

## Population structure and breeding system of the sex-role reversed, polyandrous Bronze-winged Jacana *Metopidius indicus*

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Bronze-winged Jacanas *Metopidius indicus* studied from 1995 to 1997 at Vembanur lake in southern India had a consistent sex-ratio bias of about 1.9 males per female. Only half of males and females defended territories and thus could breed; the remaining birds were non-resident floaters. Floaters were lighter and younger than residents. Bronze-winged Jacanas were sex-role reversed: females were 60.3% heavier and behaviourally dominant to males, which carried out all the incubation and chick care. The ratio of potential reproductive rates was skewed to females by about 4:1, indicating that strongly reversed sexual selection probably operates in this species. Each year about 60% of resident females were monogamous and 40% were polyandrous with up to four males. Over 60% of resident males were in polyandrous groups. Heavier females had larger harems and produced more clutches per season. The peak breeding season was late July to early September. Over 90% of clutches were depredated before hatching. Nearly half of clutches of artificial eggs were attacked by rodents, the rest by birds. Mean clutch mass was only 16.8% of female mass, giving this species one of the greatest capacities of any shorebird for laying multiple clutches. High predation rates and low energetic costs of parental care may have been important factors influencing the evolution of sex-role reversal and polyandry in jacanas.

To develop and test ideas on the evolution of social systems, a better understanding of polyandry is required (Jenni 1974). A detailed understanding of the ecology of polyandrous species is a prerequisite for comprehending why such a breeding system occurs and is maintained in some populations, and for formulating hypotheses about how such mating patterns may have evolved. Here I present such data on the polyandrous Bronze-winged Jacana *Metopidius indicus*.

The Jacanidae, a circumtropical family of shorebirds (Charadriiformes), is an ideal group in which to study polyandry, as there is evidence that seven out of eight species show highly developed sex-role reversal and polyandry (Jenni 1996). Jacanas have characteristic long legs and elongated toes and claws that spread their weight over a large area and allow them to inhabit floating and emergent aquatic vegetation in freshwater wetlands (Jenni 1996). Jacanas show more extreme

reversed sexual size dimorphism than any other group of birds or mammals (Jenni 1996). Males carry out all incubation and nearly all care (e.g. brooding and guarding) of the precocial chicks. Polyandry has been convincingly demonstrated and studied in Wattled Jacana *Jacana jacana* (Osborne & Bourne 1977, Emlen *et al.* 1989), Northern Jacana *J. spinosa* (Jenni & Collier 1972) and African Jacana *Actophilornis africana* (Tarboton 1992a). Females simultaneously defend the exclusive territories of several males, mating and providing clutches for each of them. Polyandry has also been inferred, but poorly studied, in Pheasant-tailed Jacana *Hydrophasianus chirurgus* (Hoffman 1949, 1950, Thong-aree *et al.* 1995), Comb-crested Jacana *Irediparra gallinacea* (Garnett 1985, Jenni 1996), Madagascar Jacana *Actophilornis albinucha* (Jenni 1996) and Bronze-winged Jacana *Metopidius indicus* (Mathew 1964).

The Bronze-winged Jacana is mainly sedentary and occurs in India through Southeast Asia to Indochina, south Sumatra and west Java (Hayman *et al.* 1986).

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There has only been one previous study of its mating system: Mathew (1964) observed a single unmarked group consisting of one female and two males for one season in Bombay, India. The female provided one male with a clutch, and then mated with the second male and produced three clutches for him that were all depredated. Only the males were observed incubating and caring for the chicks, and males appeared to be behaviourally subordinate to the female. His description of the breeding behaviour therefore suggested that the birds were sex-role reversed and polyandrous.

I present the first detailed data on the population structure, mating patterns and breeding behaviour of a population of Bronze-winged Jacanas at Vembanur lake in southern India, confirm the occurrence of sex-role reversal and polyandry in these birds, and speculate on the factors favouring the evolution of such a breeding system.

## STUDY AREA

I studied a population of jacanas at a freshwater lake called Vembanur, located at 9°11'N 77°23'E in Kanyakumari district, in the state of Tamil Nadu, at the southern tip of India. Set at an altitude of 30 m, the lake is surrounded by paddyfields, coconut and banana plantations, and other small lakes. The surface area of the lake was about 18 ha, of which 85% (in 1995) to 98% (in 1997) was covered in floating and rooted vegetation including: Lotus *Nelumbium speciosum*, Water Lily *Nymphaea lotus* and *Limnanthemum* sp., Water Hyacinth *Eichhornia crassipes*, pond weed *Hydrilla* spp., Water Lettuce *Pistia stratiotes*, sedge *Scirpus articulatus* and grass (Graminae). Temperatures averaged 25–35°C, and mean annual rainfall was about 1000 mm, with monsoonal peaks in June and October. The water level of the lake and thus the density of the vegetation was influenced both by rainfall and by artificial control using sluice gates to let out water for irrigation.

## METHODS

I carried out fieldwork at Vembanur lake for three breeding seasons between mid-May and mid-October 1995–97. I captured jacanas in 10-cm mesh nylon mist-nets erected above the water from canoes. I gave each bird an individual combination of two to four coloured plastic leg rings, and took the following biometrics: mass (to 1 g), bill-length (to 0.05 mm from the tip to the proximal edge of the nares), shield height (from the distal edge of the nares to the highest part of

the fleshy shield), maximum shield width, wing-length (flattened chord to 0.5 mm using a stopped ruler), tarsus (to 0.5 mm using a stopped ruler), tail (to 1 mm), toe span (maximum distance to 0.5 mm between the tips of the claws of the splayed middle and rear toes). I calculated an index for the area covered by the spread toes of both feet as  $2\pi r^2$  ( $r = 0.5 \times \text{toe span}$ ). I calculated an index of body condition as an estimate of mass relative to body size, using  $(\text{mass}/\text{tarsus}^3) \times 10^4$ .

I estimated the numbers, sex, age and status of all jacanas on the lake each month. Males and females showed no plumage dimorphism, but birds in the hand could be distinguished unambiguously by mass and bill-length. Unringed birds were sexed by estimating their size relative to ringed birds of known sex, and by noting unequivocal sex-specific calls and sexual behaviour (Butchart 1998, Butchart *et al.* 1999a). I aged jacanas by plumage characteristics (Hayman *et al.* 1986). I defined each bird's status as resident, floater or dependent chick. Residents foraged consistently in the same restricted area and persistently defended this territory from conspecifics of the same sex. Floaters did not show consistent territorial behaviour, and usually ranged widely over the lake to forage. A female often paired with several males, termed co-mates, who comprised her harem. Pairing was defined as when the female consistently foraged together with the male, defended a large proportion (usually all) of his territory, responded to his calls by approaching him, and persistently interacted with him sexually.

I measured the lake water level daily, and each month I mapped all the aquatic vegetation by drawing the shape and location of patches of vegetation with reference to a permanent grid of flagpoles spaced at 50-m intervals across the lake. I defined territory boundaries by drawing maximum convex polygons around at least 90 points marked on a map showing a resident's position every 15 min or every time it moved 5 m or more.

Throughout each season, I attempted to follow all pairs and polyandrous groups of jacanas on the lake, determining group composition and recording breeding attempts. I carried out focal watches on each pair or group at least every few days from the raised bank of the lake, or from a canoe, from dawn (about 06:45 h) until at least 09:30 h and from 15:30 h to dusk (about 19:00 h). To determine breeding status I recorded the contexts and details of sexual interactions, calls, nesting behaviour, intrusions by conspecifics and the responses of territory holders.

I recorded all nesting attempts, located clutches and

followed their fate. As breeding activities were quite conspicuous, I believe that the large majority of clutches were successfully located during the egg-laying period, but high rates of predation (see below) mean that a few may have been missed. Nests were checked daily without approaching them using a 30× telescope. During focal watches I recorded the time spent incubating to the nearest 30 s by continuous sampling, and the distance to the nearest chick (<5 m, 5–20 m, or >20 m) for the male and for the female when she was on the territory.

To investigate clutch predation, I created a series of artificial nests, each with four plasticene model eggs painted with acrylic paints to resemble jacana eggs (cf. Bensch & Hasselquist 1994). I set out the artificial clutches during the breeding season on realistic nest platforms which were checked daily from a canoe, and I removed the eggs when I found marks on the plasticene from a predation attempt. To catch depredated eggs that had been pushed off the nest platform, I placed a 1-m<sup>2</sup> rigid-framed nylon net underneath the floating vegetation. I measured the width of the bird pecks and rodent bite marks found on depredated eggs and compared these to the widths of marks made by known potential predators. I obtained a series of peck impressions for at least six individuals of 11 potential avian egg predators by gently pressing into plasticene the beak of a bird captured in a mist-net, or from the collections at the Natural History Museum (N.H.M., Tring) and the University Museum of Zoology (U.M.Z., Cambridge). Using rodents captured around the lake in rat traps, and skulls from two museum collections (N.H.M., London and U.M.Z., Cambridge), I obtained a similar series of measurements of rodent incisors for ten rodent species found in the area which were potential egg predators.

I used two-tailed non-parametric statistical tests corrected for ties where appropriate. For comparisons

between the morphology of males and females I used two-tailed unpaired *t*-tests with Bonferroni corrections where appropriate. Means are presented  $\pm$  1 se.

## RESULTS AND DISCUSSION

### Population structure and sex ratio

I captured and ringed a total of 96 jacanas; the proportion of the population ringed each year was 75.6% (1995), 72.1% (1996) and 90.3% (1997). The population in late August (the peak of breeding) increased by 5% from 1995 to 1996, and by 44% between 1996 and 1997 (Table 1). This may have resulted from an increase in the proportion of the lake covered in vegetation (85.0% in 1995, 87.2% in 1996 and 97.9% in 1997). In particular, low water levels between 1996 and 1997 permitted the spread of rooted lotus plants, increasing the area of breeding habitat by 50%.

Over the three years, the mean proportion of floaters was  $50.5 \pm 3.9\%$ . This proportion did not vary significantly between years ( $\chi^2_2 = 1.06$ , ns), nor did it differ significantly between sexes (males:  $53.9 \pm 3.1\%$ , females:  $42.9 \pm 4.1\%$ ,  $\chi^2_1 = 0.443$ , ns). The floater population included a small number of independent juveniles and immatures in transitional plumage, which comprised  $16.4 \pm 1.0\%$  of the floaters over the three years. Floaters did not form a cohesive flock, but usually foraged in those areas of habitat that were not defended by residents. They frequently attempted to intrude onto residents' territories, but being subordinate to residents they were usually successfully chased out of territories.

The mean percentage survival between seasons for adults (both sexes) was  $63.5 \pm 4.2\%$ , based on resightings of ringed birds. Eight males which were sighted in more than one year changed status between seasons: five floaters settled as residents, and three residents lost

**Table 1.** Bronze-winged Jacana population size and composition at Vembanur, 1995–97. Data were taken from population estimates in late August each year.

Year	Males		Females		Total population	Sex ratio (M/F)		
	Res.	Flo.	Res.	Flo.		Res.	Flo.	Total
1995	14	13	9	5	41	1.55	2.60	1.93
1996	12	17	8	6	43	1.50	2.83	2.07
1997	18	22	11	11	62	1.64	2.00	1.82
Mean	14.7	17.3	9.3	7.3	48.7	1.56	2.48	1.94
se	0.82	1.63	0.41	0.41	0.82	0.02	0.10	0.06

Res, residents; Flo, floaters.

their territories and became floaters. No females changed status between seasons.

The sex ratio of the population was estimated in two ways. First the population estimates at the peak of breeding gave a mean sex ratio for the three years of  $1.94 \pm 0.06$  males per female (Table 1). This ratio differed significantly from parity in each of the three years (1995:  $\chi^2_1 = 4.12$ ,  $P < 0.05$ , 1996:  $\chi^2_1 = 5.23$ ,  $P < 0.05$ , 1997:  $\chi^2_1 = 5.23$ ,  $P < 0.05$ ). Secondly the total number of birds captured in mist-nets (58 males and 38 females) gives a sex ratio of 1.52 males per female, which is also skewed significantly ( $\chi^2_1 = 4.17$ ,  $P < 0.05$ ). The sex ratio for residents, floaters and all birds combined did not vary significantly between years (residents:  $\chi^2_2 = 0.022$ , ns; floaters:  $\chi^2_2 = 0.384$ , ns; all birds:  $\chi^2_2 = 0.097$ , ns). Each year the sex ratio of floaters was significantly male-biased ( $\chi^2_2 = 12.48$ ,  $P < 0.01$ ), but the sex ratio of residents was not significantly different from parity ( $\chi^2_2 = 3.58$ , ns). This may be simply due to the small sample sizes, because the sex ratios of residents and floaters did not differ significantly in any of the three years (1995:  $\chi^2_2 = 0.582$ , ns; 1996:  $\chi^2_2 = 0.945$ , ns; 1997:  $\chi^2_2 = 0.142$ , ns). The number of independent juveniles and immatures which were captured in mist-nets (11 males and 4 females), gives a sex ratio of 2.75 males per female, which is non-significant ( $\chi^2_1 = 0.142$ , ns), but the sample size is small.

If the apparent male bias in the sex ratio of immatures is real, this suggests that it may be present at the egg stage, or it may result from differential hatch rates or chick survival. The larger size of adult females is likely to be a consequence of faster growth rates in female chicks. Greater food demands by the young of the larger sex in sexually size-dimorphic vertebrates generally result in greater mortality rates in that sex when food availability is reduced (Clutton-Brock *et al.*

1985). However, I have no data on food availability to assess whether resources might have been limiting. In Wattled Jacanas, there were no significant differences in tarsus length between male and female chicks aged 30–40 days (P.H. Wrege and S.T. Emlen, pers. comm.), but this species is less sexually dimorphic than the Bronze-winged Jacana.

Greater female mortality might also be predicted from comparisons of the mass/wing-length and mass/foot area ratios, which are significantly less favourable for females (*t*-tests, Table 2). This suggests that females may be more limited in their choice of foraging habitat (because they cannot walk on less supportive floating vegetation), and that females may have greater energetic costs of flying. Tarboton (1992a) invoked this explanation for male-biased sex ratios in African Jacanas, and my data show that it is also plausible for Bronze-winged Jacanas. However, the relevance of this idea is difficult to assess without more data on how the sex ratio bias arises and at what age.

Jenni and Collier (1972) presented data on a population of Northern Jacanas in Costa Rica giving an overall adult sex ratio of 1.31 males per female. Osborne (1982) reported a sex ratio of 1.79 males per female in Wattled Jacanas trapped in Guyana. Tarboton (1992a) estimated the sex ratio of a population of African Jacanas to be about two males per female (1.40 to 2.26 males per female). Thus in all four jacana species for which data are available, there is a consistent pattern of male-biased population sex ratios. Whichever mechanism is responsible for producing this bias, it seems to apply to populations over a wide geographical area.

## Morphology

Adult females were significantly larger than adult

**Table 2.** Mean  $\pm$  se (and range) of biometrics for adult male and female jacanas. Data are from 43 males and 25 females including both residents and floaters.

	Males	Females	<i>P</i>
Mass (g)	176.2 $\pm$ 1.68 (147–202)	282.4 $\pm$ 5.22 (226–354)	< 0.0001
Bill (mm)	22.5 $\pm$ 0.96 (21.6–23.8)	25.1 $\pm$ 0.15 (23.9–27.3)	< 0.0001
Shield height (mm)	20.9 $\pm$ 0.17 (17.5–23.3)	24.1 $\pm$ 0.34 (17.8–27.4)	< 0.0001
Shield width (mm)	10.7 $\pm$ 0.18 (7.8–13.4)	11.3 $\pm$ 0.42 (6.1–14.0)	ns
Wing (mm)	162 $\pm$ 0.46 (154–168)	189 $\pm$ 1.03 (164–190)	< 0.0001
Tarsus (mm)	70.2 $\pm$ 0.36 (65.5–76.0)	78.7 $\pm$ 0.60 (72.5–84.5)	< 0.0001
Tail (mm)	45.5 $\pm$ 0.47 (41–55)	51.2 $\pm$ 0.73 (41–59)	< 0.0001
Toe span (mm)	194 $\pm$ 3.62 (182–222)	215 $\pm$ 5.55 (200–233)	0.0071
Mass/wing-length	1.086 $\pm$ 0.010	1.506 $\pm$ 0.024	< 0.0001
Mass/foot area	0.0029 $\pm$ 0.00009	0.0036 $\pm$ 0.0002	0.0051

*P*-values are from unpaired *t*-tests.

**Table 3.** Mean  $\pm$  se of mass, body condition index and shield size of resident and adult floater Bronze-winged Jacanas.

		Residents	Floaters	P
Males	Mass (g)	179 $\pm$ 2.3	171 $\pm$ 2.5	0.031
	Body condition	5.06 $\pm$ 0.10	4.99 $\pm$ 0.10	ns
	Shield height (mm)	21.2 $\pm$ 0.23	20.1 $\pm$ 0.30	0.0040
	Shield width (mm)	11.1 $\pm$ 0.22	10.0 $\pm$ 0.33	0.010
Females	Mass (g)	293 $\pm$ 6.9	266 $\pm$ 7.6	0.024
	Body condition	6.19 $\pm$ 0.21	5.23 $\pm$ 0.22	0.0046
	Shield height (mm)	24.5 $\pm$ 0.31	23.6 $\pm$ 0.55	ns
	Shield width (mm)	11.5 $\pm$ 0.34	11.1 $\pm$ 0.67	ns

Residents: 23 males, 14 females; Floaters: 28 males, 12 females. *P*-values are from unpaired *t*-tests.

males for nearly all measurements (*t*-tests, Table 2), and there was no overlap between males and females for mass and bill-length. On average, females were 60.3% heavier than males. The only other published data on the mass of Bronze-winged Jacana refer to ten unsexed individuals with a mean mass of 154.6 g (Johnsgard 1981). The range was 94–210 g and therefore presumably included some immatures.

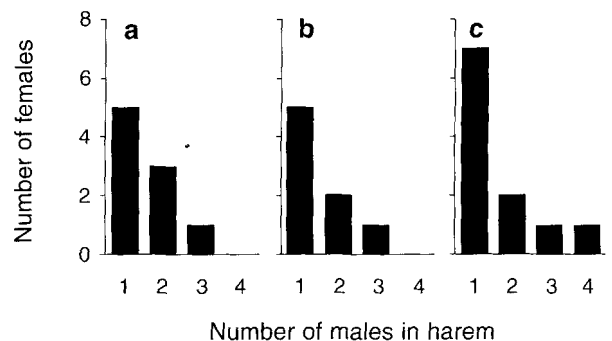
Female residents were significantly heavier than adult female floaters and they had a significantly higher index of body condition (Table 3). Male residents were significantly heavier than adult male floaters, and had significantly larger shields (Table 3). Harem size was significantly correlated positively with female mass (using each female as a single data point with her maximum harem size achieved, Spearman rank correlation:  $r_s = 0.64$ ,  $n = 14$ ,  $P = 0.021$ ). There was no significant correlation between male mass and harem size ( $r_s = 0.20$ ,  $n = 23$ , ns). There was no evidence for assortative mating: female mass did not correlate significantly with the mass of the heaviest male in the harem, nor with mean mass of all males in the harem (Spearman rank correlations; heaviest male  $r_s = -0.046$ ,  $n = 12$ , ns; mean males  $r_s = -0.081$ ,  $n = 12$ , ns). Female body mass was significantly correlated positively with the number of clutches produced each season ( $r_s = 0.74$ ,  $n = 8$ ,  $P = 0.047$ ), and over the three-year period ( $r_s = 0.85$ ,  $n = 8$ ,  $P = 0.025$ ), but there were no significant correlations between male mass and the number of clutches received each season or over the three years (Spearman rank correlations:  $n = 13$ ).

### Mating system

Females paired with up to four males simultaneously. The mean harem size for all females over the three seasons was  $1.5 \pm 0.18$  males ( $n = 21$ , using the largest harem size achieved by each female), and ranged from  $1.5 \pm 0.27$  males in 1996 to  $1.6 \pm 0.31$  males in 1997

(Fig. 1). Hence the degree of polyandry was fairly consistent between years. This contrasts with the situation for a population of African Jacanas in South Africa (Tarboton 1995) where the degree of polyandry varied widely within and between seasons as a result of variation in habitat availability and quality. The habitat at Vembanur and thus the pattern of territories were more stable (Butchart *et al.* 1999b), so population turnover was lower and the composition of breeding groups was less variable. The proportion of resident females which were polyandrous averaged  $39.4 \pm 2.50\%$  over the three years. For resident males, the mean proportion which were in polyandrous groups was  $61.2 \pm 1.73\%$ .

Five females were resident in two seasons, and one female held a harem in all three years. Harem size increased for three of these birds, remained equal for two, and decreased for one. Nine males were resident for more than one year (seven for all three years). Again there was no consistent pattern of changes in harem size: harem size increased between seasons for three males, remained the same for four, and decreased for two. Harem sizes changed within seasons because of changes in the vegetation that altered the availa-



**Figure 1.** Frequency of different-sized harems held by female Bronze-winged Jacanas at the peak of breeding (late August) 1995–97. (a) 1995; (b) 1996; (c) 1997.

bility of breeding habitat, and because of females taking over males from neighbouring females. Through the study, three females increased their harem sizes during a season, and three ended seasons with fewer males than at the start.

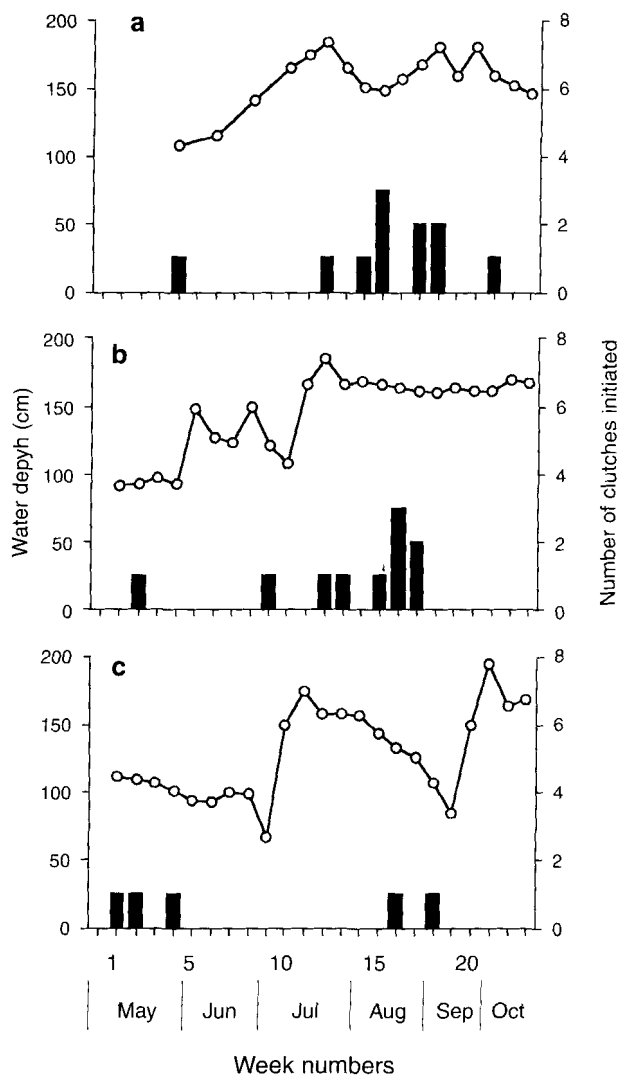
Resident male and female jacanas defended all-purpose territories which were almost exclusive within the sexes, and each female territory overlapped one to four male territories. Polyandrous females spent time on the territories of each their male mates in turn, and typically copulated with all available males before laying each clutch (Butchart in press). However, insufficient clutches survived to hatching (see below) to allow determination of paternity.

### Nesting behaviour

Males built one to five small (15–20 cm diameter), crudely constructed nesting platforms from aquatic vegetation (commonly *Pistia*, *Nymphoides*, *Hydrilla*, and *Eichhornia*). Females also carried out platform building behaviour in the days immediately prior to laying. Both sexes almost invariably flew or walked to a platform before soliciting copulations, and sexual behaviour was usually preceded or followed by platform building by the male or female.

Most clutches (77%,  $n = 26$ ) were initiated between late July and early September (Fig. 2), although the earliest and latest dates were 14 May and 25 September respectively. Mathew (1964) reported Bronze-winged Jacana clutches initiated on approximately 14 August, 27 August and 10 September in Bombay, and Ali and Ripley (1969) reported the breeding season for this species to be June to September. My data support this, but point to a peak of breeding in August. However, observations of a few juveniles and immatures that must have hatched from clutches initiated in April indicate that breeding may occur at low frequencies at other times of year at Vembanur. In the 1997 season, fewer clutches were discovered (five versus 11 in 1995 and ten in 1996), and this was presumed to have been a response to lower and fluctuating water levels in 1997 (Fig. 2) resulting from low rainfall and human management of the rate of inflow to the lake.

All eggs were laid between 07:25 h and 10:13 h. Mean ( $\pm$  se) clutch size was  $3.8 \pm 0.1$  eggs. Of 16 complete clutches, three (18.8%) contained three eggs, and the remainder (80.2%) had four eggs. Mean clutch mass was  $50.6 \pm 0.61$  g (using egg mass on the morning of laying from six complete clutches). Mean clutch mass as a percentage of female mass (measured



**Figure 2.** Weekly water level at Vembanur lake (circles), and the number of Bronze-winged Jacana clutches initiated each week between May and October 1995–97 (bars). (a) 1995; (b) 1996; (c) 1997. Week 1, 1–7 May; week 2, 8–14 May etc. to week 24, 9–15 October.

at the beginning of the season) was  $16.8 \pm 0.72\%$  ( $n = 6$  clutches/females). This compares to 15.3% for African Jacana and 21.3–27.0% for the five other species of jacanas which lay four-egg clutches (using unmatched data, i.e. mean clutch mass/mean female mass; Tarboton 1992b). Thus, Bronze-winged and African Jacanas lay proportionally the lightest clutches of all the jacanas, and the family Jacanidae has the lowest clutch mass: female mass ratios of all Charadriiformes (Ross 1979). These two species would therefore seem to have the greatest capacity of all shorebirds for laying multiple clutches (Tarboton 1992a, 1992b). The low rate of clutch survival of



jacanas (Jenni 1996) combined with a relatively high chick survival rate (Tarboton 1992b) and long tropical breeding seasons mean that laying multiple clutches of small eggs is likely to be more adaptive than laying fewer clutches of larger eggs.

### Egg predation

Of the jacana clutches located during the laying period where the fate was accurately known, 94.4% ( $n = 18$ ) were completely depredated before hatching. Eight of these were only partly depredated initially (surviving for  $7.3 \pm 1.7$  days before any eggs were lost), but the remaining eggs disappeared before hatching. Two further clutches survived to hatching but were not found at the laying stage (both were laid very early in the season).

Artificial clutches of plasticene eggs were also depredated at a high rate (all 30 were depredated within 13 days), and they survived for significantly less time until initial predation ( $3.4 \pm 0.5$  days) than real clutches (Mann–Whitney test:  $U = 161$ ,  $n = 30$  artificial nests, 18 real nests,  $P = 0.010$ ). This suggests that nest defence by adults may have reduced predation of real nests, or that the artificial nests may have been more easily detected by predators. For 24 clutches, I obtained evidence of the identity of the predator from marks (pecks and bites) left in the plasticene. Half (50.0%) were depredated by birds, 45.8% by rodents, and one clutch (4.2%) had marks and striations on one egg presumed to have resulted from an attack by a small turtle (perhaps *Lissemys punctata*).

To refine the identification, the width of at least six marks from each of seven clutches that had been pecked by avian predators were compared with measurements taken from 11 potential predator species. Mean ( $\pm$  se) widths of peck marks on the eggs ranged from  $1.42 \pm 0.72$  mm to  $2.1 \pm 0.06$  mm. Six species of potential predators had peck measurements that were not significantly different (using Mann–Whitney tests) from the marks on at least one of these clutches: Grey Heron *Ardea cinerea*, Purple Heron *A. purpurea*, Night Heron *Nycticorax nycticorax*, Moorhen *Gallinula chloropus*, Pheasant-tailed Jacana *Hydrophasianus chirurgus* and male Bronze-winged Jacana. Of these species, only Purple and Night Herons were sufficiently common to explain plausibly the frequency of egg predation. However, as the pecks of resident male Bronze-winged Jacanas also did not differ significantly from the marks on most artificial clutches, it is possible that jacanas identified the artificial eggs as those of conspecifics, and attacked

clutches found on their territory (jacanas are unlikely to be natural egg predators: intruders were never seen near nests during 131 h nest watches).

The widths of rodent bite marks on each of eight artificial clutches ranged from  $2.79 \pm 0.05$  mm to  $3.93 \pm 0.08$  mm. Two species of potential predators had bite measurements which were not significantly different (using Mann–Whitney tests) from the marks on at least one of these clutches: Indian Mole Rat *Bandicota bengalensis* and Brown Rat *Rattus norvegicus*. In 20 trap-nights using rat traps set out on the lake bank, I caught six rodents, all Black Rat *R. rattus*. This species had bite marks which fell within the range of those on the artificial nests, but were significantly smaller (Mann–Whitney tests). Thus, Indian Mole Rat is a strong candidate, but the evidence is inconclusive. Rodent predation of clutches has also been reported for Pheasant-tailed Jacanas (Thong-aree *et al.* 1995).

These rodents are primarily terrestrial, so nests located nearer to the lake shore might have been at greater risk of rodent predation. However, there was no evidence for this effect from the artificial clutches (Spearman rank correlation between the number of days surviving until initial predation and the distance to the lake shore, for rat-depredated clutches only:  $r_s = 0.21$ ,  $n = 11$ ,  $P = 0.50$ ), or the real nests ( $r_s = 0.11$ ,  $n = 19$ ,  $P = 0.65$ ).

### Parental care

Males incubated  $56.0 \pm 3.0\%$  of the time after the clutch was completed ( $n = 8$  males, mean = 21.9 h focal watches per male, range = 11.9–70.3 h). They incubated less during the egg-laying period:  $2.3 \pm 1.25\%$  on the day the first egg was laid, and  $24.1 \pm 11.9\%$  by the final day of egg-laying. The estimates may be slightly biased, because data came from the cooler hours of the day (two males observed between 09:30 h and 15:30 h incubated for  $38.2 \pm 13.8\%$  of the time). Less incubation may be required during the warmer hours, but more shading may be needed (Tarboton 1993). These incubation levels compare with 49% for Northern Jacanas in Costa Rica (Jenni & Collier 1972) and 53% for African Jacanas in South Africa (Tarboton 1993). Such low levels of incubation are probably the result of solar incubation reducing the requirement for body heat to keep the eggs warm (Tarboton 1995). Females only visited the nest during the egg-laying period and spent  $2.4 \pm 0.5\%$  of the time on the nest during this period. I never observed females incubating after the clutch was completed ( $n = 6$  females, 12 clutches, mean = 21.9 h focal watches

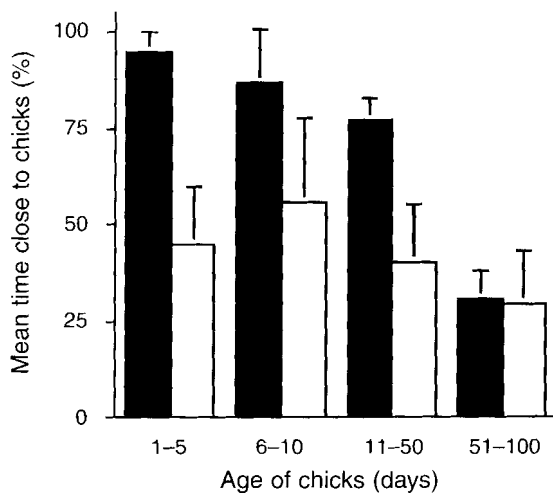


Figure 3. Percentage time that male (■) and female (□) Bronze-winged Jacanas spent <5 m from the nearest chick, for four age-classes of chicks ( $N = 5$  pairs). For polyandrous females, I used the total time spent on the male's territory, excluding time spent on other males' territories. Bars show means with standard errors.

per female, range = 11.9–70.3 h). The incubation period (from the date the first egg was laid to the day before the chicks hatched) was 29 days for two clutches for which accurate data were available.

Males guarded chicks very closely during the first seven weeks, and spent much more time close to them than females did (Fig. 3), but the sample sizes are inadequate to test this. Males brooded the chicks for up to 60% of the time during the first five days after hatching, but only rarely after 4–6 weeks. Females were never seen to brood the chicks but, given the small sample sizes, I may have missed some rare instances of females brooding or guarding chicks as described by Jenni and Betts (1978) for Northern Jacana. However, on the basis of my observations, parental care seemed to be largely if not entirely carried out by males, and therefore this population can be characterized as sex-role reversed.

### Potential reproductive rates and reproductive success

Juveniles became independent after about 70 days ( $n = 5$  broods), although they still spent much of their time on the natal territory for up to five weeks after this period. The total duration of male parental care (incubation plus post-hatching care) was therefore approximately 100 days. In a harem of four males, two could therefore hypothetically raise two broods per season because the interval between the earliest and

latest clutches found over the three years was 134 days. Females produced clutches at intervals of 12–36 days between the first days of egg laying in consecutive clutches. Mean interclutch interval was  $16.3 \pm 3.4$  days ( $n = 4$  females for which accurate data were available, excluding cases where no second clutch was laid). A quadandrous female could therefore hypothetically produce six clutches per season which males could care for. The ratio of potential reproductive rates (PRR, Clutton-Brock & Vincent 1991) is therefore skewed to females by about 4:1. This is higher than figures calculated from data reported for other sex-role reversed shorebirds e.g. 1.4:1 in Spotted Sandpiper *Actitis macularia* (Oring & Knudson 1972, Oring *et al.* 1983), 2:1 in Red-necked Phalarope *Phalaropus lobatus* (Reynolds 1987) and 2:1 in Grey Phalarope *P. fulicarius* (Ridley 1980), but it is similar to estimates for African Jacana (4:1, Tarboton 1992a, 1992b) and Wattled Jacana (about 5:1, S.T. Emlen & P.H. Wrege pers. comm.). Although other factors modify the correspondence between PRR and the intensity of sexual selection, these data suggest that sexual selection in jacanas may be more strongly reversed than in any other bird species.

As clutch survival was very low (see above) there were insufficient data to estimate mean reproductive success for males and females in different-sized harems. Although the total number of clutches produced by a female or received by a male was influenced by predation (resulting in production of replacement clutches) and by the number of years resident during the study, it might be expected to correlate positively with an individual's lifetime reproductive success. For females there were non-significant trends for the total number of clutches produced to correlate positively with the number of years resident (Spearman rank correlation:  $r_s = 0.60$ ,  $n = 8$ ,  $P = 0.157$ ), the maximum harem size achieved ( $r_s = 0.67$ ,  $n = 8$ ,  $P = 0.097$ ) and the cumulative number of males defended i.e. the number of male-years ( $r_s = 0.66$ ,  $n = 8$ ,  $P = 0.094$ ). For males the total number of clutches received was significantly positively correlated with the number of years resident ( $r_s = 0.58$ ,  $n = 13$ ,  $P = 0.046$ ), but considering all males, the number of clutches received per season was negatively correlated with harem size ( $r_s = 0.48$ ,  $n = 18$ ,  $P = 0.048$ , using one randomly selected year's data for males which were resident in more than one year). The sample sizes are small, but these results are consistent with the pattern found in Wattled Jacanas, in which reproductive success increases with harem size for females, but males have to wait longer to receive clutches in larger



harems (Wrege & Emlen 1998), and so their reproductive success may decline in larger harems.

### Evolution of sex-role reversal and polyandry

Bronze-winged Jacanas at Vembanur suffered high rates of clutch predation. High rates of natural clutch loss (including predation) have also been reported for other species of jacanas, e.g. 83% in African Jacana (Tarboton 1992a), >50% in Northern Jacana (Jenni 1974) and about 50% in Wattled Jacana (Osbourne 1982, P.H. Wrege pers. comm.). It seems likely that tropical wetlands have high densities and diversities of predators, that open nests on floating vegetation are vulnerable to egg predators, and that such nests are susceptible to variable and unpredictable water levels. The exploitation of tropical wetland habitats by an ancestral lineage of shorebirds may therefore have been associated with exposure to high rates of clutch loss, and thus selection for the ability of females to produce multiple clutches. Furthermore, the energetic costs of parental care in such a situation are likely to have been low because high ambient temperature and humidity permit low levels of incubation, and precocial chicks do not require provisioning.

These two factors seem likely to have favoured the evolution of sex-role reversal in jacanas. Once females had become emancipated from care, long tropical seasons and high productivity of wetland habitats may have permitted multiple clutch production, and polyandry may have developed when some females monopolized more than one male. The precise reason why males originally took on more parental care and females became emancipated from care remains unclear. It seems unlikely that sex-role reversal was favoured by high energetic or nutritional costs to females of clutch production and incubation (Erckmann 1983). Instead, an explanation for sex-role reversal based on the different costs and benefits to males and females of clutch desertion to seek further mating opportunities seems most likely. For example, selection for territoriality in wetland habitats with patchily distributed resources may have been an important factor favouring increased male care and influencing the evolution of sex-role reversal and polyandry in jacanas (Butchart 1998).

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