Collier). The relative tameness of the birds on this pond greatly facilitated field observations. Binoculars, spotting telescope and reflex telephoto equipment were usually employed, especially to identify marked birds. Jaçanas used regular routes to fly between the pond and nearby lawns. Mist nets strung across these routes caught birds that were then marked. The birds quickly learned to avoid the nets and we had to move them to new sites every few hours. After a few days of netting it was necessary to leave the birds undisturbed for several days. Each year a few jaçanas left the pond so rarely that we were unable to mark them. In 1963 we marked jaçanas individually with rings of fingernail polish painted directly on the lower tibiotarsi and upper tarsometatarsi. In 1964, 1969, and 1970 we used colored plastic bands placed

TABLE 1
THE NUMBERS OF MATURE-PLUMAGED AMERICAN JAÇANAS ON THE IICA POND, TURRIALBA, COSTA RICA, DURING JULY AND AUGUST

| Year | Territorial | | Nonterritorial | | Total population |
|---|---|---|---|---|---|
| | Males | Females | Males | Females | |
| 1963 | 9 | 3 | (12) | | 24 |
| 1964 | 7 | 3 | 6 | 6 | 22 |
| 1969 | 9 | 4 | 4 | 8 | 25 |
| 1970 | 7 | 4 | 5 | 4 | 20 |

on the lower tibiotarsi. The number of mature-plumaged birds newly marked was 20 in 1963, 13 in 1964, 20 in 1969, and 11 in 1970. In addition to these birds, one bird in 1969 wore a band from 1964, and in 1970 8 birds wore bands from 1969. Faded plastic bands were replaced when the birds were recaptured.

## RESULTS

The American Jaçana apparently breeds the year round at Turrialba. We have records of clutches for late January, March, June, July, August, and October. We have not yet been able to study the population for a single consecutive 12-month period, but we have no reason to expect short refractory periods in November–December or April–May. We have not yet been able to determine the relationship between molt timing and breeding.

The American Jaçana at Turrialba is almost exclusively insectivorous. Adults occasionally take very small fish, but we have never seen the young do so. Feeding jaçanas search the substrate from which they apparently glean whatever small animals they find. They occasionally peck at water lily flower buds and tubers that Purple Gallinules have opened. Collier is making an intensive study of the species' food habits. The number of territorial jaçanas at the Turrialba pond averaged 12.3 for the 4 years, and the number of adult-plumaged nonterritorial jaçanas averaged 11.3. The population remained fairly constant for the 4 years (Table 1).

### SEXUAL DIMORPHISM

The sexes have identical plumage, but the females are so much larger than the males that we could usually distinguish the sexes of adult jaçanas in the field, and always in the hand.

In 1969 and 1970 we weighed 16 males and 12 females in adult plumage. The males averaged 86.9 g and the females averaged 145.4 g. The difference in weight is significant ($t = 13.23$, $P < 0.001$). Individuals that maintained territories on the ponds were significantly heavier than unestablished resident birds. Five territorial females averaged 160.9 g while seven nonterritorial females averaged 134.6 g (Mann-Whitney Test, $U = 1$, $P = 0.006$). Eight territorial males averaged 91.4 g while eight nonterritorial males averaged 82.3 g (Mann-Whitney Test, $U = 12$, $P = 0.038$).

TABLE 2

AVERAGE TERRITORY SIZE OF JAÇANAS IN FOUR DIFFERENT YEARS

| | Average territory size in acres | | | | |
|---|---|---|---|---|---|
| Year | Males | (n) | Females | (n) | |
| 1963 | 0.35 | (4) | 1.30 | (1) | |
| 1964 | 0.45 | (7) | 1.33 | (3) | |
| 1969 | 0.30 | (9) | 0.68 | (4) | |
| 1970 | 0.38 | (9) | 0.68 | (5) | (3 polyandrous females average 0.80 acre)<br>(2 monogamous females average 0.52 acre) |
| Average: | 0.37 | (29) | 0.88 | (13) | |

Size differences become apparent within 3 to 4 weeks of hatching, but we have been unable to capture and weigh such young birds. Three immature-plumaged jaçanas banded on the pond 23 July 1964 all belonged to the same brood. They were approximately 10 weeks old and weighed 80.5, 96.5, and 100.5 g. The 96.5-g bird, a female, was an established breeding bird during June and July 1969. None of the other 15 birds banded in 1964 was seen in 1969, and none in 1970.

## TERRITORIES

Sites defended in 1963 and 1964 were located in the heterogenous vegetation. Some of the territories included small portions of adjacent water lily patches. Between 1964 and 1969 the heterogenous zone was removed and in 1969 and 1970 all territories the jaçanas defended were in the water lily zone. All breeding behavior occurred inside the territories. Although the males fed within their territories, prior to incubation they foraged outside the territories, especially on the nearby lawns. Females did more of their feeding on the lawn at all times than did the males.

Male territories averaged 0.37 acre or approximately 40 × 40 m for the 4 years of this study. Average territory size differed little from year to year (Table 2). Female territories averaged 0.88 acre and included from one to four male territories. Females defend only those areas that were also defended by males. The average size of female territories varied more from year to year than did male territories. The small average size of female territories in 1970 correlates with the decreased number of male territories per female territory.

In all years a small expanse in the east end of the pond remained undefended and several small patches in the middle of the pond also were not included in any territories. These places and the papyrus were the only parts of the pond that unmated birds were able to use. Territory owners sometimes invaded these areas and behaved aggressively toward jaçanas there, but they made no consistent effort to exclude other jaçanas from them.

On 29 July 1963 the four territories along the east edge of the pond were already established. One of these males was replaced during the summer, but no detectable modifications of boundaries were associated with this change. During late July another male successfully established a territory on a large and previously unclaimed patch of water pennywort completely surrounded by water lilies. The floating mat of vegetation was less stable than the other territories; it also differed in being surrounded by unoccupied and apparently less suitable habitat. During late July another male established a territory, built a nest, and obtained a mate, but did not succeed in breeding on the open lawn approximately 50 m east of the southeast corner of the pond.

Territories of American Jaçanas studied elsewhere in Central America by Collier have averaged consistently larger than those in Turrialba. From July through September 1965, near Villa Union, Sinaloa, Mexico, where individually marked American Jaçanas occupied shallow roadside ponds, male territories averaged 1.7 acres. Females defended from one to three male territories and both sexes foraged occasionally in adjacent pastures and cultivated fields. At Juan Mina, Rio Chagres, Panama Canal Zone, from June through August 1962, male jaçanas were so dispersed that their territory boundaries were difficult to determine but the territories averaged at least 2.5 acres (most authors consider the Panama form a separate species, *J. jacana*, which ranges from Panama south (Eisenmann, 1955; Wetmore, 1965)). The extensive river-border floating swamps in Panama adjoined tall forests with few open areas and jaçanas rarely moved outside their territories except to inhabited clearings. One marked female appeared to defend at least parts of two male territories, but with such a widely dispersed population it probably was impossible for females to maintain superterritories large enough to include three or four male territories. The aquatic environments in both Mexico and Panama lacked the diversity of microhabitats that characterized the Turrialba pond.

### Territorial Defense

Males defended their territories against all conspecifics except their mates. They usually succeeded in defending their territories against neighboring or nonterritorial males, but were usually unable to exclude the large females. When a male was unable to evict other jaçanas from his territory, his highly vocal attacks attracted his mate who either took over territorial defense or helped the male drive the intruder away. In addition to helping her mates defend their territories, the female independently defended her entire superterritory against other jaçanas, especially unmated or neighboring females.

Territorial males responded to conspecific aerial intruders with loud,

strident calls and by fluttering up toward them. This form of defense was especially conspicuous when an unestablished male circled the pond and one territorial male after another flew toward the intruder as it traversed his area. The fluttering up often included a loud whirring of wings and vocal calling by the territorial resident. When an unestablished male intruder alighted in a territory, the owner flew at him in an aerial attack. Nonterritorial members of the pond population did not release this form of aerial pursuit in the territory holders, but immigrants or transients invariably did so, and such birds typically remained at the pond only briefly.

When a neighbor entered a territory, the owner responded with either a shallow aerial dive or a running charge. Typically a neighboring male ran or walked back to his own territory, but intruding females often reacted aggressively. The attacking territorial male responded with loud, rasping cries and scurried about in a half-crouch with the wings partly extended and arched downward, which usually attracted his mate. Neighboring superterritorial females usually reached a standoff in which they stood erect a few feet apart and flicked their heads rapidly from side to side. These standoffs were followed by retirement of the birds to distant parts of their territories. When attacked by superterritorial females, unestablished females immediately retreated to the undefended areas or to the lawn.

Jaçanas also defended their territories against intrusion by other species, most commonly Purple and Common Gallinules, Masked Ducks, Least Grebes, and Green Herons. Jaçanas responded to these other species more consistently when they had eggs in the nest. Interspecific defense was least effective against Common Gallinules. They paid little attention to the threatening jaçanas, and wandered through their territories with impunity. Purple Gallinules were much more abundant and preyed on jaçana eggs and chicks. Male jaçanas were especially persistent in attempts to drive Purple Gallinules from their territories, and were often joined by the females in so doing. Purple Gallinules generally ducked their heads and ran from one or two highly vocal jaçanas making shallow dives at them, but they often appeared unresponsive to threats and calls delivered from the substrate; sometimes they threatened back and displaced the jaçanas.

### SEX ROLE REVERSAL

In the American Jaçanas the roles of the sexes are reversed. The male builds the nest with no help from the female. Copulation occurs at a variety of sites before nest construction begins. It is tempting to conclude that the male selects the site because he does the building, but we have no insight into the mechanism of nest site selection.

That the females perform any effective incubation during egg-laying or other brief visits to the nest is unlikely. After the clutch is complete all

incubating is done by the male alone, and when a male is off his nest, the eggs remain unattended. Although females help their mates defend their territories, they never relieve them at their nests. Our observations agree with Miller's (1931) that only male American Jaçanas have incubation patches.

The males care for the precocial young after hatching. Parental care includes brooding, attending, and defending the young, but never feeding them. The females never care for the young directly, although they continue to help the male drive intruders from the territory. Although usually accompanied by the male, the young are seen alone at times. The males often feed away from the young, and sometimes they fly to the lawn to feed leaving the young unattended on the pond. The young do not come out on the lawn to feed until they are about 5 weeks old and first able to fly. Although some adults walk from the pond to the lawn, the only jaçanas we have seen on the lawn were capable of flight.

Females are occasionally seen with chicks older than about 4 weeks. At this age the chicks are much less closely attended by the male and often wander independently for relatively long periods. At these times they often feed near the female and may associate with her for some time, but the association appears rather fortuitous to us. The young are not being brooded at this age and we have never seen either parent feed the young. The female helps the male with the brood only in the sense that she helps him repel conspecifics and interspecific intruders. She helps the male defend his territory at all times, irrespective of the presence of the young. The relationship may be that the female is simply tolerant of the young.

### Polyandrous Breeding Organization

The American Jaçana population at Turrialba had a polyandrous breeding organization during all 4 years. The total number of breeding jaçanas during the four seasons was 15 females and 34 males, an average of 2.2 males per female. Table 3 shows the numbers of territorial males per territorial female for all 4 years.

In 1963 the four territorial males under close observation were all paired with the same female. The only other females seen in these territories were driven away by the resident female, usually helped by the male. This same superterritorial female solicited copulation with a fifth male who built a nest on the lawn approximately 50 m east of the pond. Although the male mounted this female at least 22 times between 29 July and 18 August 1963, cloacal contact was never achieved and no eggs were laid in the nest. The same female laid at least three 4-egg clutches, including one replacement clutch, in nests of at least two of her mates with whom she had successfully copulated.

TABLE 3
FREQUENCY DISTRIBUTION OF POLYANDROUS MATESHIP GROUPS OF DIFFERENT SIZES DURING THE FOUR YEARS

| Year | Number of groups | Number of males per group | | | | Average number of males per female |
|---|---|---|---|---|---|---|
| | | 4 | 3 | 2 | 1 | |
| 1963 | 3 | 1 | 1 | 1 | | 3.0 |
| 1964 | 3 | | 1 | 2 | | 2.3 |
| 1969 | 4 | | 1 | 3 | | 2.3 |
| 1970 | 5 | | 1 | 2 | 2 | 1.7 |
| TOTALS | 15 | 1 | 4 | 8 | 2 | 2.2 |

During 1964 the numerical relationship of three active females paired simultaneously with three, two, and two males each remained constant even though two individuals were replaced during the season. Again in 1969 the polyandrous groups remained constant in size through the summer.

In 1970 a superterritorial female mated to two males was hit by an automobile, and although she managed to return to her territory she was unable to defend it, and disappeared at the end of the 2nd day. Two previously unmated females each took half her territory and one of her mates. We consider this a relatively unnatural development because numerical relationships remained constant following natural replacements in all 4 years. Table 3 shows the 1970 mateship groups as they existed before this accident.

The simultaneous nature of the polyandrous bonding is proved by the pattern and frequency of copulation of females with their various males. For example on several days in 1963, the female in the east end attempted copulation with all four territorial males and the aberrant male on the lawn. On 3 August this female assumed the copulatory position 13 times on the nest platforms of four different mates, and copulation appeared complete a total of six times with three of these males. Apparently complete copulation occurred with three different males within one 20-minute period. Although actual transfer of sperm to the female is impossible to prove in a field study, these copulations appeared equally complete in all important aspects, including performance of postcopulatory behavior (described below) by both male and female. Again in August 1964 and 1970 marked females copulated with three different males in single afternoons.

Frequency of solicitation and copulation with a particular male quickly decreased to a very low level and was in many cases not seen after the female laid a clutch for a male and he began incubating. Still the bond between the two birds clearly persisted through incubation, and the female continued to visit, forage in, and defend the male's territory as before. If

a clutch was lost, copulation resumed. Solicitation and mounting was resumed during the parental phase. Apparently complete copulation again became frequent when the chicks were about 4 or 5 weeks old.

### Copulation

Prior to copulation one or both birds may be in the territory. If the male or female is alone it attracts the other to the territory by calling or posturing. If both birds are in the territory, the bird who invites copulation typically postures, but does not usually call. When the female assumes the precopulatory position, or solicits, the male may fly from distances up to 10 m or more. Although he usually lands directly on her back, he sometimes lands next to her and then hops quickly onto her back. When a male solicits, he assumes the same precopulatory posture that the female uses. When the female arrives (she usually runs or walks quickly but does not fly to him) she assumes an identical posture just behind or to the side of the male. Sometimes the male promptly turns and mounts her, at other times he first walks away from her and then flies to land on her back. Once the male is mounted, both birds remain motionless for several seconds. Then, while balancing himself with his wings, the male begins to lift his feet alternately, shuffling them slightly toward the female's tail and regrasping her back with his long toes. Lowering his body, he gradually works his way toward her tail. This stage lasts from 10 to 40 seconds. Finally, after the male has positioned himself far enough back, the female turns her tail up and to one side while the male lowers his tail and abdomen over the other side. In this position the male flutters his wings rapidly for as long as 3 seconds, while the cloacae are presumably in contact. Contact is broken when the male lifts his tail; with little apparent change in wingbeat from the rapid strokes made while balancing over the female's tail, he flutters forward off her back to land nearby.

Successful copulations are often accompanied by male vocalizations. Presenting, mutual presenting, and incomplete copulations are more frequent than successful copulations. The female may interrupt copulations with sudden side-to-side head and neck movements, and by raising her body to a normal, upright position. The mounted male immediately starts to slide off and he flutters to one side. After copulation, either the male or female often begins to feed while walking away from the copulation site. Instead of feeding, the female may throw bits of vegetation to one side or the other as she walks away from the nest. This female postcopulatory behavior sometimes moves potential nest material closer to the platform and at other times moves material that the male has brought to the nest farther from the nest.

REPLACEMENTS

Established males or females were occasionally replaced by other individuals of the same sex. Each new occupant assumed the same territory, territorial boundaries, and mate, or in the case of female replacements, mates, as the previous occupant held.

In 1964 two recorded instances of replacement both involved jaçanas at the east end of the pond. Red-banded female, banded on 9 July and mated to three males, was driven out and replaced on her superterritory 11 July between 15:30–16:00. The new occupant was an unmarked and previously unestablished female. Red-female returned at least once each day through 15 July, and was driven away each time by the unmarked female. After that she became a member of the "surplus" population of papyrus-roosting, lawn-feeding jaçanas. The initial replacement occurred within orange-banded male's territory. He made incipient attacks toward the new female at least six times on the day she replaced his former mate, 11 July, and once on the next day. The attacks were limited to shallow dives toward the female; he usually alighted a few feet away and stood erect, craning his neck toward her. Orange-male first attempted copulation with the new female on 13 July. He made three attempts all of which seemed unsuccessful. No overt aggression was apparent between the new female and her other two mates whose territories she included in her superterritory.

The second replacement was of orange-male, who disappeared during the night of 22 July. An unbanded male was on the territory at sunrise the next morning. The unmarked female made several aerial and running attacks on the new male but she always stopped abruptly very close to him without completing the attacks. Within 15 minutes both birds were feeding quietly inside the territory. The male was marked with a yellow band the next day, 23 July. During the week following his establishment he was occasionally aggressive toward the female and made several shallow dives at her. These two birds attempted copulation at least five times during the male's first day on the territory, 22 July. The new superterritorial female was banded blue on 30 July. Both of these replacement birds defended their areas through the end of the 1964 observations on 25 August. Yellow-male's territory boundaries corresponded exactly to those of orange-male whom he replaced.

Replacement males initially responded aggressively to all jaçanas entering their newly assumed territories. They successfully repelled intruding males, but were unable to drive out the previous owner's mate. The female failed to drive out a new male although she attacked him. It is not obvious why the already established female failed to drive the replacement male away, but it is our impression that attacks on new birds were abbreviated

and, more importantly, that the replacements did not respond to the attacks by fleeing the way intruding, unestablished birds invariably did. Squatting and prostrate postures by a male in response to attacks by a replacement female on 22 July 1963 appeared to be appeasement behavior, as the female did not attack him when he assumed such postures. Overt aggressive interactions disappeared almost completely within a few hours in most cases. Tolerance of each other and attempts at copulation followed, but coitus was never consummated at the first several invitations to mount nor even during the first several actual mountings.

### Nonbreeding Population

In addition to the breeding birds, the populations in all 4 years contained many jaçanas in mature plumage that were not actively breeding (Table 1). Excluded from most of the pond by the territorial birds, these nonbreeders fed on the nearby lawns, rested in the papyrus, and occasionally congregated in patches of low growth not claimed by the territorial birds.

This large reserve of nonbreeding birds in mature plumage is a conspicuous feature of the jaçana population at Turrialba. The occasional replacement of established individuals by birds from this population proves that at least some of them are capable of breeding. Still we cannot exclude the possibility that some of these replacements were immigrants from elsewhere. Immigrants appeared frequently and, although they usually left soon after appearing, some joined the nonbreeding population.

Our trapping techniques took individuals from all segments of the population, but as we caught disproportionately more adult males than females (4.5 to 1 during 1963 and 1964), clearly our techniques were selective for males. The total number of breeding birds during the 4 years of our study was 34 males and 15 females (not including replacements). The nonbreeding population for the 3 years for which we have data included 15 males and 18 females. The sex ratios at Turrialba thus varied from slightly to heavily biased in favor of males during the months of July and August. We are hesitant to place much emphasis on these data, for the sample is certainly inadequate to suggest a sex imbalance in the species.

Hourly censuses recorded maximum numbers of jaçanas present during early morning and midafternoon. However more birds fed on the lawn in cooler overcast weather, during light to moderate rains, or immediately after a heavy downpour rather than in hot sunny weather regardless of time of day. The number of birds visible on the pond sometimes dropped below 10 during the hottest, brightest hours when many jaçanas moved into the heavy papyrus. Cool overcast weather brought birds out into the open even in midday.

### REPRODUCTIVE SUCCESS

Nests were not visited, and we could not see into all nests from the shore. Our observations are also limited to late June, July, and August. The normal clutch size is four. We never saw more than four eggs in a nest, and four eggs were laid in every nest we had under observation from the start of egg-laying. Eggs were lost from clutches under observation and entire clutches were lost.

One clutch was destroyed by two Purple Gallinules who visited the nest and ate one egg while the male jaçana was feeding on the lawn. The male returned and drove off the gallinules, but they took the second egg the next day, and the remaining two eggs were gone the following day. Other likely mortality factors include rapid fluctuations of water level during rainstorms, and upset of the fragile floating nests by other species.

Of 22 young in six broods seen on 7 July 1964, 19 were still present on 25 August. Similarly of 24 immatures present 25 June 1969, 20 were still present (16 of them color-banded) on 25 August. Two additional broods of four downy chicks each hatched 6 and 14 August 1969 and all eight of these chicks survived at least until 25 August. In 1970 all seven chicks seen 25 June were still present on 19 August. A brood of three that hatched on 9 July disappeared, and no other chicks were produced before 19 August 1970, although at least three clutches were lost. Although one or two chicks were sometimes lost from broods, we did observe the loss of one entire brood, apparently from starvation. One of the chicks in a brood of three that hatched on 9 July 1970 did not prosper and appeared less agile than the other two. It disappeared between 07:00 and 08:00 on the 3rd day after hatching. When the two remaining chicks were 10 days old, they seemed small and their heads were large in proportion to their bodies. They disappeared sometime during the late morning of their 10th day. Their mother (banded yellow over dark blue in 1969) was hit by an automobile when they were 7 days old. The male spent much time with the new female (banded orange in 1969) with whom he eventually formed a pair bond. During this time he spent very little time with the chicks, which were already in relatively poor condition. His lack of attention apparently hastened their starvation. Jenni is testing the hypothesis that parental attention directly influences the rate of food intake by jaçana chicks.

## DISCUSSION

Although the ecological conditions at Turrialba are artificially maintained, polyandry in the American Jaçana is not an aberrant function of this unique situation. While never before studied in a marked population, polyandry has been reported for other jaçanas and is known with reasonable certainty in at least the Pheasant-tailed and Bronze-winged Jaçanas. Col-

lier has also observed polyandry in a marked population of American Jaçanas in Mexico. Though polyandry has not been substantiated in the rest of the family to our knowledge, sexual dimorphism and the information in the literature suggest that the other Jacanidae are also polyandrous.

The suitable space available to the jaçanas for breeding territories and for rearing the young at Turrialba is very small. The extensive lawns provide supplementary feeding areas. The idea that food for chicks may be limited is supported by the apparent starvation of three chicks in 1970. It appears to us that food for young, or space for food production, is the critical resource. The other requisites that the males gain from their territories could be provided in much less space than they defend, except possibly food for the male, who can leave the territory temporarily to feed, which the chicks cannot.

At the Turrialba pond almost all of the low vegetation is occupied by territorial male jaçanas. Evidence that the suitable habitat is completely occupied is the fact that in four seasons we saw only one bird add itself to the population, while six others established themselves by displacing already established birds. If our hypothesis is correct that food is the critical resource, it would be advantageous for the adults to reduce their competition for food with the young. Competition can be reduced by evolving a breeding system that reduces the number of adults on the pond, but which maintains or maximizes reproductive potential.

The development of promiscuity, polygyny, or polyandry are all possible ways of reducing adult use of the prime habitat to a level below that required in a monogamous system, while maintaining the breeding potential. Promiscuity would not be helpful under present conditions because effective defense of the territory depends on the presence of two adults throughout the breeding cycle. Two adults are potentially available in both polygynous and polyandrous systems. Polygyny would appear to be more economical than polyandry because a superterritorial male can potentially mate with a large number of females, while the number of males for which one female could provide eggs is presumably more limited by the greater energy demands for egg production. The number of mates a jaçana can have is limited at least partly by its ability to assist its mates in territorial defense. Thus the theoretical advantage of polygyny over polyandry could probably not be realized. Two other aspects of the American Jaçana's breeding biology are important in considering the relative adaptiveness of polyandry and polygyny, size differences between the sexes and sex role reversal.

Polyandry could evolve only in association with sex role reversal, or in a species that had already evolved sex role reversal. Parental care by one parent will evolve if one parent is more successful than two, or if one

parent is as successful as two and the other parent somehow increases its reproductive potential by not participating in natal care. Sex role reversal occurs in birds that have not evolved polyandry, for example the phalaropes. Thus although polyandry is dependent on sex role reversal, the reverse is not true. Unfortunately there appears to be some confusion in the literature because of the assumption that birds with sex role reversal are also polyandrous. Sex role reversal and the size difference between the sexes in the American Jaçana appear to be closely related phenomena.

Breeding female American Jaçanas weigh 75 percent more than the males, and are analogous to large egg-laying machines. They are able to acquire and mobilize sufficient energy to produce up to three, four, or more clutches in a few weeks. With sex role reversal, the female is able to feed away from the male territory and there is therefore no strict premium on minimizing her weight to reduce competition with the male or the chicks. A female with more than one mate can feed in their several territories and thereby reduce her competition with any one male and his chicks. The large females play the dominant role of territory defense and probably of courtship, and apparently there has been no selection for large male size for these purposes. The male and the chicks both depend on the food resources inside the territory and the male's small size has the advantage of reducing his competition with young for food. Small size may also be an adaptation for reducing competition among the males by allowing them to reproduce successfully on smaller territories. The ability to cover a four-egg clutch places a lower limit on male size.

Polygamous organization in the American Jaçana reduces the number of breeding adults per territory below what a monogamous population would require. Sex role reversal allows the larger female to spend most of her time outside the territory of any one mate, and allows her to exploit other food resources. Freedom from parental duties with its concomitant restriction to one territory in jaçanas allows the female to establish pair bonds with other males. The need to help the male in intra- and interspecific territorial defense limits the number of males with whom she can form pair bonds, as does her ability to produce eggs. At least some females are able to acquire the energy needed to produce several clutches. That this breeding system makes heavy demands on the female's energy is suggested by the relative frequency with which females are replaced; 21 percent of the breeding females, but only 9 percent of the males were displaced by other birds during 5 months of observation.

There is little evidence to support the hypothesis that polyandry in the American Jaçana is the consequence of a surplus of males. It is difficult to imagine how selection could have favored a male surplus before the evolution of a polyandrous system. Although adult-plumaged males outnumbered

females 49 to 33 during the four seasons, this ratio does not differ significantly from a 1 to 1 ratio ($\chi^2 = 3.12$, $P > 0.05$). The regular appearance of transients during the breeding season is evidence that the resident population may represent a select portion of the species population. Ascertaining the sex ratio of an unbiased sample of the species would be difficult. In all years some resident females remained unmated while other females had more than one mate. A biased sex ratio may be a secondary effect of polyandry, but we do not consider it to be the cause of polyandry.

On the basis of percent of body weight, jaçanas all lay rather small eggs (Schönwetter, 1962), proportionately smaller than the eggs of other shorebirds, and proportionately smaller than the eggs of several nidicolous groups (Lack, 1968). The comparatively small egg size appears inconsistent with the need for precocity in jaçanas. Small egg size is very likely an adaptation that allows the female to lay one egg every day for 4 days and to produce a large number of such clutches in a short period of time. As a consequence of the small egg size, the precocial young are quite small and probably have little or no food reserve. Consequently they can survive only if food is relatively abundant and dependable at hatching.

Several comparisons with phalaropes tend to reinforce our ideas about the adaptiveness of the jaçana system. All three species of phalaropes are migratory and nest at comparatively high northern latitudes. They average one-third to two-thirds as heavy as breeding male American Jaçanas, depending on sex and species (Höhn, 1965). They breed on open, low profile, semiaquatic prairie or tundra habitat. Female phalaropes are larger than the males and have brighter breeding plumage. The female is active and aggressive in seeking a mate and initiating copulation. She furnishes a single male with four eggs that are large compared to her body size (Höhn, 1967; Lack, 1968). The male provides all subsequent parental care. After the brief period of mating and egg-laying, female phalaropes abandon the males, wander off to feed elsewhere, and presumably recover the energy used in egg production. The system of monogamy with sex role reversal is well suited to the open habitat with short breeding season where the phalaropes nest. It is virtually certain that monogamy prevails. Höhn (1967) has shown that in both sexes of Wilson's Phalarope sexual activity of the gonads lasts only a few weeks on the central Alberta breeding grounds. He could find little evidence of a possible second clutch production. In the short summers of these high latitudes the females are probably unable to acquire enough energy to produce a second clutch early enough in the season for the young to mature before the onset of inclement weather. Apparently the phalaropes have evolved a large egg size rather than multiple clutches as a way of maximizing reproductive potential.

Evidence from Collier's observations in Mexico and Panama where

jaçana territories were much larger than at Turrialba and from the literature further suggests that habitat quality correlates with the density of jaçana populations. For example between 1963 and 1967, the water in Gatun Lake, Panama Canal Zone, was kept at an abnormally high level. Jaçanas around Barro Colorado Island, previously limited to a few individuals, increased by several dozen (E. O. Willis and M. L. Cody, pers. comm.). This increase accompanied a great proliferation of floating vegetation (especially *Hydrella* sp.). A second example comes from Lake Kariba, Zambesi River, Rhodesia. By 1962, 4 years after the dam was built, approximately 1,000 sq km of sheltered water was covered by thick growths of the introduced aquatic fern, *Salvinia auriculata*. A virtual explosion of the previously small population of African Greater Jaçanas followed. Although both the amount of aquatic vegetation and the number of jaçanas have fluctuated subsequently, both remained very large on Lake Kariba (Lowe-McConnell, 1966; Jarman, 1968). During brief visits along the shallow north shore of Lake Olomega, El Salvador, 29 July through 8 August 1925, Miller (1931) estimated 17 to 20 nests of eggs plus several broods of young American Jaçanas. Miller indicated that the floating vegetation (a photograph shows water hyacinth, water lettuce, and aquatic fern) extended about 100 yards out from shore, but did not state how extensive an area he visited. He leaves the impression of a dense jaçana population in a relatively small area. When Collier visited 15 sq km Lake Olomega on 31 July 1970, the aquatic vegetation along the north shore was generally much taller and denser than shown in Miller's 1925 photograph, but he found many open stretches of low vegetation, especially along the northwest shore, that were similar to the Turrialba pond. Densities of jaçanas in these open areas were at least as great as at Turrialba.

From the preceding evidence we conclude that the density of jaçanas and the small territories at Turrialba are correlated with the relative richness and diversity of the environment. While the occurrence of polyandry in the American Jaçana does not depend on the unusual densities, the high ratio of males to females in the Turrialba breeding population probably does.

A distinct problem connected with simultaneous polyandry is that of paternity. When one female mates with three males in less than 20 minutes as observed in 1963, the probability of a male rearing his own offspring must be reduced. On the other hand the likelihood that a particular male fathers the chicks he later raises is enhanced by the more intense behavioral and temporal relationships of the male and the female. She spends a greater amount of time in the male's territory just before and during the days of oviposition, and the frequency of copulation with that particular male increases substantially during the same period. The frequent solicitations and copulations probably serve at least three functions in addition to in-

seminating the female. First the copulations probably perpetuate the pair bonds throughout the protracted breeding season. Secondly they may allow the birds to test and monitor the receptiveness of one another. Thirdly such multiple interactions may coordinate the reproductive physiology of the birds so that eggs will be available when the male has built a nest and is prepared to care for a new set of eggs. Males who lost a clutch were ready to accept a new clutch within a week. Although copulation stopped during incubation, males whose broods were approaching independence began responding to female solicitations by mounting, and by the time their broods were 5 or 6 weeks old, the males were once again copulating successfully.

The floating substrate the jaçanas exploit is analogous to the shoreline, short grass prairie, and tundra habitats used by other charadriiforms. Suitable marsh habitat is limited in the tropics and has a dispersed patchy distribution. The rapid succession of tropical swamps and marshes simply increases the unpredictability of such habitat over time. Furthermore, as Orians (1969) and others have pointed out, marshes may differ tremendously from one another in their productivity. Productivity may also differ greatly from one part of a marsh to another part. This further adds to the uneven distribution of suitable breeding habitat. The floating vegetation is analogous to temperate grasslands and marshes in being essentially two-dimensional where the resources are limited to a narrow vertical belt. The jaçanas limit their feeding to the surface of the substrate. In the temperate zones, several marsh and grassland dwelling passeriforms have evolved polygyny (Verner and Willson, 1966). In the tropics, with long breeding seasons, the jaçanas have evolved a polyandrous system.

Polyandry appears to be especially adaptive to the problem of patchy food distribution in marshes. The females hold larger territories and are less restricted to them than are the males. Thus, they are better able to take advantage of both spatial and temporal variation in food abundance. They can shift their feeding to an area of more abundant food inside their superterritory or to undefended areas; or if food is scarce in the superterritory or undefended parts of the marsh, they can feed in fields or grasslands.

ACKNOWLEDGMENTS

The initial portion of this work was done while we were research participants in the Seminar in Tropical Biology (N.S.F. Grant 21977, Jenni) and the Organization for Tropical Studies (N.S.F. Grant GE 4705, Collier). Further support to Jenni was provided by N.S.F. Grant GB 21279. Collier was additionally funded by the American Philosophical Society with the cooperation of the Smithsonian Institution and the Gorgas Memorial Hospital for the work in Panama, by the Chapman Memorial Fund of the American Museum of Natural History for work in Mexico, and by the San Diego State College Research Foundation and the Society of the Sigma Xi for recent work in Turrialba.

This study was possible only through the cooperation and support of the staff at the

Instituto Interamericano de Ciencias Agricolas, Turrialba, Costa Rica. We are especially indebted to them for facilities and tolerance during our various tenures at the Institute. Sr. Roger Morales has been extremely helpful. We are also indebted to Mildred E. Mathias, University of California, Los Angeles, for assistance in identifying the flora of the Turrialba pond.

## SUMMARY

American Jaçanas had a polyandrous breeding organization at a small pond near Turrialba, Costa Rica, during July and August, 1963, 1964, 1969, and 1970. The 15 breeding groups studied during the 4 years averaged 2.2 males per female. The numbers of males per female were 4 (one group), 3 (four groups), 2 (eight groups), and 1 (two groups). So far as we know this is the first study in which polyandry has been proved in a population of birds banded for individual identification, and the first unequivocal demonstration of simultaneous polyandry.

The behavioral roles of the sexes are nearly completely reversed. Males establish small territories, build the nest, incubate the eggs, and care for the young alone. Females establish territories that include the contiguous territories of from one to four males. They are aggressive and help their mates repulse territorial intruders. Breeding males average 91 g and are able to repel other males, but not females, which average 161 g.

In all 4 years a resident population of mature-plumaged, nonbreeding birds roosted and fed primarily in parts of the pond unsuitable for nesting territories and on the lawns adjoining the lake. The breeding birds also fed extensively on the lawns, but males that were incubating or caring for very young chicks foraged almost entirely within their territories. Individuals from this resident nonbreeding population occasionally established territories on the pond (one case), displaced breeding males or females and took over their territories and mates (six cases), or replaced an individual that was disabled (one case of two birds replacing one).

Polyandry apparently allows the American Jaçana to produce a maximum number of young on the limited amount of suitable breeding habitat by reducing competition between adults and chicks, thus insuring a maximum amount of food for a large number of chicks. Polyandry can occur only in conjunction with sex role reversal. In the American Jaçana the female has become a large bird that specializes in egg production and in helping her much smaller mate(s) defend their territories. Small male size is probably adaptive because it reduces competition for food with the young and may also allow for smaller male territories. With a smaller biomass of adults harvesting food from the limited breeding habitat, more food is available for the young and a greater reproductive potential can be realized. Polyandry provides all the requisites for successful reproduction in the tropical marsh habitat where these substrate-feeding insectivores breed.

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