THE AUK
A QUARTERLY JOURNAL OF
ORNITHOLOGY

VOL. 106 JANUARY 1989 NO. 1

EXPERIMENTAL INDUCTION OF INFANTICIDE IN FEMALE WATTLED JACANAS

STEPHEN T. EMLEN,[1,2,4] NATALIE J. DEMONG,[1] AND DOUGLAS J. EMLEN[3]

[1]*Section of Neurobiology and Behavior, Division of Biological Sciences, Cornell University, Ithaca, New York 14853 USA,*
[2]*Smithsonian Tropical Research Institute, P.O. Box 2072, Balboa, Republic of Panama, and*
[3]*45 Lone Oak Road, Ithaca, New York, 14850 USA*

ABSTRACT.—We induced infanticide experimentally in a free-living population of Wattled Jacanas (*Jacana jacana*). These tropical shorebirds have a polyandrous mating system and females compete among themselves for breeding opportunities with males. Severe fights occurred between females, leading to takeovers of male mates. Under these circumstances, infanticidal behavior (the killing of young of the previous female) by the replacement female would be adaptive if it led to more rapid reproduction with the usurped male. When opportunities for takeovers were created experimentally (by removal of resident females), replacement females killed or evicted three of four existing broods of chicks and sexually solicited four of five usurped males. These findings strengthen the hypothesis of sexually selected infanticide by extending its applicability to a species in which sex roles are reversed.
Received 5 April 1988, accepted 1 September 1988.

INFANTICIDE refers to the killing of conspecific young. Among certain social carnivores such as lions, (Bertram 1975, Packer and Pusey 1984) and polygynous primates such as langurs (Hrdy 1974, 1977; Hausfater and Hrdy 1984), adult males may forceably "take over" a group of females and young after which they often kill the offspring sired by the previous male owner. Such sexually selected infanticide (Hrdy 1979, Sherman 1981) has been hypothesized to cause a rapid recycling of sexual activity in the females, and thus increase the fitness of the replacement male. The hypothesis of sexually selected infanticide makes specific predictions about the context in which killings will occur (following takeovers), the identity of the perpetrators (replacement males—in polygynous species) and the adaptive gain to the killer (increased reproductive access to mates). We tested these predictions by attempting to experimentally induce infanticidal behavior in the Wattled Jacana (*Jacana jacana*), a polyandrous species in which females compete for access to males.

Jacanas are tropical shorebirds that exhibit marked reverse size dimorphism (females are larger than males) and behavioral sex role reversal (males are the caretakers of the eggs and young) (Jenni and Collier 1972, Osborne and Bourne 1977, Jenni and Betts 1978, Stephens 1984a). Jenni and Collier (1972) and Stephens (1984a) documented that *J. spinosa* in Costa Rica exhibits a polyandrous mating system where females pair with up to four male mates simultaneously. Less rigorous evidence suggests that polyandry occurs in at least three of the world's five other species of jacana as well (Hoffmann 1949, Mathew 1964, Osborne and Bourne 1977, Osborne 1982).

In *J. spinosa*, males perform virtually all parental care duties that include incubation (for 28 days) of the clutch and tend the precocial

[4] Reprint requests should be sent to the first address.

chicks until they reach independence, some 56 days later (Stephens 1984a). Once a male begins incubation of a clutch, he becomes unavailable to care for another clutch for almost three months, assuming the young survive until independence (Jenni and Collier 1972, Stephens 1984a). Competition is expected to be intense among members of the limited sex (females) for access to any available partners of the limiting sex (males). Jenni and Collier (1972) and Stephens (1984a) describe intense fights between resident and intruder females, fights which frequently led to territory (and male) takeovers by the challenger.

When such a takeover occurs, the males are usually caring for eggs or chicks of the former female. Jacanas have a prolonged breeding season and males often rear two or more broods in succession (Jenni and Collier 1972, Osborne and Bourne 1977, Stephens 1984a). Consequently, if a replacement female actively caused the failure of the ongoing nesting attempt of a usurped male, she might cause him to recycle and become ready to accept her clutch of eggs more rapidly. Using this adaptive reasoning, Stephens (1982) predicted that infanticide by replacement female jacanas should occur. He also reported an observation of suspicious egg loss in *J. spinosa* consistent with the hypothesis.

We tested the hypothesis of sexually selected infanticide by attempting to induce it experimentally in the Wattled Jacana.

METHODS

We studied Wattled Jacanas in the Republic of Panama from late April through early June of 1987. Our study site comprised 4 ha of floating vegetation in the Chagres River, near the town of Gamboa. The Chagres River in this area supported a large, dense population of many hundred jacanas. Thirty-one individuals (roughly one third of the birds inhabiting the study site) were captured in bow nets and marked with unique combinations of colored leg bands.

We spent ca. 300 h observing the birds from canoes. We mapped the territorial boundaries of all males and recorded the chronological stage of each nesting attempt. We recorded behavioral interactions between males and females (in particular, which females came to the defense of different males and their chicks) to identify unambiguously the current female mate of each breeding male. Female territories were mapped and found to overlie the male territories. Individual females defended areas that encompassed 1–3 male territories. Sixteen of twenty-eight females (57%) were polyandrous by this definition. The social organization of *J. jacana* at this location was similar to that of *J. spinosa* in Costa Rica.

We attempted to induce infanticide by experimentally removing two breeding females. Observations during 10 days prior to the removals indicated that both were polyandrous, one (YY/GM) had three male mates on her territory (two with chicks), the other (OM/RR) had two male mates (both with chicks). Each female was collected in the hour before dusk and its male mates (and chicks) were watched closely for the following 4–5 days.

RESULTS

REPLACEMENT OF FEMALES

Replacement females were present on the "vacated" territories within 1 h of the following dawn (by the time of our arrival at the study site). Three different females were involved in takeovers; each was a neighbor that expanded its former territory to encompass the area occupied by one or more undefended males (Fig. 1). Two replacement females (called 1 and 2) each usurped 2 males; the third obtained one, but only after fighting with female 2 who initially expanded her range to include all 3 former males of removed female YY/GM. Of the 3 female replacements, two had previously been monogamous; one, biandrous.

INFANTICIDAL BEHAVIOR OF REPLACEMENT FEMALES

Each of the replacement females aggressively attacked the chicks of the former female resident. Three of the four males with chicks vigorously attempted to drive off the new female and to protect their young. Females dominated males, and the final results were the known or presumed deaths of 2 broods of chicks, the permanent driving away of a third, and injury to the fourth (Table 1). The details of the attacks varied according to the age of the dependent young. A description of the behavior of each of the replacement females is presented below.

Female 1.—Resident female OM/RR had on her territory 2 males (A and B), each tending chicks. The young of male A were 35–40 days old. They were 80% of full adult size and were capable of sustained flight. The young of male B were 15–20 days old. They were only 50% of adult size, flightless, and still covered in downy

plumage. At this age the chicks forage in close proximity to the male parent (Jenni and Collier 1972, Jenni and Betts 1978).

On the morning following OM/RR's removal, female 1 occupied the full extent of OM/RR's former territory. She began chasing the 2 young of male A and repeatedly drove them from the area. At first these young returned to small pieces of floating vegetation located on the periphery of the territory. Female 1 consistently harrassed them, forcing them to land in the water and then attacking them when they again became airborne. By mid-morning both young had disappeared. Over the next 2 days, a similarly aged young (the chicks were not marked) was seen nearby on 2 occasions; each time it was driven off by female 1. No young was seen on or adjacent to the territory thereafter. Male A did not intervene during any of the female attacks on his chicks.

Female 1's attacks on male B's 2 chicks were more direct. She flew and ran at them, pecking them on the head, nape and back. During these attacks, male B vigorously interfered. He dove and struck the female with his feet and repeatedly landed between the female and the chicks. We witnessed 19 separate attacks. Each lasted from 30–200 s. Seven of these resulted in the female pinning down a chick and striking it repeatedly and forcefully, pulling out numerous feathers in the process. By mid-morning both chicks were injured; one was bleeding from the head. Later, the female twice picked up a chick, tossed it back down, and left it limp on the ground. Her final attacks forced each chick to swim out into the current of the river, thereby leaving the territory entirely. We followed the chicks for 20 min, until the current had carried them some 170 and 200 m away from the territory. Male B hovered over 1 chick while it was within 6–8 m of the territory boundary; thereafter he made no attempt to maintain contact with either young. We collected one chick; the other was not seen again.

Female 2.—Resident female YY/GM originally had 3 males (C–E) on her territory. Male C had 3 chicks ca. 25–30 days of age. They were two-thirds adult size but could not yet fly. Male E was tending 2 small downy chicks, estimated to be 8–10 days old. Male D was without eggs or young.

By 0745 on the morning following the removal of YY/GM, female 2 had expanded her activities westward to occupy the territories of both males C and D. Unfortunately, our observations were cut short (90 min) because of severe thunderstorms. However, we witnessed two intensive attacks on the 3 young. Each time, male C intervened by giving high intensity dis-

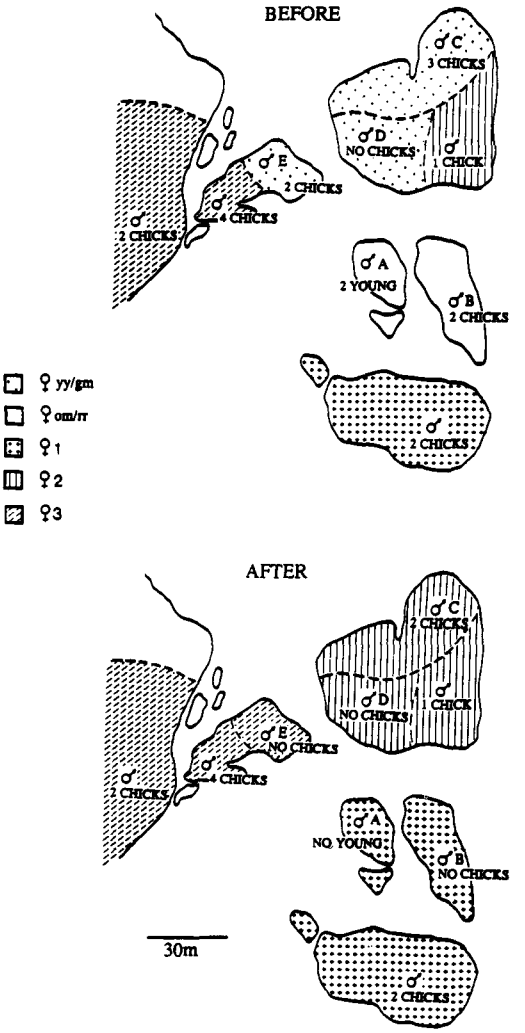

Fig. 1. Before: Map of the territory boundaries of 5 female and 9 male jacanas at the start of observations. Three of the females are polyandrous (OM/RR, YY/GM, and no. 3); two are monogamous. Territories are located on floating mats of vegetation surrounded by open water of the Chagres river. After: Similar map of territory boundaries 2 days after experimental removal of 2 resident females (OM/RR and YY/GM). Note that the 3 remaining females have expanded their territories to encompass all of the undefended areas and to usurp all 5 male mates of former residents. Note also that 7 of the 9 chicks originally being tended by the usurped males have been eliminated.

TABLE 1. Summary of behavioral interactions between resident male and replacement female jacanas following the experimental removal of the original female mate.

Resident male I.D.	Original female I.D.	Replacement female I.D.	Male nesting stage at takeover	Fate of dependent chicks	Male sexual behavior with replacement female
A	OM/RR	1	Tending 2 chicks, aged 35–40 days	Permanently evicted from territory by replacement female 1.	Consorted with, and sexually solicited by, replacement female 1; repeatedly mounted female.
B	OM/RR	1	Tending 2 chicks, aged 15–20 days	Presumed killed. Both seriously injured and chased into the water by replacement female 1 (last seen swimming away from territory).	Consorted with, and sexually solicited by, replacement female 1; repeatedly mounted female.
C	YY/GM	2	Tending 3 chicks, aged 25–30 days	Injured (one possibly killed) by replacement female 2. Four days after removal, 2 chicks still survived.	None
D	YY/GM	2	No eggs or chicks		Consorted with, and sexually solicited by, replacement female 2; repeatedly mounted female
E	YY/GM	2/3	Tending 2 chicks, aged 8–10 days	Killed by replacement female 3. Previously attacked by replacement female 2.	Consorted with, and sexually solicited by, replacement female 3; repeatedly mounted female.

tress calls and counterattacking the female. The following morning, only 2 chicks remained on this territory; one was limping. We cannot be certain of the cause of the disappearance of the missing chick.

On the second day, female 2 attempted to take over the territory of male E. She aggressively attacked E's chicks but was evicted by female 3 (see below). By noon of the second day, female 2 was consorting exclusively with male D (who was without eggs or chicks). She continued to direct sporadic attacks at male C's remaining chicks, but without the previous intensity. When observations were ended 4 days after this takeover, male C's 2 remaining chicks were still alive.

Female 3.—No female intruded onto the territory of male E until the morning of the second day when female 2 flew in and directly attacked E's two small (8–10 day old) chicks. She pecked them repeatedly, pulling out bits of down feathers. Male E responded with cries, dives, and counterattacks on female 2. The resulting commotion attracted the neighboring resident from the west (Fig. 1). This bird (female 3) flew in, and a fight ensued between the 2 females. Female 3 evicted female 2 and took over the territory.

During the following 35 min, female 3 seemed to search for the chicks. She crisscrossed the territory, her head stretched high, and peered down into the thin mat of floating vegetation. This behavior was unlike food searching (the neck typically is not held high during foraging) and female 3 did not consume any food items during this time. Meanwhile, male E performed nearly continuous distraction displays leading away from the location of the chicks. First, he hovered over the female, giving intense distress calls. Next he landed on the side of the female farthest from the hiding chicks and began to walk away, hunched low and with wings drooping. As he got farther from the female, he decreased both the intensity and repetition rate of his calling. Finally, he remained mostly silent and motionless, still hunched low. This sequence was repeated every 2–4 min. Similar distraction behavior in response to intruding females was observed in *J. spinosa* (Stephens 1984b). At no time did female 3 appear to alter

her direction of search or follow the displaying male.

These behaviors ended abruptly when the female spotted the chicks, ran directly to them, and attacked both of them vigorously. During the attack, she struck one chick 8 or 9 times, picked it up by the neck and wings, shook it, and dropped it in the water. Within minutes the chick was dead. During this attack, the male took to the air and repeatedly dove and struck the female. The exchange ended with the female breaking off her attack on the chicks and chasing male E. At this time the second chick was badly injured and unable to maintain its balance while walking. It remained in hiding and was seen only once during the following 4 h. A thorough search of the territory later in the day was unsuccessful. We presume it died from its injuries.

Sexual Behavior of Replacement Females

Each of the 3 replacement females began loosely consorting with one or more of her new males on the day of the takeover. The consortship became tighter on the second day and by the third and fourth days each female performed sexual solicitation displays to a preferred male. Female 1 solicited, and was repeatedly mounted by, both males A and B. Females 2 and 3 solicited and were mounted by males D and E, respectively. Thus all incoming females initiated sexual behavior with the usurped males within 48 h of killing or driving off the males' offspring. Similar rapid solicitation by replacement females was reported for *J. spinosa* (Jenni and Collier 1972, Stephens 1982). Unfortunately, our observations ended 4 and 5 days after the replacements, before new clutches of eggs could be laid. But incoming females in both *J. jacana* and *J. spinosa* are known to lay clutches for new males within 8–10 days of a takeover (Jenni and Collier 1972; Osborne 1982; Stephens 1982, 1984a).

Discussion

Infanticide associated with territory or mate takeover has been reported in two other well-studied bird species and implicated in several others (e.g. Schifferli 1978, Stacey and Edwards 1983, Fujioka 1986, Goldstein et al. 1986, Moller 1987). In Barn Swallows (*Hirundo rustica*), Crook and Shields (1985) describe eight instances in which unpaired males killed (or presumably killed) newly hatched young. In three cases, the male was a replacement that arrived at the nest following the death or disappearance of the original male mate. In the remaining five cases, the male attacked the young of an intact pair. The victimized female later renested with the infanticidal male in four of the eight instances. The behavior was interpreted as an advantageous tactic used occasionally by unpaired males to obtain mating partners (Crook and Shields 1985).

Freed (1986) reported that nesting tropical House Wren (*Troglodytes aedon*) activites were disrupted by usurping individuals in 13% of all breeding attempts. Both males and females committed infanticide in association with territory takeovers. The usurpers were unpaired individuals that frequently succeeded in becoming replacement mates following the failure of the original nesting attempt (76% of males; 50% of females). Freed also believes that infanticide is an adaptive behavior, promoted by limited breeding opportunities for individuals not already part of the breeding population.

We observed infanticide when a new bird took over a territory on which nesting was in progress. When we experimentally removed two resident female Wattled Jacanas from their territories, three neighboring females rapidly expanded into the undefended areas. At the time of the removals, five different males resided on these territories; four of them were tending chicks. Each of the replacement females aggressively attacked the chicks of the resident male, causing injury or death. Within 48 h of the removal of the original females, seven of their nine offspring had been eliminated and three of their four actively breeding male mates had been "relieved" of parental care duties. The replacement females consorted with the usurped males on the day of the takeover, and the males repeatedly mounted the replacement females within three to four days.

According to the hypothesis of sexually selected infanticide, the benefit gained from killing young (or destroying eggs) is increased access to reproductive partners that would otherwise be unavailable (Hrdy 1979, Sherman 1981). In polyandrous jacanas, the males are the limiting sex. A male is not available to incubate a new clutch for a replacement female so long as he is engaged in tending the brood (or clutch)

of a former female. If killing young (or destroying eggs) is to be viewed as an adaptive behavior on the part of a replacement female, it must increase the reproductive "availability" of new male mates.

If the incoming females had not eliminated the chicks of the resident males, only one of the five usurped males (male D) would have been reproductively available. Assuming that the new pairs reproduce together [documented for *J. spinosa* by Jenni and Collier (1972) and Stephens (1984a)] and that at least one chick in each brood being tended at the time of takeover survives to independence, we can calculate the magnitude of the benefit of being infanticidal. A non-infanticidal female must wait until the young tended by the usurped male become independent before she can initiate breeding. An infanticidal female can initiate breeding immediately by removing such young (or eggs, if the male is incubating). To estimate these savings we subtract the ages of the males' broods at the time of takeover from the age of chicks at independence (56 days). The savings are 16–21 days, 36–41 days, and 46–48 days, respectively, for females mating with males A, B, and E. Through infanticide, replacement females cause the taken-over males to recycle and become reproductively available considerably sooner than would otherwise be the case.

Four alternate hypotheses have been proposed to explain infanticidal behavior (see table 1 *in* Hrdy 1979). First, infanticide is a means of exploiting immatures as a food resource. This can be ruled out in the case of jacanas because the perpetrating females made no attempt to consume the killed or injured young. Second, the killing of vulnerable young reduces competition for valuable resources located on the territory. Although we cannot rule this out as a partial explanation, we favor the sexual selection hypothesis because of the previous breeding success of the perpetrators and the speed with which they directed sexual behavior toward the newly usurped males. Third, according to a parental manipulation hypothesis, parents maximize their fitness by eliminating weak or malformed young, thereby concentrating their parental investment in their healthiest offspring. The fact that the perpetrators of infanticidal attacks were take-over females and not the original female breeders is inconsistent with this explanation. Finally, a null hypothesis would predict that infanticide is nonadaptive to the perpetrator. Such behavior is considered abnormal, perhaps caused by unusual local circumstances (such as very high densities, human intervention with the habitat, etc). The fact that infanticidal behavior does appear to be beneficial to those individuals engaging in it argues against this interpretation.

We therefore conclude that Stephens' (1982) original suggestion was correct. Female jacanas practice sexually selected infanticide following the takeover of a male engaged in parental care activities. By so doing, they presumably increase their reproductive success by minimizing the time until they can breed with their newly aquired male.

Our observations on experimentally induced infanticide in jacanas are remarkably similar to reports on naturally occurring infanticide following male takeovers in lions and various species of primates (Hrdy 1974, 1977, 1979; Bertram 1975; Packer and Pusey 1984). In these mammalian species, the mating systems are polygynous and males compete for breeding opportunities with females. In jacanas, the mating system is polyandrous, and females compete for breeding opportunities with males. The context of infanticide, the identity of the perpetrators, and the presumed reproductive benefit to the killer are all in agreement with predictions, and strengthen the generality of the hypothesis of sexually selected infanticide by extending it to a species in which sex roles are reversed.

ACKNOWLEDGMENTS

We thank James Karr and Neal Smith for sponsorship while at the Smithsonian Tropical Research Institute; Donald Jenni and Martin Stephens for helpful advice concerning the fieldwork; and James Davis, Frank and Sarah Follett, Stanley Rand, and Nicholas Smythe for the loan of equipment. The manuscript benefited from comments by James Davis, Lenny Freed, Lewis Oring, William Shields, and Martin Stephens. Financial assistance was provided by the Smithsonian Tropical Research Institute and the National Science Foundation through grant BNS85-17725.

LITERATURE CITED

BERTRAM, B.C.R. 1975. Social factors influencing reproduction in wild lions. J. Zool. (London) 177: 463–482.

CROOK, J. R., & W. M. SHIELDS. 1985. Sexually selected infanticide by adult male Barn Swallows. Anim. Behav. 33: 754–761.

FREED, L. A. 1986. Territory takeover and sexually

selected infanticide in tropical House Wrens. Behav. Ecol. Sociobiol. 19: 197–206.

FUJIOKA, M. 1986. Infanticide by a male parent and by a new female mate in Colonial Egrets. Auk 103: 619-621.

GOLDSTEIN, H., D. EISIKOVITZ, & Y. YOM-TOV. 1986. Infanticide in the Palestine Sunbird. Condor 88: 528–529.

HAUSFATER, G. & S. B. HRDY (Eds.). 1984. Infanticide: comparative and evolutionary perspectives. New York, Aldine.

HOFFMANN, A. 1949. Uber die brutpflege des polyandrischen Wasserfasans, *Hydrophasianus chirurgus*. Zool. Jarhb. 78: 367–403.

HRDY, S. B. 1974. Male-male competition and infanticide among Langurs (*Presbitis entellus*) of Abu, Rajahsthan. Folia Primatologica 22: 19–58.

———. 1977. Infanticide as a primate reproductive strategy. Am. Sci. 65: 40–49.

———. 1979. Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. Ethol. Sociobiol. 1: 13–40.

JENNI, D. A., AND B. J. BETTS. 1978. Sex differences in nest construction, incubation, and parental care in the polyandrous American Jacana (*Jacana spinosa*). Anim. Behav. 26: 207-218.

———, & G. COLLIER. 1972. Polyandry in the American Jacana (*Jacana spinosa*). Auk 89: 743–765.

MATHEW, D. N. 1964. Observations on the breeding habits of the Bronze-winged Jacana (*Metopidius indicus*). J. Bombay Nat. Hist. Soc. 61: 295–302.

MOLLER, A. P. 1987. Advantages and disadvantages of coloniality in the swallow, *Hirundo rustica*. Anim. Behav. 35: 819–832.

OSBORNE, D. R. 1982. Replacement nesting and polyandry in the Wattled Jacana. Wilson Bull. 94: 206–208.

———, & G. B. BOURNE. 1977. Breeding behavior and food habits of the Wattled Jacana. Condor 79: 98–105.

PACKER, C., & A. E. PUSEY. 1984. Infanticide in carnivores. Pp. 31–42 *in* Infanticide: comparative and evolutionary perspectives (G. Hausfater and S. B. Hrdy, Eds.). New York, Aldine.

SCHIFFERLI, L. 1978. Die Rolle des Mannchens wahrend der Bebrutung der Eier beim Hausperling *Passer domesticus*. Ornithol. Beob. 75: 44–47.

SHERMAN, P. W. 1981. Reproductive competition and infanticide in Belding's Ground Squirrels and other animals. Pp. 311–331 *in* Natural selection and social behavior (R. D. Alexander and D. Tinkle, Eds.). New York, Chiron.

STACEY, P. B., & T. C. EDWARDS JR. 1983. Possible cases of infanticide by immigrant females in a group-breeding bird. Auk 100: 731–733.

STEPHENS, M. L. 1982. Mate takeover and possible infanticide by a female Northern Jacana *Jacana spinosa*. Anim. Behav. 30: 1253–1254.

———. 1984a. Maternal care and polyandry in the Northern Jacana, *Jacana spinosa*. Ph.D. thesis. Chicago, Illinois, Univ. Chicago.

——— 1984b. Intraspecific distraction displays of the polyandrous Northern Jacana, *Jacana spinosa*. Ibis 126: 70–72.