Division of labour in parental care behaviour of a sex-role-reversed shorebird, the wattled jacana

STEPHEN T. EMLEN*† & PETER H. WREGE*†

*Department of Neurobiology and Behavior, Cornell University
†Smithsonian Tropical Research Institute, Balboa, Republic of Panama

Jacanas represent the extreme in avian sex-role reversal. We studied the division of labour between the two sexes in parental care of the eggs and chicks in wattled jacanas, *Jacana jacana*, in the Republic of Panama. Males were the sole incubators of the eggs (515 clutches). Males were also the sole caretakers of chicks for 97% of broods ($N = 252$). Caretaking activities included continuous close association with the young, leading them to foraging locations, brooding them during cold temperatures and rain, and maintaining nearly constant vigilance against threats of predation. Although females were also observed to perform all of these direct chick care behaviours, they did so very rarely (3% of broods) and only when the male was unavailable to provide such care himself. This happened either when females laid new clutches for males that were still tending dependent chicks, or when predators killed males, leaving broods defenceless and untended. The only regular contribution to chick care by females was providing defence against predators. The male was usually the first parent to detect a predator, but he recruited the female to join him in confronting threats that he could not deter alone. We conclude that, although males perform the overwhelming majority of parental care in wattled jacanas, females provide critical backup support. By displaying parental behaviours facultatively, only when the male is unable to provide them adequately himself, female wattled jacanas are able to enhance the survival of their eggs and young while typically expending only minutes per day in such efforts.

2004 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd.

Parental investment refers to anything done for an offspring that increases its chance of survival while decreasing the parents' ability to produce additional offspring (Trivers 1972). It includes the cost of producing the gamete plus any additional time or effort expended on behalf of the offspring until it becomes independent. In the vast majority of animal species, parental investment by females exceeds that by males. In birds, for example, females produce extremely large and costly eggs, and when there is an asymmetry in egg care behaviour by the two sexes, it is usually the female that performs the majority (or all) of the incubation (Lack 1968; Clutton-Brock 1991).

Differences in the relative parental investment of the two sexes often cause females to be unavailable for future reproductive events longer than males. The potential reproductive rate of males then exceeds that of females (Clutton-Brock & Vincent 1991). Females and the parental investment they provide become valuable 'resources' for males, and males compete among themselves for access to females (Williams 1966; Trivers 1972; Andersson 1994).

In a small minority of animal species, the asymmetry of relative parental investment is reversed. Among birds, females always invest more in gametes than males, but males of some species expend much more time and effort in the care of eggs and young than do females. Such sex-role reversal in the provisioning of parental care behaviour has been reported in about 35 species of birds in 13 families (Jenni 1974; Ridley 1978; Oring 1982, 1985).

One of these avian families, Jacanidae, comprises eight species of shorebirds, all of which have adapted to live on mats of aquatic vegetation in freshwater marshes and swamps throughout the tropics. Seven of the eight species

Correspondence and present address: S. T. Emlen, Department of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853, U.S.A. (email: ste1@cornell.edu). P. H. Wrege is at the Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY 14853, U.S.A.

of jacana show nearly complete sex-role reversal. Females lay extremely small eggs relative to their body size (Ross 1979), thus reducing the costliness of egg production. Males appear to be the sole incubators of eggs and to provide the majority of care for the dependent young (Jenni 1974, 1996). As would be predicted, the potential reproductive rate of females greatly exceeds that of males (Butchart 2000; Emlen & Wrege 2004) and females compete among themselves for access to males and the attendant parental care that males provide. Females are also much larger than males in all sex-role-reversed jacanas, with female mass being 148–183% that of males (reviewed in Emlen & Wrege 2004). In six of these species, females form pair bonds with multiple males, a mating system known as simultaneous polyandry (Jenni 1996). Males in such associations share their female with other males, termed 'comates'.

In this paper, we quantify the roles of male and female wattled jacanas, *Jacana jacana*, in providing parental care to their eggs and young. The research was part of a broad, 7-year study of the behavioural ecology of the species. We confirm that males are the sole providers of direct care for all clutches and for the overwhelming majority of broods. However, we also document that females are fully capable of showing the full suite of chick care behaviours under rare but predictable circumstances. Females also play a regular role in predator defence of both the eggs and young. We conclude that females play an important role in supplementing the parental care activities of the male. We speculate that the reason why division of labour is not more complete in jacanas is that females are able to contribute significantly to nest and chick survival without significantly compromising their ability to engage in other activities.

METHODS

Study Area

We studied the parental behaviour of wattled jacanas at a study site on the Chagres River, 2.5 km northwest of the town of Gamboa, in the Republic of Panama. The area is part of the Soberania National Park, which lies within a zone of semideciduous lowland rain forest. At our study site, the river was approximately 0.9 km wide; it supported extensive mats of floating aquatic vegetation on which many hundreds of wattled jacanas resided. The Chagres River is a permanent body of water and jacanas bred on it during all months of the year. The river runs into, and provides the main water source for, the Panama Canal.

Jacanas established territories, constructed their nest platforms and reared their young on a floating vegetative habitat that consisted primarily of three species: hydrilla, *Hydrilla verticillata*, water hyacinth, *Eickhornia crassipes*, and water lettuce, *Pistia stratiotes*. Resident jacanas from the study site spent virtually all of their time within the confines of their defended territories and, to our knowledge, never ventured ashore. The habitat was essentially two-dimensional and afforded great visibility, both to the birds and to human observers. Hyacinth extended less than 1 m above the water surface, whereas the dominant water lettuce grew only 10–15 cm in height.

Study Population

We focused our attention on a 13-ha area (approximately 325 × 400 m) located in the centre of the Chagres River. The site was part of a larger area of contiguous habitat that stretched over 0.6 km east–west and 0.3 km north–south. On a monthly basis, an average of 18 resident females (range 4–29), 30 resident males (range 9–40), and a variable-sized population of nonresident 'floaters' occupied the site. The network of territories of our study birds merged imperceptibly into neighbouring territories of less-studied individuals. No part of the study area was closer than 0.2 km to the nearest shore and water depth typically varied between 4 and 9 m.

Data were obtained during seven field seasons, typically beginning in January and averaging 7.5 months (1990: March–June; 1991 and 1993: January–June; 1992: February–July; 1994 and 1995: January–December; 1996: February–June). Depending on the time of year, the research team varied from one to six persons, with effort concentrated between February and June.

Capture and Marking

We attempted to capture all resident jacanas, including chicks and juveniles, as well as many floaters, on the study area. We did so using a variety of techniques, including the use of mist nets, walk-in traps and playbacks of 'comfort' calls to chicks. By the end of each field season, an average of 78% of all resident females and 90% of all resident males had been banded. Overall, a total of 150 females, 311 males and 172 juveniles were captured, measured and had blood samples collected. Each bird was fitted with a unique combination of one to three colour leg bands plus a numbered aluminium band. All bands were placed above the tarsal–metatarsal joint to increase visibility.

Nest Checks

We monitored 515 nests, 342 (66%) of which were found before or during egg laying. Nests were checked every 2 days throughout incubation until the day of hatch. Broods of chicks were checked every 4 or 5 days until 25 days of age, and less frequently thereafter.

Behavioural Observations of Mating System and Parental Care

We obtained behavioural data using focal, scan and ad libitum techniques (Altmann 1974). Each resident female was observed at least twice weekly, for 2 or more hours, to confirm her number of mates and to gauge reproductive activity. A female was considered to be paired with a male when she met four criteria: (1) she consistently foraged with the male; (2) she defended most or all

of the male's territory against other females; (3) she responded to the 'rally' calls of the male by flying to the male's location; and (4) she solicited the male for copulations. A female was considered to be polyandrous when she met the four criteria with two or more males simultaneously.

To quantify the role of the two sexes in incubation, we conducted 38 scan samples at 17 nests. At 5-min intervals, for a total of 57 h, we recorded the location of the female and male relative to their nests. Incubation constancy was calculated as the percentage of scans during which either bird was at the nest site. Additionally, we recorded the sex of the incubating bird present during regular (alternate day) checks of the contents of all nests ($N > 2500$ visits).

To quantify the roles of male and female in nest and chick defence, we conducted focal samples on 15 territories for a total of 45 h. The identity of each intruder (purple gallinule, *Porphyrula martinica*, common gallinule, *Gallinula chloropus*, female jacana or male jacana) onto the territory was recorded, as was the behavioural response of the resident pair of jacanas. From these data we calculated the frequency of intrusions by nest and chick predators, the responses of both male and female jacanas to such predators, and the success of any antipredator defences. Differences between the sexes in the probability of being the first to detect and respond to an intruder were examined, for each intruder type, by chi-square tests. Differences in the responses of each sex to different types of intruder (whether first responders recruited their mates for joint defence) were tested by logistic regression analysis (single degree of freedom orthogonal contrasts) incorporating band number as a factor to control for unequal numbers of observations of different individuals. We first compared responses to male conspecific intruders against those to all types of predators (gallinules and female jacanas), combined. We then omitted male conspecific intruders and compared responses to gallinules against those to intruding female conspecifics.

Finally, many ad libitum observations were made during the course of daily research activities on the study site. Behavioural observations were concentrated in the morning hours from first light until 1100 hours and again in the afternoon from 1500 hours until dark. Observations were made from canoes, using binoculars and spotting telescopes. A total of 137 person-months of observations were compiled during the study.

Statistical Tests

The SAS statistical software system, version 8.1 and SYSTAT version 5.2 were used for statistical analyses. Mean values are reported $\pm$SE, unless otherwise indicated. Experiment-wise type I error rates were held at the 0.05 level.

RESULTS

Males as the Sole Caretakers of Eggs

Parental care in wattled jacanas was typified by marked division of labour and extreme sex-role reversal. Only the male incubated the clutch, which was almost invariably four eggs. Of 342 clutches found before laying was complete, 339 had a final clutch size of four eggs whereas three had three eggs. The incubation interval (measured from the laying of the last egg until hatch) was 25 days.

Females were never seen to incubate. In 57 h of scan sampling of 17 females paired to incubating males, no female ever ventured closer than 8 m to an active nest. Furthermore, in none of more than 2500 checks of nest contents was the female ever observed to incubate or to be at the nest site. On more than 30 occasions, we continued incubation observations until dark and, in every instance, the male was the member of the pair on the nest. Females roosted solitarily, elsewhere on the territory.

On nine occasions, incubating males disappeared (presumably predated), leaving clutches untended. In no instance was a female observed to incubate, or even to defend, these unguarded nests, and the clutches disappeared by the following day.

Male incubation constancy was extremely low. Males with active nests spent, on average, 41% of their time at the nest. This included time spent both incubating and shading the eggs.

Despite this low incubation constancy, males lost weight while tending the eggs. We captured and weighed five individual males both early and late during their incubation. Each of the five males lost weight as incubation progressed, with an average weight loss of 0.3 g per day (Table 1). Assuming a constant rate of loss, this would represent a loss of 7.5 g over the 25-day incubation period, or 8% of average male body mass.

Hatching usually occurred synchronously, with all four eggs typically hatching within a few hours of one another. As each chick emerged, the male removed the eggshells, carrying and dropping them several metres from the nest area.

Males as the Primary Providers of Chick Care

The precocial chicks were mobile within hours of hatching and were actively led away from the nest by the male. It was the male that set the direction of travel and determined the location of foraging. He brooded the chicks under his wings in the cold and rain. The male occasionally led very young chicks back to the nest platform at night and brooded them there for several nights following hatching. During their first few weeks of life, the chicks remained within a few metres of the male. As they became older, they wandered more widely, although they continued to forage as a loose unit and to follow and respond to the male's vocalizations and other behaviours until they were about 2 months old.

The male maintained vigilance over the dependent chicks at all times and communicated to them when conditions merited alert or alarm. To minor disturbances and distant predators, he uttered repetitive 'kek-kek' (alert) calls and led the chicks in a direction away from the danger. If a potential predator (or human) approached more closely, he gave a staccato rattle (danger) call to which the chicks responded by running short distances

Table 1. Weight loss of male wattled jacanas during incubation

Male ID	Date	Day of incubation	Weight (g)	Interval between weighings (days)	Actual weight change (g)	%Weight loss*
496	5 April 2002	6	92			
	24 April 1992	25	90	19	−2	2.9
630	18 February 1993	2	95			
	10 March 1993	22	94	20	−1	1.3
669	13 March 1993	2	89			
	4 April 1993	24	83	22	−6	7.7
670	21 March 1993	5	100			
	9 April 1993	23	90	18	−10	13.9
704	27 April 1993	4	96			
	18 May 1993	25	85	21	−11	13.6
491†	13 May 1991	NA	80			
	10 June 1991	NA	86	28	+6	

NA = nonapplicable.
*Percentage of weight loss was calculated over the full 25-day incubation period.
†Bird 491 was a nonbreeding male and served as a control.

and then either crouching and freezing in the vegetation or sinking under the water. In the latter situation, the chicks could remain immobile under the water with only their bills extending above water for periods as long as 25 min (see also Bosque & Herrera 1999). The male signalled when the danger had passed by giving a soft, repetitive, clucking (comfort) call to which the chicks responded by reappearing and following him once again.

Chicks remained in the care of the male until they were capable of flight. This occurred at 8–10 weeks of age. We used the attainment of flight as our criterion for defining chick independence (the end of parental care). Young birds generally left their natal territories within 1–2 weeks of flying. Occasionally, juveniles were tolerated on the natal territory for up to 8 months.

The time required for a male to successfully rear a clutch from receipt of eggs to independence of the brood was thus nearly 3 months (4 days of receiving eggs, 25 days of incubation and 50–60 days of chick care).

Females as Backup Providers of Chick Care

Female jacanas typically did not associate at all with dependent chicks. This pattern occurred for 235 of 242 observed broods (97%). On very rare occasions, however, a female provided full and active care for her young. Such instances occurred in only seven (3%) of the observed broods. These seven exceptions occurred under two very specific circumstances: first, when a male was simultaneously tending both a brood of young and a clutch of eggs, and second, when predation upon a male with chicks left a brood defenceless and untended.

We observed 17 cases where a female laid a clutch of eggs for a male before the young from his previous brood had reached independence (Table 2). In none of these 17 cases did the female have another, 'unoccupied', mate available to receive the clutch of eggs. Thus, the males that received these clutches were, in essence, attempting to perform 'double duty', alternating their activities between incubating a clutch of eggs and tending and protecting

a mobile brood of chicks. In four of these instances, the female provided direct care to the chicks and thereby freed the male to spend more time incubating the clutch. These females foraged with the chicks, brooded them during the morning cold and afternoon rain showers, and alerted them to impending threats (e.g. the approach of purple gallinules and common gallinules).

We also observed five cases where males were predated while caring for broods of dependent young. In each of the three cases where the chicks did not disappear along with the male, the female mate took over full care of the chicks following the male's death and continued to provide active care until the young either became independent or were lost to predation. One female provided such care for a full month. During this time, she showed the entire suite of species-specific parental care behaviours, including leading, brooding, defending and giving of the 'danger' and 'comfort' calls. Only after her two young reached independence 28 days after the death of her mate did she accept a new male mate onto the territory.

We examined the influence of age and number of chicks on a female's decision to provide or not to provide active chick care. We used the sample of 12 males performing 'double duty' for which we had sufficient data (>3 observation periods) plus the sample of three broods for which the male parent disappeared, leaving chicks untended. When broods were partitioned into two groups based on chick age (young broods: <35 days; old broods: >35 days) at the time the male received the new clutch or was predated, females were significantly more likely to provide active care to the young broods (five of six young broods received care versus two of nine old broods; $\chi_1^2 = 5.40$, $P < 0.025$). In a logistic regression analysis incorporating both age and number of young, age was nearly significant in predicting active care by the female (Wald's $\chi_1^2 = 3.57$, $P = 0.06$), whereas number of young was not (Wald's $\chi_1^2 = 0.39$, $P = 0.53$). Because the sample size was small, the corresponding power of the regression analysis was weak, and this result should be considered as suggestive rather than definitive.

Table 2. Behaviour of female wattled jacanas when the male was incubating a clutch of eggs while still caring for dependent young

Female ID	Male ID	Date (month/year)	Number of young	21–25	26–30	31–35	36–40	41–45	46–50	Female parental care
259	546	4/1994	3	X						Yes
136	475	4/1990	1	X						Unknown
148	467	4/1990	1	X						Unknown
22	814	8/1995	3	X						Yes
284	602	9/1996	3	X						No
20	795	10/1996	3	X						Yes
180	496	5/1992	1			X				Unknown
2606	735	10/1996	3			X				Unknown
247	665	5/1994	2				X			No
393	667	5/1994	4				X			No
284	602	9/1996	3				X			No
919	879	9/1996	4				X			No
138	535	2/1991	3					X		Yes
284	841	7/1995	2					X		No
292	602	8/1995	3					X		No
179	602	7/1994	1						X	Unknown
20	795	8/1996	1						X	No

The age of young column header spans: Age of young (days)

The Role of Both Sexes in Predator Defence

Predation threats to jacana eggs or chicks were frequent. During 45 h of focal observations on 15 nesting pairs, we recorded 280 territorial intrusions by potential predators, or an average of just more than six intrusions per hour. Both male and female breeders played major roles in defending the nest and chicks. We partitioned the focal data according to whether the threat was from a hetero-specific predator (purple and common gallinules), a con-specific predator (intruding female) or neither (male jacana). Female jacanas were considered potential preda-tors because they routinely destroy both eggs and small young when they successfully intrude and take over a male from another female (Emlen et al. 1989). Male jacanas constitute no known threat to eggs and young, but are a threat to the territory ownership of the resident male.

They were included for purposes of comparison. We asked (1) which parent first responded to the threat, (2) whether the male called to the female for assistance in the defence, and (3) whether the female, if called upon, joined the male in attacking the source of the threat.

Male jacanas were significantly more likely than females to be the first to respond to an intruder on the territory (Table 3). This was true regardless of the type of intruder (heterospecific intruder: $\chi^2_1 = 10.9$; female jacana in-truder: $\chi^2_1 = 29.4$; male jacana intruder: $\chi^2_1 = 328.8$; all $P < 0.0001$). More than two-thirds (44/62) of potential heterospecific predators were first detected by the breed-ing male. In roughly one-half (20/44) of these cases the female played no role and the male, by himself, deflected the threat away from the nest, led the chicks away from the threat, or distracted the potential predator while the young ran to safety. The results were similar for intruding

Table 3. Differences between male and female responses to various predation threats. Data are from 45 h of focal sampling on 15 nesting pairs of jacanas

	Heterospecific predators*	Female jacana intruders	Male jacana intruders
Sex of first responder			
Male	44 (71%)	149 (68%)	548 (86%)
Female	18 (29%)	69 (32%)	90 (14%)
Total	62	218	638
Did male give rally call?			
Yes	24 (55%)	103 (69%)	31 (6%)
No	20 (45%)	46 (31%)	517 (94%)
Total	44	149	548
Did the female join in predator defence?			
Yes	21 (88%)	74 (72%)	16 (52%)
No	3 (12%)	29 (28%)	15 (48%)
Total	24	103	31

Column group header: Type of threat

*Heterospecific predators included purple gallinules, *Porphyrula martinica*, and common gallinules, *Gallinula chloropus*.

female jacanas. Again, two-thirds (149/218) of the first sightings were by males, and in roughly one-third (46/149) of these instances, the male quietly led the chicks away from the potential danger.

The female was the first responder to the remaining predator intrusions. When females responded to conspecific females, they almost always attacked the intruder. When they responded to gallinules, they more often blocked the approach to, or deflected the intruder from, the location of the nest or young. This behaviour by the female provided the male with time to lead the chicks to safety.

Often, when the male was the first responder, he alerted the female to the presence of the intruder and, together, they confronted the source of the threat (95 of 193 instances). This occurred primarily when a purple or common gallinule or a trespassing female jacana came very close to the nest or the location where the chicks were hiding. In these cases, the male gave a shrill, high-pitched rally call to which the female typically responded by flying immediately to the male's location. Responses to intruding female jacanas did not differ from those to heterospecific predators. In both cases, males were equally likely to call to the female (Wald's $\chi_1^2 = 1.90$, NS) and, if alerted, the female was equally likely to join the male in defending against both intruder types (Wald's $\chi_1^2 = 2.65$, NS).

The form of the joint defence depended on the type of predator. Against gallinules, both male and female actively attacked the threatening individual, running at it with wings outstretched and striking it repeatedly from the air with their feet. In contrast, only the female actively attacked an intruding female jacana. Males maintained a close presence, but restricted their activities to running at the female with outstretched wings or facing the intruder in a crouched position with wings outstretched and head and neck feathers erected.

Conspecific male intruders were treated very differently. The male resident was the sole responder in 81% (517/638) of such instances (Table 3). Separate orthogonal contrasts (see Methods) indicated, in comparison to other types of intruders, that (1) resident males were significantly more likely to be first responders to intrusions by male jacanas (Wald's $\chi_1^2 = 196.7$, $P < 0.0001$), and (2) males were significantly less likely to alert their females to such intrusions (Wald's $\chi_1^2 = 31.3$, $P < 0.0001$). In only 2.5% (16/638) of incursions by trespassing males did the breeding pair show a joint defence in chasing the male intruder from the territory. In contrast, joint defence occurred in 34% of intrusions by gallinules or trespassing female jacanas (21 of 62, and 74 of 218 cases, respectively).

Most defensive attacks against potential predators were successful. Of the 280 observed predator detections, including the 95 more severe cases where joint defence occurred, only four resulted in actual loss of eggs or chick(s).

DISCUSSION

The Role of the Male Parent

Male wattled jacanas performed the overwhelming majority of parental care. Incubation lasted 25 days and young became independent (i.e. they could fly) at 50–60 days of age. A successful breeding cycle thus occupied nearly 3 months of a male's time.

Males were the sole incubators of the eggs. In the course of 57 h of scan sampling, and in more than 2500 nest checks, no female was ever observed to incubate eggs. On nine occasions when a male disappeared (presumably predated) while incubating eggs, in no instance did the remaining female incubate the untended eggs. We suggest that incubation is no longer present in the females' physiological or behavioural repertoire. Incubation has not been confirmed in females of any of the sexually dimorphic jacana species (pheasant-tailed jacana, *Hydrophasianus chirurgus*: Hoffmann 1949; northern jacana, *J. spinosa*: Jenni & Collier 1972; Jenni & Betts 1978; African jacana, *Actophilornis africanus*: Tarboton 1993; bronze-winged jacana, *Metopidius indicus*: Butchart 2000; comb-crested jacana, *Irediparra gallinacea*: Mace 2000).

The cost of incubation to the male is presumably low. The high solar radiation that typifies the nesting habitat of jacanas relieves the male of much of the incubation load (Jenni 1974; Tarboton 1995; Butchart 2000; Mace 2000). Scan samples indicated that males tending clutches spent only 41% of the daylight hours at the nest site, either incubating eggs or shading them from the sun. Osborne & Bourne (1977), in a study of *J. jacana* in Suriname, reported a value of approximately 60%. Similarly low estimates of incubation constancy have been found in the other sex-role-reversed jacana species (44% for northern jacana, Betts & Jenni 1991; 47% for pheasant-tailed jacana, Hoffman 1949; 53% for African jacana, Tarboton 1993; 56% for bronze-winged jacana, Butchart 2000; 54% for comb-crested jacana, Mace 2000).

Incubation in wattled jacanas was not without some costs, however. Based on a sample of five males that were recaptured both early and late in incubation, we estimated that males lose approximately 8% of their body weight during their 25 days of incubating. This is consistent with detailed time budget studies of wattled jacanas by Osborne & Bourne (1977) who reported that incubating males spend approximately 50% less time foraging than do nonbreeding males. Similar reductions in time spent foraging by incubating males have been reported for northern jacana (Betts & Jenni 1991) and comb-crested jacana (Mace 2000).

Males were also the primary caretakers of the chicks. Of 242 broods monitored during this study, females were only observed to provide direct chick care to seven (3%). Chicks thus spent the overwhelming majority of their time under the direct care of the male parent. During the first 3–4 weeks after hatching, the chicks followed the male closely. It was the male who determined the chicks' foraging and resting locations. He brooded them under his wings in the cold of early morning and during Panama's frequent afternoon rainstorms. He also provided nearly constant vigilance, sending the chicks scurrying for cover at the threat of danger, and calling them back to him when the threat had passed.

As the chicks became older, the male continued to perform all of these parental behaviours, and the male and chicks still moved as a unit, but the distance the chicks

foraged from the male increased. Similar patterns of male care have been reported for all of the sexually dimorphic jacanas (Hoffmann 1949; Jenni & Collier 1972; Tarboton 1992; Butchart 2000; Mace 2000). Male parental care in wattled jacanas continued until the chicks were able to fly, which occurred at approximately 50–60 days of age. Young were tolerated by the male parent after this age, but they typically left the territory and joined the mobile population of floaters a few weeks after attaining flight.

We assumed that the cost of chick care in wattled jacanas is low because the young are precocial and able to forage for themselves within hours of hatching. There is no provisioning of young jacanas in the sense of adults bringing food to the young. Rather, the male leads the chicks to different areas of the territory where they feed themselves. Time budget studies of northern jacanas (Betts & Jenni 1991) show that, although males do reduce their time spent foraging when caring for chicks, the reduction is minor because they are able to forage for themselves while simultaneously tending the young.

Chick care in wattled jacanas is nondepreciable (Wittenberger 1979; Walters 1982) in the sense that the cost of providing care for multiple chicks is not significantly greater than the cost of providing care for a single chick. This is true whether leading chicks to favoured foraging sites, brooding them in inclement weather, communicating danger or comfort calls, or even driving off a potential predator. Thus, whereas efficient chick care by a male jacana is incompatible with simultaneous incubation of a second clutch, it is not incompatible with simultaneous foraging and vigilance for himself.

The Role of the Female Parent

In marked contrast to the incubation behaviour and nearly continuous chick care behaviour provided by the male, female wattled jacanas spent minimal time in parental activities. Females never incubated eggs and spent, on average, only minutes per day in chick-related behaviours. The importance of this female care, however, was much greater than its minimal quantity might suggest. As such, female parental care represents a previously underappreciated aspect of jacana breeding biology.

There were two ways in which female wattled jacanas directly contributed to clutch and chick survival. First, on very rare instances, females displayed the same suite of chick care behaviours as those regularly shown by males. And second, females routinely provided essential predator protection.

Active female chick care only occurred under two highly specific but predictable conditions: (1) when a male mate was tending chicks while simultaneously incubating a clutch of eggs, and (2) when a parental male disappeared permanently, leaving a brood untended.

Although extremely rare in their occurrence, these observations confirm that all of the basic chick care behaviours of leading, brooding and providing vigilance are present in the behavioural repertoire of female wattled jacanas. However, females only displayed active chick care when their mates were temporarily or permanently unavailable, and even then, only under circumstances when the chicks were likely to die if no care was provided at all. Thus, females were more likely to care for chicks of a deceased male than for a male doing 'double duty', and were significantly more likely to care for younger (presumably more vulnerable) chicks than for older ones (Table 2). We hypothesize that female parental care in wattled jacanas is conditionally expressed only in circumstances when the benefit of providing such care is exceptionally high.

Among jacanas, active chick care by females is not unique to wattled jacanas. Rare observations of brooding by females have been reported for northern jacanas (Jenni & Betts 1978; Betts & Jenni 1991) and pheasant-tailed jacanas (Hoffmann 1949), but not for African jacanas (Tarboton 1992) or comb-crested jacanas (Mace 2000, personal communication). In their study of northern jacanas, Jenni & Betts (1978; Betts & Jenni 1991) noted that females brooded and accompanied chicks only after times of unusually heavy rain when, they speculated, food availability was low. They also reported one instance where a female tended chicks of an incubating male doing 'double duty'. These observations are consistent with active female care being both rare and conditional upon the male's inability to provide sufficient parental care alone.

Mutual Dependency of the Pair in Predator Defence

Female wattled jacanas played a regular and essential role in defence against nest and chick predators. This was only possible, however, because of the territorial and parental behaviours of the male. By being territorial, the male was vigilant to intruders, and by tending the nest and young, he was vigilant to predation threats. Not surprisingly, males were the first to detect and respond to greater than two-thirds of predator intrusions (by purple gallinules, common gallinules and conspecific females). In roughly one half of such cases, the male, unaided by the female, was able to deflect the predator from the nest vicinity or to lead the chicks away to safety.

However, male jacanas depended on their female mates to back them up in cases where the predation threat escalated beyond their ability to deal with it alone. Under such circumstances, the male alerted his female to the danger by giving a shrill, high-pitched vocalization that usually brought her rapidly to his side. The pair, together, then confronted the predator.

Such joint defence was the response to one-third of all intrusions by potential predators (gallinules or female conspecifics). Because of her much larger body size (wattled jacana females and males, on average, weigh 129 g and 88 g, respectively; Emlen & Wrege 2004), the female was presumably more effective than the male in deterring predators. Stephens (1984) confirmed this assumption for the northern jacana. He reported that purple gallinules were driven furthest when attacked by pairs, less far by females alone, and least far by attacking lone males.

Wattled jacanas thus have a two-tiered system of predator defence. The male typically is the first responder but, if needed, he can count on the female for backup support. Similar behaviours, whereby males recruit their females to jointly attack predators, have been reported for all of the sex-role-reversed jacanas (Hoffmann 1949; Jenni & Collier 1972; Jenni & Betts 1978; Stephens 1984; Tarboton 1992; Butchart et al. 1999; Mace 2000).

Responses to intruding male jacanas were very different. Females were significantly less likely both to be the first to respond to, and to join in defending against, a male trespasser. This is consistent with the fact that male jacanas do not constitute a known threat to the female or to the eggs or chicks, but only to the territorial ownership status of the resident male.

Several features of the jacanas' habitat facilitated the ability of females to provide backup support in predator defence even though they frequently foraged far from the vicinity of the nest or young. First, the floating mats of vegetation on which jacana territories were established seldom exceeded 1 m in height, thus allowing the birds easy visibility over large areas. Second, male territories were small, averaging only 40 m in diameter (unpublished data). Third, the expansiveness of the vegetation meant that male territories often abutted one another in a checkerboard matrix. Both the high density and the two-dimensional aspect of male territories increased the effectiveness of predator detection and defence. A jacana typically could see directly across the entirety of its own territory and those of several immediate neighbours. Thus, when a male alerted his female to a serious threat, the female often had line-of-sight access to information that enabled her to locate, assess and rapidly respond to that threat.

Jacana sex roles in predator defence were thus mutually interdependent. The female relied on her mate to alert her to the presence of most intrusion threats, and the male relied on his female to back him up when predation threats escalated. This mutual dependency made it possible for the female to play a critically important role in increasing the survival probability of her eggs and chicks without having to spend more than minutes per day engaging in such behaviours.

This two-tiered system of predator defence was highly effective. Of the 280 intrusions by potential predators, only four resulted in the loss of eggs or chicks. Yet, paradoxically, despite this high success in predator deterrence, rates of nest loss were high in our study population. Fully one-half of all clutches were lost prior to hatching and two-thirds of hatchlings disappeared prior to reaching independence (unpublished data). The most common cause of such loss was predation.

We suggest that the reason for the high predation losses was not an inability of parental pairs to successfully defend against those predators that were detected early enough for deterrence to be effective. Rather, we suspect that most losses occurred when lapses in vigilance made it possible for predators to gain close access to the nest or chicks without being detected. Stephens (1984) similarly suggested that successful predation by purple gallinules only occurs on northern jacanas when the eggs or chicks are temporarily unattended by the male parent.

Parental care in wattled jacanas is thus typified by a marked division of labour, but with two unusual twists. First, although females no longer incubate eggs, they retain the ability to perform all aspects of chick care. They display such chick care, however, only under exceptionally rare circumstances when their mates are physically unable to perform these behaviours themselves. Second, although almost completely emancipated from all direct care of eggs or young, females nevertheless play a critically important role in predator defence. By relying on the male to provide vigilance for the eggs and young, yet responding when alerted to threats by the male, female wattled jacanas reap the benefits of a system of male uniparental care that can be facultatively transformed into one of biparental defence when required.

References

Altmann, J. 1974. Observational study of behaviour: sampling methods. *Behaviour*, **49**, 227–267.

Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.

Betts, B. J. & Jenni, D. A. 1991. Time budgets and the adaptiveness of polyandry in northern jacanas. *Wilson Bulletin*, **103**, 578–597.

Bosque, C. & Herrera, E. A. 1999. 'Snorkling' by the chicks of the wattled jacana. *Wilson Bulletin*, **111**, 262–265.

Butchart, S. H. M. 2000. Population structure and breeding system of the sex-role reversed, polyandrous bronze-winged jacana, *Metopidius indicus*. *Ibis*, **142**, 93–102.

Butchart, S. H. M., Seddon, N. & Ekstrom, J. M. M. 1999. Yelling for sex: harem males compete for female access in bronze-winged jacanas. *Animal Behaviour*, **57**, 637–646.

Clutton-Brock, T. H. 1991. *The Evolution of Parental Care*. Princeton, New Jersey: Princeton University Press.

Clutton-Brock, T. H. & Vincent, A. C. J. 1991. Potential reproductive rates and the operation of sexual selection. *Quarterly Review of Biology*, **67**, 437–456.

Emlen, S. T. & Wrege, P. H. 2004. Size dimorphism, intrasexual competition and sexual selection in wattled jacanas (Jacana jacana), a sex-role reversed shorebird in Panama. *Auk*, **121**, 391–403.

Emlen, S. T., Demong, N. J. & Emlen, D. J. 1989. Experimental induction of infanticide in female wattled jacanas. *Auk*, **106**, 1–7.

Hoffmann, A. 1949. Uber die Brutpflege des polyandreschen Wasserfans, *Hydrophasianus chirurgus*. *Zoologische Jahrbucher-Abteilung für Systematik Okologie*, **78**, 368–403.

Jenni, D. A. 1974. Evolution of polyandry in birds. *American Zoologist*, **14**, 129–144.

Jenni, D. A. 1996. Family Jacanidae (jacanas). In: *Handbook of the Birds of the World. Vol. 3* (Ed. by J. del Hoyo, A. Elliott & J. Saratal), pp. 276–291. Barcelona: Lynx Edicions.

Jenni, D. A. & Betts, B. J. 1978. Sex differences in nest construction, incubation, and parental behaviour in the polyandrous American jacana (*Jacana spinosa*). *Animal Behaviour*, **26**, 207–218.

Jenni, D. A. & Collier, G. 1972. Polyandry in the American jacana (*Jacana spinosa*). *Auk*, **89**, 743–765.

Lack, D. 1968. *Ecological Adaptations for Breeding in Birds*. London: Methuen.

Mace, T. R. 2000. Time budget and pair-bond dynamics in the comb-crested jacana, *Irediparra gallinacea*: a test of hypotheses. *Emu*, **100**, 31–41.

Oring, L. W. 1982. Avian mating systems. In: *Avian Biology. Vol. 6* (Ed. by D. S. Farner, J. R. King & K. C. Parkes), pp. 1–92. New York: Academic Press.

Oring, L. W. 1985. Avian polyandry. In: *Current Ornithology. Vol. 3* (Ed. by R. F. Johnston), pp. 309–351. New York: Plenum.

Osborne, D. R. & Bourne, G. R. 1977. Breeding behavior and food habits of the wattled jacana. *Condor*, **79**, 98–105.

Ridley, M. W. 1978. Paternal care. *Animal Behaviour*, **26**, 904–932.

Ross, H. A. 1979. Multiple clutches and shorebird egg and body weight. *American Naturalist*, **113**, 618–622.

Stephens, M. L. 1984. Interspecific aggressive behavior of the polyandrous northern jacana (*Jacana spinosa*). *Auk*, **101**, 508–518.

Tarboton, W. R. 1992. Aspects of the breeding biology of the African jacana. *Ostrich*, **63**, 141–157.

Tarboton, W. R. 1993. Incubation behaviour of the African jacana. *South African Journal of Zoology*, **28**, 32–39.

Tarboton, W. R. 1995. Polyandry in the African jacana: the roles of male dominance and rate of clutch loss. *Ostrich*, **66**, 49–60.

Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man 1871–1971* (Ed. by B. Campbell), pp. 136–179. Chicago: Aldine.

Walters, J. R. 1982. Parental behavior in lapwings (Charadriidae) and its relationship with clutch sizes and mating systems. *Evolution*, **36**, 1030–1040.

Williams, G. C. 1966. *Adaptation and Natural Selection*. Princeton, New Jersey: Princeton University Press.

Wittenberger, J. F. 1979. The evolution of mating systems in birds and mammals. In: *Handbook of Behavioral Neurobiology. Vol. 3 Social Behavior and Communication* (Ed by P. Maler & J. Vendenberg), pp. 271–349. New York: Plenum.