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## ASPECTS OF THE BREEDING BIOLOGY OF THE AFRICAN JACANA

W. R. TARBOTON

Department of Zoology, University of the Witwatersrand, P.O. Wits, 2001, Johannesburg, South Africa.

Present address: P.O. Box 327, Nylstroom 0510, South Africa.

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### SUMMARY

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The breeding of a marked population of African Jacanas was studied for eight successive years (1980-1988) on the floodplain of the Nyl River in the central Transvaal, South Africa. Numbers varied from 0 to c.1000 birds depending on the extent of flooding; individual turnover at one site averaged 57% per month. The sex ratio was significantly skewed towards males by about 2:1. Egg laying occurred mainly between November and March (85% of 256 records). Females were polyandrous and males undertook all parental care. Courtship was initiated by both sexes (72% by male) and culminated in full copulation in 20% of cases. Copulation lasted 35-63 sec. Sexually active birds copulated, on average, 0.4x/h. Nine marked females laid 7-10 clutches in one season; clutches were laid at 4-21 d intervals and 92% of clutches comprised four eggs. The eggs in a clutch were laid on successive mornings between 06h07-07h55. Males began incubating when the third egg was laid. The incubation period varied between 23-26½ d; the fledging period was more variable, from 39 d to >75 d. Nests were frequently built up during incubation and eggs occasionally moved to new positions when water levels rose. Clutch survival was low, averaging 26% and ranging from 0-39% between low and high flood years. Predators were suspected of causing 83%, and rising water 8% of clutch losses. Chick survival was 57-74%, this high survival being attributed to their predator avoidance behaviour. Higher female mortality is attributed to the handicaps in foraging and flying resulting from their much greater weight and less favourable wing-length:weight and foot-span:weight ratios than males. Aspects of copulatory behaviour are considered adaptive in avoiding sperm competition. Chick-carrying behaviour appears confined to those Jacanidae having modified radii.

### INTRODUCTION

The African Jacana *Actophilornis africana* is a conspicuous, widespread and locally common bird of Afrotropical wetlands, but it has not been studied extensively and most published information is anecdotal. Two unusual habits of the species that have attracted particular interest are those of brooding and carrying its young under its wings (Pitman 1960; Simpson 1961; Cunningham-van Someren & Robinson 1962; Hopcraft 1968) and of scooping its wings under its eggs while incubating (Miller 1951; Cunningham-van Someren & Robinson 1962; Dutton 1968). These observers noted that incubation and chick rearing was undertaken by the smaller bird of the pair which they incorrectly assumed to be the female. Maclean (1972) drew attention to this misinterpretation and to the improbability that eggs were actually incubated under the birds wings, as suggested by Miller (1951) and Cunningham-van Someren & Robinson (1962). Vernon (1973) provided the first evidence of the African Jacana having a polyandrous mating system when, sexing the birds on the basis of their size, he reported finding two males incubating clutches and being attended by one female. Hodgson (1983) reported that the male of a breeding captive pair undertook all parental care and that the young were never fed by the parent.

Fry (1983a) related the African Jacana's chick-

carrying and egglifting behaviour to the bird's unusually shaped radius and suggested that this flanged, bow-shaped wing-bone facilitates these behaviours as well as serving a possible purpose in fighting. The regional handbooks of Maclean (1985) and Urban *et al.* (1986) provide general accounts of the breeding biology of this species, some data of which were derived from unpublished information arising from this study.

The purpose of this paper is to describe aspects of the breeding biology of the African Jacana and so provide the background to a broader investigation into the species' polyandrous mating system (Tarboton, 1992, In press a, b, In prep.). The study was conducted during eight successive summers between 1980/81 and 1987/88 on a nomadic population that frequented a large, ephemeral wetland in the central Transvaal, South Africa.

### STUDY AREA

The study area extended along 20 km of the floodplain of the Nyl River around Nylsvley Nature Reserve, near the town of Naboomspruit, in the central Transvaal, South Africa (Fig. 1). Most data were collected at Deekraal Dam (24°40'S, 28°40'E) but marked birds moved back and forth between the localities indicated in Fig. 1; additional observations were made at these sites. Nylsvley has a subtropical climate with average tempera-

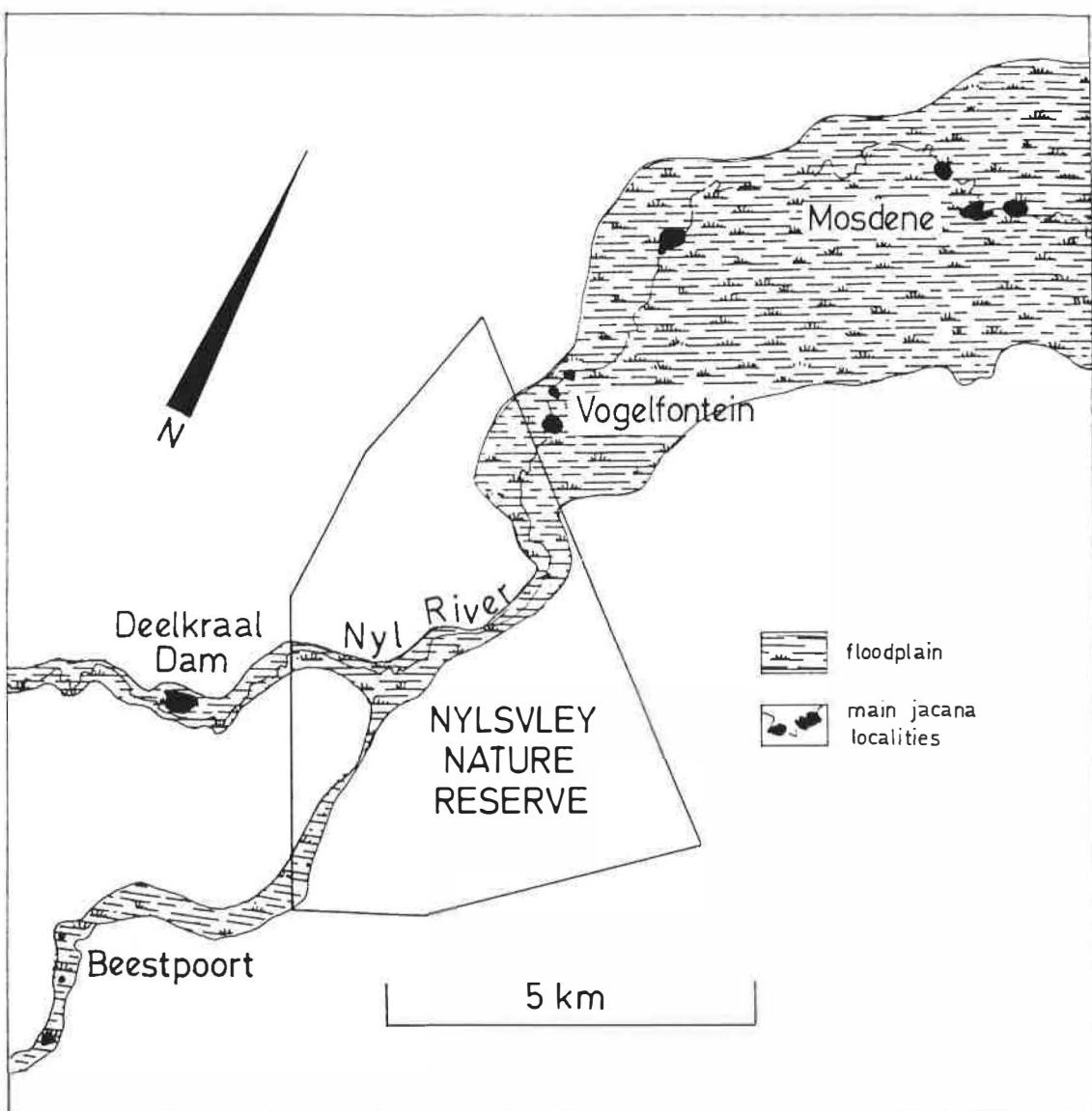


FIGURE 1

The study area, showing the localities mentioned in the text.

tures (at 14h00) in midsummer (January) of 27,5°C (extremes = 10,0 - 38,8°C) and in mid-winter (July) of 20,6°C (extremes = -1,3 - 28,8°C) (South African Weather Bureau 1986). It receives a mean annual rainfall of 620 mm, most of which falls in a single annual wet season between November and April (Frost 1987). The Nyl floodplain is an ephemeral wetland that extends for 40-50 km along a 2-6 km wide grassy plain and derives its water from a 500 km<sup>2</sup> catchment in adjacent hills (Tarboton 1987). The extent, timing and duration of flooding depends on how much rain falls in this catchment, fluctuating between no flooding in drought years to a maximum of 16 000 ha flooded in years of high rainfall. The region's annual rainfall is variable, deviating, on average by 17 % from the mean each year, hence the variable conditions that occur on the floodplain. In the period 1960-1987 little or no flooding occurred in 12 years, moderate flooding in nine years and ex-

treme flooding in six years (Tarboton 1987).

During the eight years of this study (1980/81-1987/88) the annual rainfall was very variable, ranging from 30,9 % below average (drought years) to 33,0 % above average (flood years). Deelkraal Dam fluctuated between being full and empty during this period, drying out twice (1983 and 1986) and filling to capacity six times (Fig. 2). In the first two years (1980/81 and 1981/82) its water level remained high and more than 50 % of the surface was covered with a floating mat of *Nymphaea caerulea*, a favoured foraging substratum for African Jacanas (Fig. 3). In the third summer *Nymphaea* was beached as the dam dried out, and in the fourth to sixth summers (1983/84-1985/86), fluctuating water levels inhibited the establishment of extensive habitat suitable for the birds. In the last two years (1986/87-1987/88) above average rains maintained high water levels in the dam and favourable conditions for jacanas

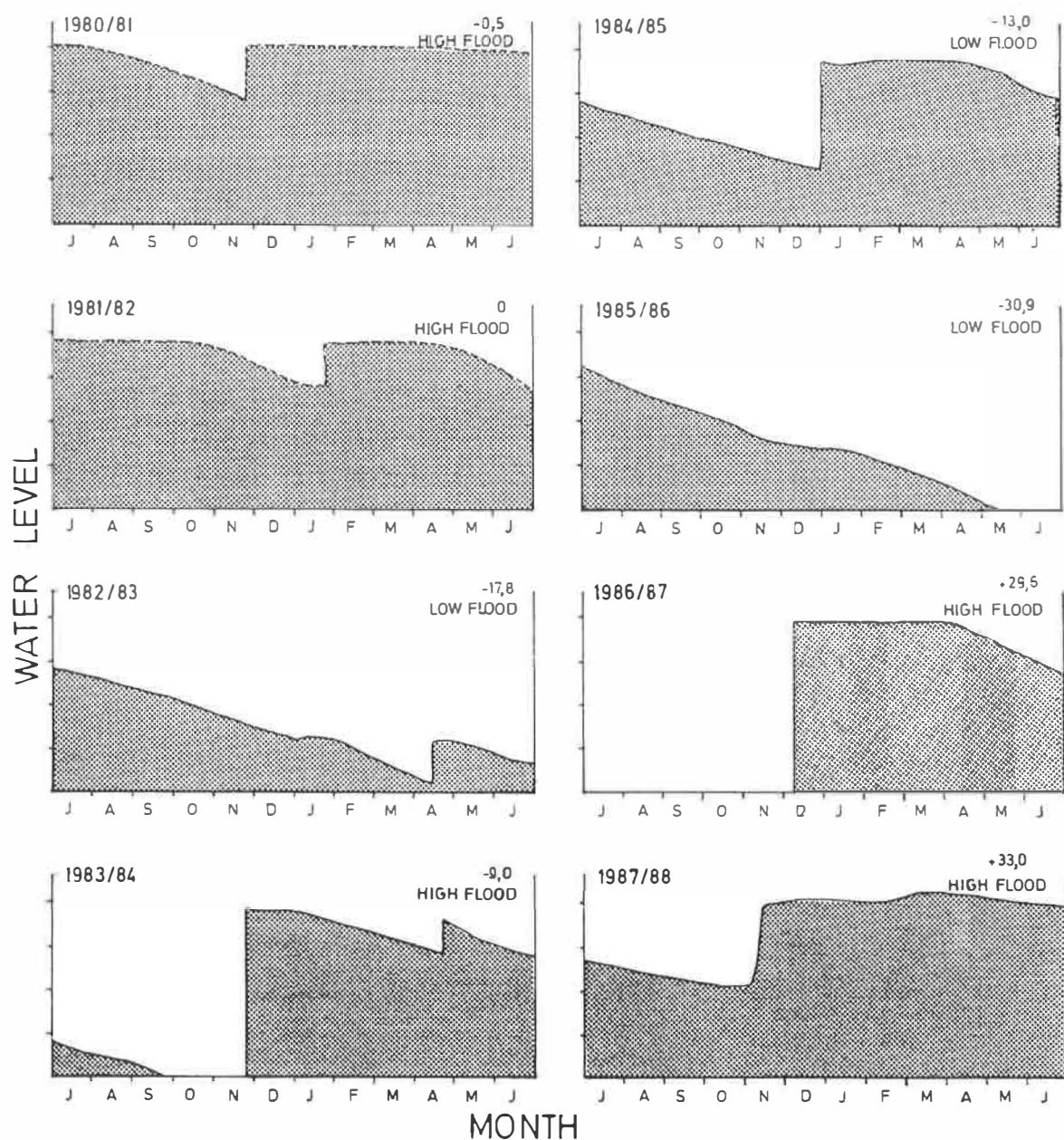


FIGURE 2

The water-level of Deelkraal Dam (measured monthly) during the study period, showing years of high and low flood.

were re-established. The pattern of events on Deelkraal Dam mirrored those occurring on the floodplain as a whole.

The years in which high water levels were maintained at Deelkraal Dam during the breeding season (November-March) (Fig. 2) are referred to hereafter as 'high flood' years while years with a decreasing, or low water level are referred to as 'low flood' years.

#### METHODS

Most records of breeding (84%; n = 256) and most observations of breeding behaviour were made at Deelkraal Dam. Three towers were

erected around the perimeter of this dam to facilitate observations and nest searches. Low level, high resolution aerial photographs of the dam were taken from a helicopter in 1981, 1982, 1983, 1987 and 1988 and a grid of numbered poles was erected in the dam to aid the plotting of nest positions and territories of breeding birds.

The main aquatic plant communities used by the jacanas were mapped monthly between November 1983 and March 1988 using the aerial photos as a base. The water level of the dam was measured monthly from July 1982 onwards (Fig. 2). Water temperatures were measured monthly between January 1984 and March 1986 at 12 fixed points on the dam. In four years (1981/82,

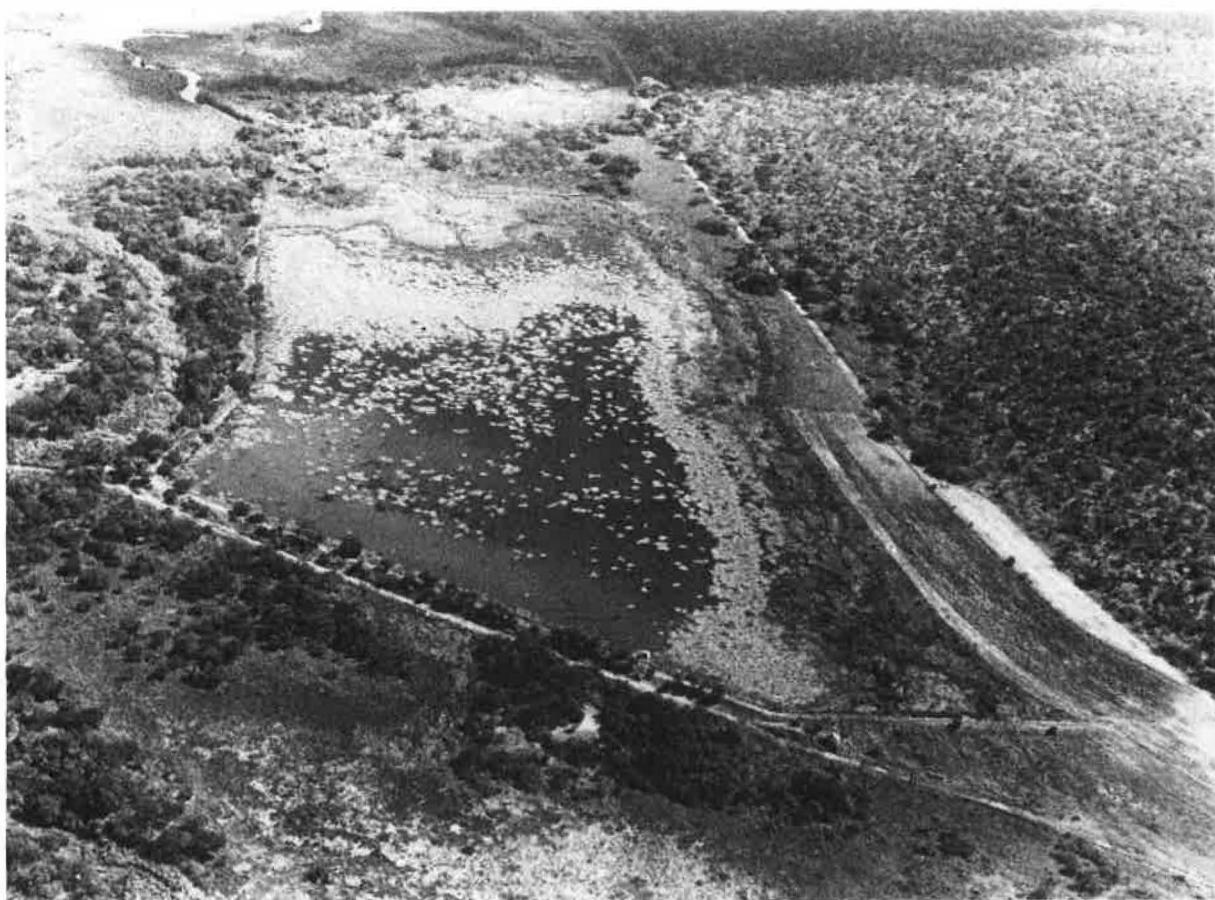


FIGURE 3

Looking west across Deelkraal Dam from the air in April 1981 when it was covered with a floating mat of *Nymphaea caerulea*.

1982/83, 1985/86 and 1987/88) an effort was made to locate every clutch laid on the dam and most were found before completion of the clutch (65%;  $n = 99$ ). The stage of incubation of clutches found after incubation had started was estimated by immersing the eggs briefly in water alongside the nest and judging the extent to which they sank or floated. This was compared with a previously determined scale in which the sink/float characteristics of eggs of known age had been assessed (Table 1). Follow-up visits to nests to determine hatching success were made as often as possible.

African Jacanas are tolerant of disturbance at their nests and none deserted clutches as a result of either their eggs being handled and marked or the males being trapped while incubating. Eighty-four birds were trapped, 16 while incubating and the others either with mist nets or with a spotlight and net at night, and these were ringed with unique combinations of four rings (one metal and three coloured) placed two on each tibiotarsus. Focal sampling of marked birds from the observation towers was done throughout the 1985/86 breeding season at c.4 day intervals ( $n = 1304$  bird-hr), from which courtship and copulation frequencies of sexually active birds were determined. One hundred and nine counts were made of the

birds present at Deelkraal Dam during 1981-1987 and each bird's identity (if ringed), age and sex was recorded.

## RESULTS

### *Population structure, sex ratios and movements*

Sex and age ratios of the population were estimated in three ways (Table 2). Birds caught for ringing had an overall sex ratio of 1,96:1 (males:females) (adults = 2,05:1; immatures =

TABLE 1  
THE STAGE OF INCUBATION AND THE RESPECTIVE SINKING OR FLOATING PROPERTIES OF AFRICAN JACANA EGGS IN WATER (DAY 1 = DAY ON WHICH FINAL EGG IN CLUTCH WAS LAID)

Stage of Incubation (d)	Sinking/floating properties of eggs
1-3	Eggs sink rapidly
3-5	Eggs sink slowly
6-8	Eggs float just below water's surface
9-11	Eggs float at the water's surface
12-14	Eggs float with cap less than 8 mm exposed
14-16	Eggs float with cap about 10 mm exposed
17+	Eggs float with cap more than 12 mm exposed

TABLE 2  
PROPORTIONS OF MALE, FEMALE, ADULT AND IMMATURE AFRICAN JACANAS OF BIRDS RINGED (I), AND OF ALL BIRDS COUNTED ON DEELKRAAL DAM DURING 1981-1987 (II) AND DURING 1985/86 SUMMER (III)

	I Number Ringed	II All Counts (1981-1987)	Sep	Oct	Counts During Nov	1985/86 Summer Dec	Only Jan	Feb	Total
Adult male	39	965	74	75	45	65	37	15	93
Adult female	19	405	21	35	38	43	24	7	168
Imm. male	12	344	20	54	15	2	—	—	91
Imm. female	7	174	19	23	16	7	—	—	65
Total	77	1888	134	187	114	117	61	22	635
<b>SEX RATIOS</b> (n males: 1 female)									
All birds	1,96	2,26	2,35	2,22	1,11	1,34	—	—	1,72
Adults	2,05	2,38	3,52	2,14	1,18	1,51	1,54	2,14	1,85
Immature	1,71	1,98	1,05	2,35	0,94	0,29	—	—	1,40

1,71:1). The adults' and the overall sex ratio differs significantly from parity ( $\chi^2 = 6,9$  and 8,1 respectively; both  $p < 0,01$ ). This sample is biased, however, because immatures were usually easier to catch than adults and, because females did not incubate, males were over-represented in the sample. The second estimate is derived from 109 counts of birds present on Deelkraal Dam during 1981-1987 in which the age and sex of each bird was assessed visually (Table 2). This sample totals 1888 birds but the same individuals were often recounted (for as long as they were present on the dam) and some data are thus pseudoreplicated. These provide an estimated population sex ratio of 2,26:1 (adults = 2,38:1; immatures 1,98:1); all three ratios differ significantly from 1:1 ( $\chi^2 = 282,3$ , 228,9 and 55,8 respectively; all  $p < 0,01$ ). The third sample is a subset of the Deelkraal Dam count data, being the monthly average for the counts made during the 1985/86 breeding season when most of the birds present were marked. These indicate that this population's sex ratio varied monthly between 1,11-2,35:1 ( $\bar{x} = 1,72:1$ ) (adults  $\bar{x} = 1,85$ ; range = 1,18-3,52; immatures  $\bar{x} = 1,40$ ; range = 0,29-2,35). The adults' and overall sex ratios differ significantly from 1:1 ( $\chi^2 = 45,0$  and 42,7 respectively; both  $p < 0,01$ ). All three methods indicate that the population sex ratio is skewed towards males (by about 2:1), that it is probably more skewed in adults than immatures, and, that it fluctuates with time in local populations. A small sample of non-flying young in five broods whose development was monitored ( $n = 16$ ) had a sex ratio slightly, but not significantly ( $\chi^2 = 0,25$ ;  $p > 0,05$ ) skewed towards males at 1,29:1.

Immatures could be distinguished from adults until they reached 9-12 months of age and moulted into adult plumage (mostly in November-December). The average age ratios for the three data sets in Table 2 are, respectively, 3,05:1, 2,64:1 and 2,54:1 (adults:immature). There was considerable variation between years: in the low flood years of 1982/83 and 1985/86 no young were reared at Deelkraal Dam (adult:immature ratio = 28:0) whereas in high flood years productivity was higher, e.g. in 1987/88 about 26-29 adults reared 30 young (ratio = 0,87-0,97:1).

African Jacana numbers fluctuated widely on the floodplain according to conditions: in years of

extensive flooding there were an estimated 500-1000 birds present whereas none remained in drought years when all suitable habitat disappeared (pers. obs.). It is not known where the jacanas moved to during these periods. When the floodplain became inundated again after the first (1983) drought 10,0% ( $n = 30$ ) of the birds that had been colour-ringed before the drought were seen again, and after the second (1986) drought 10,4% ( $n = 67$ ) of the previously marked birds were resighted.

During the 1985/86 breeding season (from September to February) when most of the birds present at Deelkraal Dam were colour-ringed ( $n = 27$ ), complete 'roll-calls' of the population were taken at, on average, four day intervals ( $n = 47$ ). The numbers dropped from about 20 present at the start of the season to about seven birds at the end of the season (Fig. 4). The decrease in numbers correlated with the monthly surface area of the dam (Spearman's  $r = 0,94$ ;  $p < 0,05$ ). At least 36 different individuals were recorded at least once during counts, although no more than 23

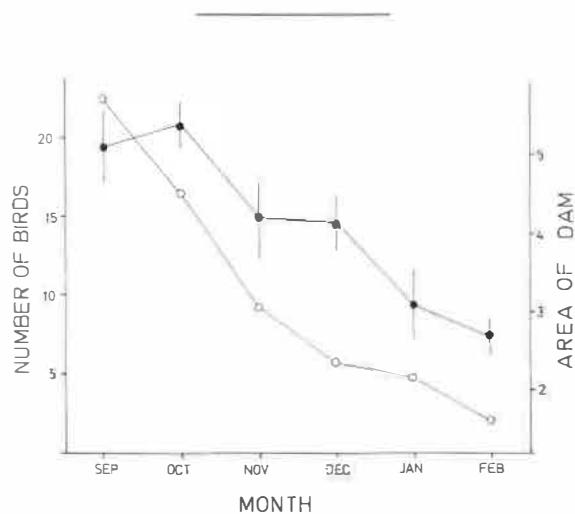


FIGURE 4

The number ( $\bar{x} \pm 1 \text{ sd}$ ) of African Jacanas present on Deelkraal Dam (●) and the area (ha) of the dam (○) in each month of the 1985/86 breeding season.

were present simultaneously. Only three individuals remained on the dam throughout the six-month period; the others came and went at an average monthly turn-over rate of 57 % (= numbers leaving or arriving/numbers staying x 100). A few were resighted at other times elsewhere on the floodplain but most were not seen again. Similarly in the 1986/87 breeding season nine of the 11 breeding males on the dam at the start of the season were colour-ringed birds but only four of these remained at the end of the season and at least six unringed newcomers had moved in to breed.

Resightings of colour-ringed African Jacanas indicated that individuals moved about the floodplain widely and frequently. Sixty birds were resighted more than a month after being ringed, 21 more than a year later, eight more than two years later and two more than four years later. Birds that remained at one locality for successive years were exceptional: one male bred for four successive years at Deelkraal Dam; another three bred there for two years, and one male bred on Beestpoort for two years and Deelkraal Dam for one year. Two females bred on Deelkraal Dam in more than one season: one bred there for one year, was absent the second, bred there at the start of the third year, then moved to Vogelfontein and bred there later in the third year. Another bred on the dam in three successive years, was sighted 20 km downstream at Mosdene during the ensuing winter and returned, but did not breed at Deelkraal Dam in the fourth year. At least eight birds initially trapped at Deelkraal Dam were resighted elsewhere on the floodplain. One bird was resighted on the Vaal River, 300 km from the study area (S. de Beer, pers. comm.).

#### Breeding season

The 256 African Jacana breeding records obtained from the Nyl floodplain during 1974-1988, backdated where necessary to the month of egg-laying, are detailed in Table 3. The same table shows breeding season data from Natal (Dean 1971), Zimbabwe (Irwin 1981), Malawi (Benson & Benson 1977) and East Africa (Brown & Britton 1980), with the respective northern- and southern-most latitudes of each region. The proportion of records falling within the November-March period for each region is positively correlated with each region's mid-latitude (Spearman's  $r = 1.00$ ;  $p < 0.0001$ ). As suggested elsewhere (Tarboton, In press, b) the latitudinal gradient in winter ambient temperatures and its effect on

water temperatures may underlie this relationship.

#### Nests

The African Jacana's nest is a flimsy, often sodden platform of aquatic plant stems heaped up on floating vegetation (Urban *et al.* 1986). Nests ranged in diameter between 95 and 330 mm ( $\bar{x} = 200$  mm; SD = 59; n = 71) and were raised up to 20 mm above the water surface. On the Nyl floodplain the submerged hydrophyte *Ceratophyllum demersum* was the most frequently used nest material, being abundant and easily dislodged and pulled to the nest site. Less often, stems of *Ludwigia stolonifera*, *Potamogeton thunbergii*, *P. crispata*, *Polygonum* spp. or *Cyperaceae* were used for nest material. Occasionally (3.7%; n = 190) the eggs were laid on a substratum without the addition of any nest material. Material was added frequently to nests during the incubation period, especially when the water level rose. The same platform was re-used rarely (3.0%; n = 133) for a replacement clutch.

The choice of substratum used for nests varied from year to year depending on hydrological conditions and the aquatic plant communities established. The site chosen had to be sufficiently supportive for a pair to stand on it simultaneously and copulate. At a few sites, which were later rejected, the female became submerged during copulation. The sites most frequently chosen, when available, were over deep water (> 1 m), on small (> 1 m diameter) islands and screened by plant stems. On the Nyl floodplain such sites were usually floating islands of *Leersia hexandra*, *Ludwigia stolonifera*, or a *Nymphaea* corm which had become dislodged and floated to the surface bringing with it some mud which became colonised by *Schoenoplectus* or another small sedge species. In drought years, when the birds bred during falling water levels, many nests were located on flat, open rafts of *Potamogeton thunbergii*, rendering the incubating bird very conspicuous. In one year (1982/83), rapidly receding water levels resulted in several nests which started off over water being beached and ending on soft mud 20 m from the water's edge.

#### Nest building and courtship

Nest building and courtship in African Jacanas are closely integrated. Courtship and copulation occur only on potential nest platforms, although these may be unrecognisable as such until nest material is pulled onto the site. A pair of birds that

TABLE 3  
THE NUMBER OF AFRICAN JACANA EGG LAYING RECORDS PER MONTH AT DIFFERENT LATITUDES

Region	Latitude	Number Of Egg Laying Records Per Month												% Between Nov-Mar	
		J	A	S	O	N	D	J	F	M	A	M	J		
Natal <sup>1</sup>	27°S-31°S	-	-	-	1	5	7	16	6	4	-	-	1	39	97
Nyl floodplain <sup>2</sup>	24°S	-	4	6	26	42	51	73	40	12	2	-	-	256	85
Zimbabwe <sup>3</sup>	15°S-23°S	7	12	9	10	16	12	27	41	32	10	6	5	187	68
Malawi <sup>4</sup>	10°S-17°S	2	8	3	2	3	5	-	8	7	2	1	7	48	48
East Africa <sup>5</sup>	10°S-05°N	9	7	4	1	5	5	4	5	4	7	10	12	71	32

Data sources: 1. Dean 1971; 2. this study; 3. Irwin 1981; 4. Benson & Benson 1977; 5. Brown & Britton 1980.

TABLE 4  
THE NUMBER OF COURTSHIP SEQUENCES INITIATED BY  
MALES, FEMALES AND BIRDS OF UNKNOWN SEX WHICH  
REACHED EACH OF THE THREE STAGES OF COURTSHIP (SEE  
TEXT)

Courtship initiated by	Total	No. of Courtship Sequences reaching		
		Stage I	Stage II	Stage III
Males	226	104	62	60
Females	90	16	51	23
Unknown sex	72	—	42	30
TOTAL	388	120	155	113

have established a bond may court and copulate on three or four platforms, the most frequently used of which becomes the site chosen for the eggs.

- A typical courtship sequence has three stages:
- I — One of the pair, usually the male (72%; n = 316) stands on the nest site and utters a characteristic soliciting call directed at its intended mate.
  - II — The target bird, if it chooses to, joins the calling bird on the nest by flying there or by walking.
  - III — The two birds copulate or attempt to copulate.

On average, 29% (n = 388) of courtship sequences culminated in full or attempted copulation and 20% in full copulation (Table 4). Significantly fewer courtship sequences (54%; n = 226) initiated by males went beyond stage I than those initiated by females (82%; n = 90;  $\chi^2 = 23.93$ ;  $p < 0.0001$ ).

The soliciting bird frequently pulls at nearby stems of vegetation and heaps these onto the site. If the target bird does not respond to his/her calling, the soliciting bird may discontinue calling and continue adding material to the nest, or fly to another platform and repeat the sequence. The soliciting call is a repetitive, low pitched, harsh monosyllabic 'hhh'. It may become higher pitched and be uttered more rapidly if the target bird is slow to respond, and the bird on the nest platform may make little jumps into the air and scrabble at the nest with its claws. Both sexes utter the same note, which is only used in courtship. The soliciting bird typically faces the target bird when calling, with head pointing down and held low. If the mate comes to the nest, it also approaches with head down (Fig. 5A). Once together on the platform (Stage II), the female stands still in the head-down position while the male walks around her prodding at her with his bill, sometimes starting at her neck and usually ending at her cloacal region (Fig. 5B). This may last up to 1 min.

The female terminates the courtship sequence at this stage more frequently (69%; n = 74) than the male (51%; n = 122), although the difference is not significant ( $\chi^2 = 3.29$ ;  $p > 0.05$ ). She does so by standing erect. Males usually terminate by flying off to chase another bird in the vicinity. The courtship proceeds to stage III when the male

jumps lightly up onto the female's back and then crouches down so that his belly is in contact with her back, holding onto her by curling his toes over her shoulders (Fig. 5C). He depresses his tail and she holds hers vertically to bring their cloacas into contact. During copulation he slowly wags his tail from side to side.

Copulation attempts frequently were terminated prematurely (30%; n = 116), usually as a result of the female standing up and the male sliding or falling off her back. Successful copulations lasted, on average, 47 sec (n = 30; SD = 7.6; range = 35–63 sec). At the end of a successful copulation the male stood up, hopped off the female, sometimes with a quick wing flap, and stood alongside her. Following copulation males often flew off to chase birds in the vicinity. Birds copulated evenly throughout the day: the number of observed copulations per hour did not deviate significantly from the distribution expected from an even occurrence ( $\chi^2 = 11.1$ ;  $p > 0.05$ ).

The frequency with which sexually active birds courted and copulated varied daily. During 291 h of observation over 43 days in the 1985/86 breeding season sexually active females copulated, on average, 0.43X/h (n = 4 females; range = 0.32–0.98) and there was no correlation between their copulation frequency and the number of clutches each laid during the season (Spearman's  $r = 0.40$ ;  $p = 0.49$ ) (Table 5). Sexually active males copulated at a similar overall frequency ( $\bar{x} = 0.44X/h$ ; n = 5 males; range = 0.31–1.11). In this season two dominant males (M91, M53) monopolised the sexually active females and received most of the clutches that they laid (six and seven respectively, Table 5). Males stopped copulating once they began incubating (when the third egg was laid) and their aggression towards other males diminished simultaneously. This enabled lower ranked males to court the females for as long as the dominant birds were committed to clutches. Their access terminated abruptly, however, if a dominant bird lost its clutch and reclaimed the female to lay a replacement. Females that were midway through laying a clutch for a lower ranked bird when this happened intervened and protected the latter from attacks from the dominant bird until the clutch was complete. The two dominant males in 1985/86 had the lowest copulation frequencies (0.31 and 0.32X/h) but, because they had the most access to the females, they secured the most copulations. The third-ranked male in this year (M87) had a higher copulation frequency (0.59X/h) and he received a total of three clutches from one of the females (but copulated with three of them). The two lowest ranked males (M93, M82) had the highest copulation frequencies (0.76 and 1.11X/h respectively) but neither had exclusive access to a female sufficiently long to have a clutch laid for it.

In some instances two or more lower ranked males courted a female simultaneously before she laid a clutch for one of them. In one such case a female (F70) copulated four times in 80 min, twice each with two males. Three days later she commenced laying a clutch for one. The dominant males' aggressive behaviour probably enhanced

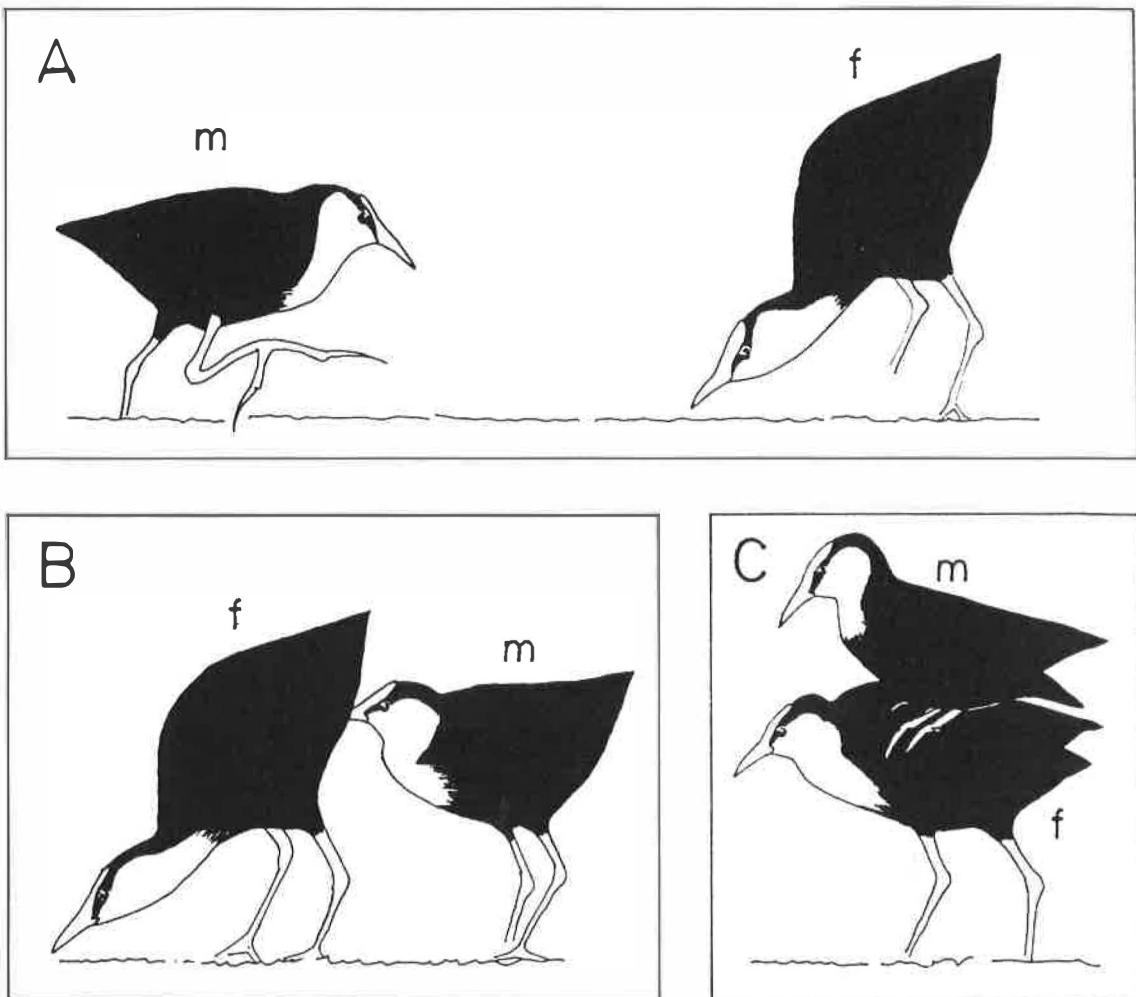


FIGURE 5

Sequence of postures used by African Jacanas in stages II and III of courtship (see text).

their assurance of paternity of the clutches they incubated. Lower-ranked males had less prospect of this because of the laying female's greater promiscuity when courting them. Even dominant males, however, probably received clutches fertilised by lower-ranked males, as when, after losing a clutch, they regained access to the female after she had been courting and copulating with a lower-ranked male. In one such case the female (F49) copulated 5X in 90 min, once with the lower ranked bird before he was ousted, followed by 4X with the dominant male after he had regained her attentions. She commenced laying for the dominant male three days later.

Males also copulated with more than one female when the opportunity arose. One male, positioned between the territories of two adjacent females, courted and copulated with the first female on his platform and 25 min later did the same with the second female on the same platform. In the 1985/86 season the third-ranked male (M87) shuttled back and forth between the two sexually active females as they laid clutches for the dominant birds and became briefly accessible to him. In the

1987/88 season several males received clutches from different females during the course of the breeding season (Tarboton, In prep.).

#### Egg laying

Ninety-two percent of African Jacana clutches on the Nyl floodplain comprised four eggs, with 12 (7.7%) three-egg clutches and one (0.6%) five egg clutch being recorded ( $n = 155$ ) (Tarboton, 1992). The individual eggs of a clutch are laid on successive mornings between 06h07-07h55, with a mean laying time of 06h50 ( $SD = 28$  min;  $n = 14$ ). In one case the four eggs were laid on successive mornings at 06h47, 06h42, 06h25 and 06h57. There was no correlation between times of egg laying and sunrise (Spearman's  $r = 0.02$ ;  $p = 0.94$ ).

Laying females went to the nest 4-12 min before laying, sometimes having to nudge off the incubating male to gain access to the nest. Then they half-crouched on the nest, restlessly changing position, pulling at nest material, briefly settling on the eggs present as if to incubate, perhaps preening, and finally, laying. One egg was watched emerging, point first, and another dropped 50 mm from the

TABLE 5

THE FREQUENCY (N/H) WITH WHICH SEXUALLY ACTIVE MALE AFRICAN JACANAS AT DEELKRAAL DAM WERE ENGAGED IN STAGE I AND STAGE III COURTSHIP SEQUENCES AND THE NUMBER OF CLUTCHES THEY RECEIVED DURING THE 1985/86 SUMMER

Sex	Bird	Observation time (h)	Frequency of courtship reaching		Clutches received/laid
			Stage I	Stage III	
Male	M53	84,2	1,12	0,31	7
	M91	107,9	1,08	0,32	6
	M87	72,9	1,80	0,59	3
	M93	18,4	1,63	0,76	0
	M82	8,1	1,97	1,11	0
	totals	291,5	1,33	0,43	16
Female	F56	106,9	1,09	0,32	1
	F49	135,3	1,38	0,38	10
	F85	29,9	1,77	0,74	2
	F55	19,4	1,75	0,98	3
	totals	291,5	1,33	0,43	16

bird onto the nest. Some females remained standing on the nest for several minutes after laying while others left immediately.

At least eight breeding females laid seven or more clutches in a single season, two laying 10 clutches each, one laying nine and one eight clutches (Table 6). Other females observed on Deelkraal Dam laid 1-5 clutches in a season but some of these left and may have continued breeding elsewhere. In 1985/86 female F85 on Deelkraal Dam known to be breeding for the first time, laid two clutches at the dam, a third clutch upstream, then withdrew from breeding and spent the rest of the season with the floaters on the dam. In the same season another female (F49) laid 10 clutches.

The interval between successive clutches laid by the same female ranged from four to 28 days ( $\bar{x} = 12,1$  d; SD = 7,3; n = 24). None of the females had a consistent inter-clutch interval; for example F49 had intervals between clutches in one season of 6, 5, 18, 21, 4, 5, 5, 8 and 13 days.

#### Incubation Period

Several observers have stated that, in African Jacanas, only one sex incubates (Cunningham-van Someren & Robinson 1962; Hopcraft 1968; Phelan 1970; Steyn 1973) and Hodgson (1983) noted that it was the male that did this in a captive breeding pair. Elsewhere (Tarboton, In press, b) I show that this was also the case in the Nyl flood-

plain population and that the male began incubating when the third egg was laid. Only rarely (3X) were females seen to settle on the eggs as if to incubate and then only during the egg-laying period: one female did so just before laying her third egg and two other females, visiting their incomplete clutches, settled briefly on the eggs; none sat for longer than 2 min.

The incubation period (time of laying of last egg to time of hatching of last chick) was measured accurately ( $\pm 6$  h) in four clutches: 23 d, 23½ d, 24½ d, 26½ d (range 23-26½ d). It was measured less accurately ( $\pm 1\frac{1}{2}$  d) in another three clutches (22 d, 22½ d, 23½ d) and two other clutches had minimum incubation periods of 20½ d and 22 d. Wilson (1974) estimated the incubation period of a clutch to be about 21-24 d and Hodgson (1983) reported that two captive-laid clutches took 24 d (when incubated by the parent) and 26 d (when artificially incubated) to hatch. The eggs hatched in their laying order in one clutch in which they had been numbered as they were laid.

Incubating males attend their eggs (incubating or shading) for 53 % of the daytime, this being higher on cool than warm days (Tarboton, In press, b). Clutches laid early in the summer are more likely to be subject to cold weather than those laid later; at Nylsvley the average minimum temperatures for October and January were, respectively, 13,3°C and 17,1°C (Weather Bureau 1986). The 26½ d incubation period recorded was

TABLE 6

LAYING PERIOD, TOTAL CLUTCHES LAID, SEQUENCE OF CLUTCH SIZES AND TOTAL EGGS LAID BY THE MOST PRODUCTIVE AFRICAN JACANA FEMALES ON DEELKRAAL DAM

Female	Year	Date of laying of		Days between first- and last-laid eggs	Total clutches laid	Sequence* and clutch size	Total eggs laid
		First egg of first clutch	Last egg of last clutch				
F49	1985/86	1 Oct	29 Jan	121	10	4434443344	37
Fk	1987/88	20 Aug	6 Jan	140	10	444444444(1)	37
F70	1981/82	5 Oct	9 Feb	128	9	4(1)4433444	31
Fd	1987/88	10 Sep	26 Mar	198	8	44(3)442+33	29-31
Fg	1987/88	28 Sep	23 Dec	87	7	4344354	27
Fw	1981/82	14 Nov	29 Jan	77	7	4434444	27
Fi	1987/88	21 Nov	27 Mar	127	7	2+4442+43	23-27
F69	1982/83	7 Oct	5 Feb	121	7	4(2)4(1)444	23

\* Clutches in parenthesis were depredated before completion. The number of eggs in clutches marked + may have exceeded this amount.



FIGURE 6

Typical incubating position of male African Jacana (drawn from photograph).

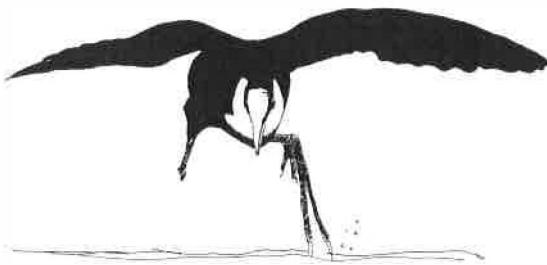


FIGURE 7

Distraction display of male African Jacana (drawn from photograph).

for an October-laid clutch whereas the others were for clutches laid after November, and this may account for its greater duration. Males did not terminate incubation if their eggs failed to hatch once this period was exceeded; one male (M07) incubated such a clutch for 53 d before it was lost to flooding.

The male often adopts a characteristic posture when incubating (Steyn 1973; Fry 1983b) in which his wings are dropped and wrapped under his body, such that the wrists are almost horizontal and touching below his belly (Fig. 6). It has been suggested that males lift the eggs and hold them against their sides with their wings to incubate them (Miller 1951; Cunningham-van Someren & Robinson 1962) but Maclean (1972) and Fry (1983a) have pointed out that the male has a well developed brood patch on his abdomen and that the eggs are probably being held against this, with the wings being used to keep the eggs off the damp nest.

African Jacanas occasionally move their eggs from one nest to another: Cunningham-van Someren & Robinson (1962) reported two instances in which clutches were moved about 4 m and 0.4 m and Wilson (1974) observed it once. In two of four such cases observed in this study (4%; n = 98) when nests had been 'beached' as a result of water levels receding rapidly, the clutches were moved, 1 m and 0.5 m respectively. In one the eggs were relocated behind a tuft of vegetation which screened the male while incubating and in the other they were relocated after a grazing bushpig *Potamochoerus porcus* had pulled up the *Nymphaea* plant on which the nest was placed. Both hatched. The other two moves occurred when rapidly rising water flooded the initial nest. Three of the four eggs in one clutch were moved to a newly built platform 2 m away and one egg in the other four egg clutch was relocated 30 m. Both attempts failed when a further rise in the water level flooded the new sites. Both clutches were within 2 days of hatching when the moves occurred and the eggs would thus have floated high in the water (Table 1), enabling the parent to push the eggs along while swimming. Recently laid eggs would

sink and thus not be moveable in this way.

Incubating males have several responses to potential predators approaching the nest. As noted by Cunningham-van Someren & Robinson (1962) they are particularly aggressive towards smaller Rallidae and other waders walking in the vicinity, and determinedly chased off Black Crakes *Amaurornis flavirostris*, Lesser Gallinules *Porphyryula aleni*, Moorhens *Gallinula chloropus*, Wood Sandpipers *Tringa glareola* and Ruffs *Philomachus pugnax*. When approached by larger birds such as Purple Gallinule *Porphyrio porphyrio*, Grey Heron *Ardea cinerea*, Spurwinged Goose *Plectropterus gambensis* and Redknobbed Coot *Fulica cristata*, males stood erect with bill pointing downwards, nape feathers raised, calling loudly. At times the bird also lifted its wings vertically during this threat display. Females sometimes responded by flying in to assist the male in driving off the predator. The jacanas frequently encountered swimming Nile monitors *Varanus niloticus* or pythons *Python sebae* and they sometimes aggregated around these, but did not attack or mob them.

Males occasionally performed an elaborate distraction display, usually when young rather than eggs were present (Simpson 1961). I only observed it during this study when I approached in a boat: the male would face the boat, crouch with wings drooped and half open, head down, calling agitatedly. It then made short runs, pausing to jump briefly and land back on the water with a splash, simultaneously clapping its wings loudly on the water (Fig. 7).

#### *Factors affecting clutch survival*

One measure of clutch survival is the percentage of clutches hatching of the total clutches observed. Mayfield (1961), Johnson (1979) and Klett & Johnson (1982) have pointed out the potential bias in this method in which the failed portion of the sample is under-represented as a result of an unknown number of early nests failing that go undetected. The hatching estimate for four subsets of African Jacana data are presented in Table 7; these show that the least biased subset (n = 79)

TABLE 7  
ESTIMATED SURVIVAL RATES OF AFRICAN JACANA CLUTCHES BASED ON DIFFERENT SUBSETS OF BREEDING DATA FROM THE NYL FLOODPLAIN (SEE TEXT)

Data set	n	% Hatched	% Hatched in year of		$\chi^2$	p
			High flood	Low flood		
All clutches, 1974-1988	134	28,7	35,2	10,5	8,35	<0,01
All clutches, 1981-1988	102	27,5	35,8	11,4	6,85	<0,01
Clutches from Deelkraal Dam, four years only*	93	25,8	34,4	9,4	6,98	<0,01
Clutches from Deelkraal Dam, found before laying complete	79	25,3	32,7	11,1	4,29	<0,05

\* years in which all clutches laid were found

gave a hatching success estimate (25,3 %) only 3,4 % lower than the most biased subset ( $n = 134$ ). Hatching success in high and low flood years is compared in the same table: a significantly higher proportion of clutches hatched during high flood (32,7 %) than during low flood years (11,1 %;  $\chi^2 = 4,29$ ;  $p < 0,05$ ).

When clutch survival is viewed in terms of the percentage of clutches surviving to different stages of incubation (Fig. 8) it can be seen that the initial rate of survival is lower in low flood than high flood years but both rates level off to the same slope during the 13-18 d stage of incubation. Thus in both cases nests that survive the early part of the incubation have about an equal chance of hatching after this: the early incubation loss is the critical difference between high and low flood years.

Predation was suspected as the main cause of egg loss (83,3 %;  $n = 102$ ) despite not a single instance of such predation being witnessed, either during 190 h of continuous nest watches or many other hours of casual observation. Many potential avian, reptilian and mammalian predators lived alongside jacanas on the floodplain, most numerous of which were Purple Gallinule *Porphyrio porphyrio*, Nile monitor *Varanus niloticus*, water mongoose *Atilax paludinosus* and Cape clawless otter *Aonyx capensis*. Several recently depredated nests had fresh signs of Purple Gallinules having been on them (faeces, eaten *Nymphaea* flower heads) and two had fresh otter tracks passing directly over the empty nest. In most cases the eggs disappeared without trace, leaving the nest intact but empty. Eight clutches (7,8 %) failed as a result of being flooded by rising water levels, notwithstanding the males' attempts to build up these nests or relocate the eggs. No flooded clutches were seen to survive as a result of such nest building efforts.

Nest site characteristics in low and high flood years were different in several respects (Table 8). An obvious difference was that in the low flood years they were, on average, in shallower water (respectively 334 and 991 mm; Mann-Whitney  $u = 6,43$ ;  $p < 0,0001$ ). Shallow water probably made them more accessible to predators, in addition to the increased risk of their being trampled by cattle and other herbivores entering the water to drink and graze. Water depth and clutch survival were significantly correlated (Spearman's  $r = 0,48$ ;

$p < 0,0001$ ). There was no significant difference between the mean distances of nests from the nearest shore in low and high flood years (23 and 17 m respectively; Mann-Whitney  $u = -1,37$ ;  $p > 0,1$ ) and no correlation between this distance and clutch survival (Spearman's  $r = 0,15$ ;  $p = 0,19$ ).

The extent to which the incubating bird was concealed by vegetation around the nest was scored on a scale between 1-5 (where 1 = no screening, incubating bird clearly visible from 50 m; 5 = maximum screening, incubating bird not visible from 50 m). Both this and the height of the vegetation surrounding the nest were significantly different in low and high flood years (Table 8). The choice of plant species that provided the substratum to the nest also differed significantly between low and high flood years (Table 9;  $\chi^2 = 17,69$ ;  $p < 0,001$ ): these three variables are clearly interdependent. In low rainfall years most

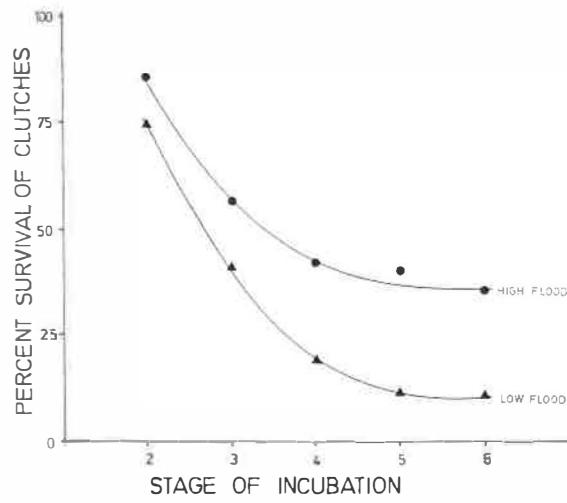


FIGURE 8

The proportion of African Jacana clutches surviving to different stages of incubation in years of high and low flood (2 = 1-6 d; 3 = 7-12 d; 4 = 13-18 d; 5 = 19-24 d; 6 = hatched or >24 d).

TABLE 8  
A COMPARISON BETWEEN FOUR SITE CHARACTERISTICS OF AFRICAN JACANA NESTS FOUND IN LOW AND HIGH FLOOD YEARS

Nest site characteristics		Low flood	High flood years	Mann-Whitney years	p
Water depth (mm)	- $\bar{x}$	333,8	991,1	-5,75	<0,0001
	-sd	227,4	537,8		
	-n	32	37		
Distance from edge (m)	- $\bar{x}$	23,0	17,3	1,52	0,13
	-sd	21,1	14,2		
	-n	25	47		
Index of nest concealment (1-5)	- $\bar{x}$	1,97	2,91	-3,72	0,0002
	-sd	21,1	14,2		
	-n	38	103		
Height of nest cover (mm)	- $\bar{x}$	47,5	170,4	-3,72	0,0002
	-sd	95,2	101,7		
	-n	16	37		

nests (76,5%; n = 34) were placed on floating mats of *Potamogeton thunbergii* or *Nymphaea caerulea* which afforded minimal cover to the incubating bird (Table 10). In high flood years nests were more evenly spread on a variety of substrata, most being on *Ludwigia stolonifera* (Table 9). *Ludwigia* had the highest mean screening value (3,85), followed by *Leersia hexandra* (3,55) and *Polygonum* spp. (3,13) (Table 10), all of which were used as nest sites to a greater extent in high than in low flood years (Table 9). The relative availability of these substrata in high and low flood years was not quantified but a subjective assessment was that the plant species most favoured for providing nest sites were least developed in drought years when water levels were receding, but flourished in high flood years when the water level of the dam remained high. In contrast, the *Potamogeton* mats were developed most extensively in shallower water and continued spreading as the level dropped.

The dispersion of nests on Deelkraal Dam was significantly correlated with their hatching success. During the high flood years when the dam remained full through the breeding season, three physiognomically different areas could be recognised (Fig. 9): a deep-water central area (A), a narrow (< 5 m) littoral zone along the south and east edges where the slope gradient was high (B) and a broad (> 5 m) littoral zone on the north and west edges where the gradient was shallower, the latter divided into the north edge which lacked a bay (C) and the western edge which was backed by two bays (D, E). In proportion to the respective areas of each, significantly more nests were located in the littoral zone than in the central deep-water area ( $\chi^2 = 78,6$ ;  $p < 0,01$ ) and hatching success of nests located in the two western bays (D, E; Table 11) was significantly higher than elsewhere ( $\chi^2 = 20,2$ ;  $p < 0,01$ ). The central deep-water area was sparsely covered with *Nymphaea* and *Polygonum*, whereas the littoral zone had the most extensive development of favoured nesting plant communities, and this was maximally developed in the two western bays where the most nests were located.

#### Post hatching period

The degree of synchrony in hatching varied be-

tween clutches. The emergence of chicks from eggs was preceded by (i) the chicks calling inside the eggs 24-48 h before hatching and (ii) the eggs pipping in the last 24 h before hatching. In one clutch three of the four eggs hatched within 45 min of one another; in two clutches all four eggs hatched within 8 h whereas in another clutch the last egg hatched at least 30 h after the first three. The shells are carried up to 30 m away from the nest by the male, as noted by Cunningham-van Someren & Robinson (1962).

The precocial chicks begin moving about within 4 h of hatching (Miller 1951) and they are led or carried away from the nest by the male. They are not fed by the male (Hodgson 1983), although they forage together and he points his bill at food items which the young pick up. Initially they remain within a few metres of the male and are frequently held or carried under his wings. They begin wandering more widely from about 10 d old and young were last seen being carried by a male when 18 d old. Some family groups remained intact for at least 70 d, whereas in others the young dispersed after 40-50 d. The age at which chicks first fly was difficult to establish as they usually ran or dived underwater when approached, even when they could fly. Three young from different broods could first fly when 39, 40 and 44 d old. In 11 other broods of young, however, the young could not fly when 41, 42, 42, 45, 46, 46, 47, 49, 59, 68 and 75 d old. In the last extreme case one young in the brood could fly when 58 d old whereas its younger sibling still could not when 75 d old. Two other non-flying siblings were examined when 59 d old and their primaries had

TABLE 9  
THE NUMBER OF AFRICAN JACANA NESTS LOCATED ON DIFFERENT SUBSTRATES IN YEARS OF LOW AND HIGH FLOOD

Substrate	Low Flood	High Flood
<i>Ludwigia stolonifera</i>	6	35
<i>Potamogeton thunbergii</i>	14	19
<i>Nymphaea caerulea</i>	12	13
<i>Leersia hexandra</i>	-	10
<i>Polygonum</i> spp.	-	9
<i>Typha</i> & sedges	1	8
Bare mud	1	5
<b>TOTALS</b>	<b>34</b>	<b>99</b>

TABLE 10  
THE EXTENT TO WHICH AFRICAN JACANA NESTS ( $n = 126$ ) WERE SCREENED BY THE SUBSTRATE ON WHICH THEY WERE LOCATED. SCREENING IS RANKED FROM 1 (NIL) TO 5 (MAXIMUM)

Substrate	Number of nests in each rank					$\bar{x}$	SD	n
	1	2	3	4	5			
<i>Ludwigia stolonifera</i>	—	3	12	8	16	3,85	1,17	39
<i>Leersia hexandra</i>	—	—	3	5	2	3,55	1,30	10
<i>Polygonum</i> spp.	—	1	2	3	1	3,13	1,45	7
<i>Potamogeton thunbergii</i>	12	11	8	1	—	1,94	0,88	32
<i>Nymphaea caerulea</i>	15	15	1	—	—	1,50	0,61	31

emerged only 10 mm at this age. They hatched at the end of a drought summer during which Deelkraal Dam's water level had receded from 53 % to 4 %, and their male parent was the last remaining adult jacana on the dam when he abandoned them there at 52 d old. Males were twice recorded breeding a second time in one season after raising a first brood. The two initial broods were 38 and 42 d old and could not fly when their male parents abandoned them and started incubating second clutches.

The role of the male in rearing chicks appears to centre on protecting them from predators. In the presence of danger a male with small chicks gathers the young under his wings and runs to cover, carrying them rather than letting them run, but as they get older and become less dependent on him, they run or dive underwater when approached. As during incubation, males with small young behave

aggressively to any waterbird species in the vicinity and females may assist males in challenging a predator. A male at Deelkraal Dam with 18 d-old young was assisted by his mate in attacking a Pygmy Goose *Nettapus auritus* family, killing at least two goslings (N. Elwell, pers. comm.). Even a bird as unlikely to be a predator of the chicks as a Malachite Kingfisher *Alcedo cristata* was observed being chased off. Females were never observed attending the young, and males sometimes left the young unattended when they went to feed outside their territories.

#### Breeding success

Only the data from Deelkraal Dam in the four years when all clutches and broods are thought to have been found (1981/82, 1982/83, 1985/86, 1987/88) have been used in assessing breeding success (Table 12). Assumptions made in calculating

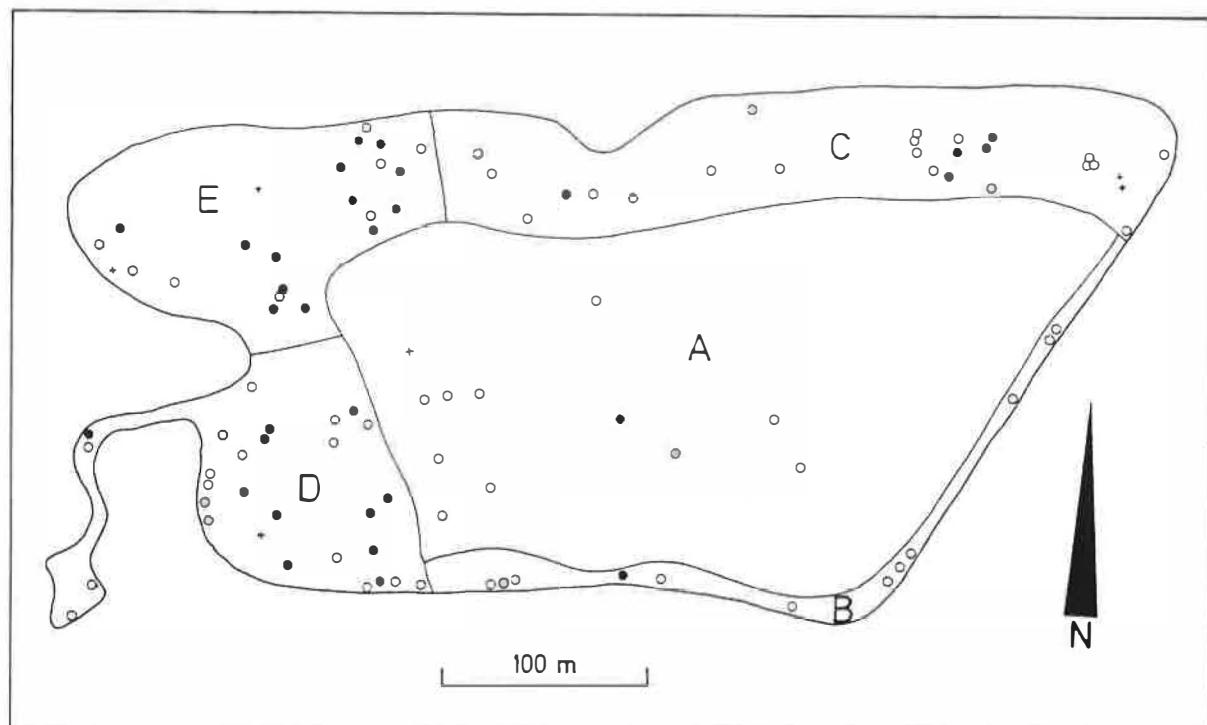


FIGURE 9

African Jacana nest positions on Deelkraal Dam in years of highflood between 1980-1988 (● = hatched; ○ = failed to hatch; x = outcome unknown).

TABLE 11  
THE RELATIVE HATCHING SUCCESS OF AFRICAN JACANA NESTS LOCATED IN DIFFERENT SECTIONS OF DEELKRAL DAM DURING HIGH FLOOD YEARS BETWEEN 1980-1988 (SEE FIG. 10 AND TEXT)

Section of dam	Area (ha)	Number of nests	Nests per hectare	% which hatched
A—central deep-water area	5,54	12	2,2	9,1
B—narrow littoral zone	0,48	12	25,0	8,3
C—broad littoral zone (N edge)	2,12	26	12,3	20,8
D—broad littoral zone (SW bay)	1,20	29	24,2	39,3
E—broad littoral zone (NW bay)	1,50	23	15,3	61,9
TOTALS	10,84	102	9,4	32,3

values are: that the unknown clutch sizes ( $n = 6$ ) were four eggs; that young reaching 30 d or more fledged successfully (in three cases younger chicks are assumed to have been successful based on the male parent's subsequent behaviour); and, that where the number of eggs hatching was not determined it was the same as the last-recorded number of eggs in the nest.

Overall clutch survival was low, with about one in 10 hatching in low flood years and one in three in high flood years (Table 7). The survival rate of individual eggs was even lower (19-24%; Table 12). However, once broods hatched, their survival rate improved to 80,8% ( $n = 26$ ; Table 12). The proportion of young reared per egg that hatched was likewise high (58-74%;  $n = 70$ ; Table 12), and significantly greater than the hatching success (19-24%;  $\chi^2 = 71,4$ ;  $p < 0,0001$ ).

The number of young reared per breeding adult could not be estimated accurately because of the movement of adults in and out of Deelkraal Dam. Several marked birds which moved off the dam during the course of a breeding season were subsequently found breeding elsewhere and their relative breeding success off the study site was not known. But the young raised per breeding adult (Table 12) show that, because of the polyandrous

mating system, females accounted for 2-3X more young per breeding bird than did males.

## DISCUSSION

African Jacanas attempted to breed on Deelkraal Dam in each of the eight summers covered during this study, but the number of birds breeding and their success each year was highly variable. Three contrasting habitat scenarios occurred at the dam during the eight years. Firstly, in the three low flood years (Fig. 2) in which little or no run-off reached the dam, the shoreline receded, previously suitable breeding habitat for the jacanas became progressively beached and the hydrophyte community was dominated by *Potamogeton thunbergii*, a plant which provided suitable foraging habitat for the jacanas but lacked cover for nests. Clutch survival ( $\bar{x} = 11\%$ ) was lowest in these years. In the five remaining high flood years two situations occurred. In three years extensive floating mats of a variety of hydrophytes became established over much of the dam; up to 29 jacanas bred and clutch survival ( $\bar{x} = 33\%$ ) was higher than at any other time. In the two high flood years when the dam refilled after having been dry during the preceding winters (1983, 1986) floating

TABLE 12  
AFRICAN JACANA BREEDING SUCCESS ON DEELKRAL DAM IN FOUR YEARS OF UNBIASED SAMPLING

Years Extent of flooding	1981/82 high	1982/83 low	1985/86 low	1987/88 high	Total
Number of males (min-max)	13	4-5	3	19-22	
Number of females (min-max)	6	3-4	5	7	
Clutches - laid	28	16	16	39	99
- hatched	8	3	0	15	26
- % hatched	28,6	18,8	0	38,5	26,3
Eggs - laid (min-max)	96-102	50	58	144	348-354
- hatched (min-max)	24-28	7	0	35-50	66-85
% hatched (min-max)	25,0-29,2	14,0	0	24,3-34,7	19,0-24,0
Young reared	19	0	0	30	49
% young reared of					
- clutches laid	67,9	0	0	76,9	54,4
- eggs laid (min-max)	18,6-19,8	0	0	20,8	13,8-14,1
- eggs hatched (min-max)	67,9-79,2	0	0	60,0-85,7	57,7-74,2
Broods reared	7	0	0	14	21
% broods reared of					
- clutches laid	25,0	0	0	35,9	21,2
- clutches hatched	87,5	0	0	93,3	80,8
Young reared per					
- breeding female	3,17	0	0	4,29	
- breeding male (min-max)	1,46	0	0	1,36-1,58	

mats of hydrophytes suitable for jacanas developed minimally: very few birds colonised the dam or bred here in these summers.

These changing conditions greatly influenced the jacanas' choice of nest sites: in high flood years nests were located over deeper water, in taller cover and were better screened from view than in low flood years (Table 8). Perhaps as a result of this, clutches had a significantly higher rate of survival. I found their nests more difficult to locate when they were hidden in vegetation and it is reasonable to assume that this would apply equally to nest predators which hunt visually. However, the survival rate of clutches only correlated significantly with water depth ( $p < 0.0001$ ) and not with the height of cover ( $p = 0.12$ ) nor with the extent to which the nest was screened ( $p = 0.23$ ) (Spearman's rank correlations). Thus while it is tempting to ascribe the better clutch survival in the high flood years to the greater availability of nest cover, this is not supported empirically. Greater water depth may simply reduce accessibility to predators.

Most jacana nests on the dam were located in the littoral zone (Fig. 9) and those positioned where this was broadest had significantly higher hatching success than elsewhere (Table 11). The 23 clutches laid in the high flood years in the north-west bay (Fig. 9, area E) had a hatching success of 62%. Several factors may account for the much higher survival of clutches laid in this bay, but none are proven. Firstly, this bay was the most sheltered position on the dam with respect to wind, so egg loss to wind action here was minimised. Secondly, the mat of floating vegetation on which the jacanas nested was wider than that found elsewhere on the dam so that many of the nests here were further away from either the dam's banks or from the fringe of tall macrophytes. The significance of this is that the suspected main predators of jacana eggs (the Nile monitor and Purple Gallinule) mainly frequented the dam's banks and the fringing vegetation respectively, and nests placed close to these would be the most prone to predation. Elsewhere I have hypothesised that the poor survival of clutches in African Jacana has been the selective force that led to the evolution of role reversal and polyandry in this species (Tarboton, In prep.).

In contrast to the egg stage, once clutches hatched, the survival rate of chicks was high: on average, 81% of the clutches that hatched produced one or more flying young, and the success rate of eggs that hatched was between 58-74% (Table 12). The avoidance behaviour that chicks perform when approached by a predator (diving under water, running for cover, being carried off underwing by the parent) probably accounts for this. The variable fledging period of young African Jacanas is unusual in Charadriiformes as it is not documented by Johnsgard (1981) in any other species in this order. In this study it ranged between cases in which young first flew at 39-44 d of age to those in which young were still flightless when 59-75 d of age. Even siblings that hatched simultaneously differed in age of first flight e.g.

with one flying by 58 d and the other not yet flying at 75 d. It is likely that food deprivation was responsible for the slow development sometimes found. The two chicks with retarded wing growth that were abandoned by their male parent at Deelkraal Dam in 1984 when 52 d of age were the last jacanas remaining at the fast-shrinking water body and it seems probable that scarcity of food was the reason for both the departure of the adults and the retarded condition of the chicks. Another case involved a family of a male parent and two young that hatched on a small (0.15 ha), isolated pond on Beestpoort (Fig. 1). The male frequently flew from the pond to feed elsewhere, indicating that food on the pond was limited. These chicks also developed slowly, the less advanced of the two still being flightless when 75 d of age.

The impression that African Jacanas are highly mobile, evidenced by the average 57% per month turnover of individuals at Deelkraal Dam during the 1985/86 breeding season, is further supported by records of their unexpected appearance in areas that lack suitable habitat or are beyond their normal range. For example, singletons have been observed at remote waterholes in southern Namibia (Maclean 1960; Carp 1961), in the Kalahari Gemsbok National Park (N. Matthews, K. Herholdt, pers. comm.), and in the Namib Desert at Sandwich Harbour (Prozesky 1960) and Gobabeb (C. F. Clinning, pers. comm.). Many of the places frequented by African Jacanas are ephemeral wetlands similar to the Nyl floodplain and nomadism allows individuals to find and exploit isolated occurrences of suitable habitat.

The sex ratio of African Jacanas at Deelkraal Dam was skewed significantly towards males (Table 2). In studies made of two races of the American Jacana *Jacana jacana* the evidence presented suggests that these populations may also be male-skewed, although the differences in the numbers of each sex are not statistically significant. Thus for *J. j. spinosa* Jenni & Betts (1972) recorded 49 males and 33 females in their study population and in *J. j. jacana* Osborne (1982) reported trapping and marking 34 males and 19 females. I suggest that the apparently male-skewed populations observed in these species are real and reflect higher female mortality that arises from the nomadic habits of jacanas. In both of these and in the African Jacana females are 60-70% heavier than males. In the African Jacana, and possibly in *Jacana jacana* as well, female wing length is only 12% greater than that in males and footspan is only 5% greater (Tarboton, In press, a). Thus when flying, females have a less favourable wing-length:weight ratio than males (0.70 vs. 1.05) and when walking on floating substrata they have a less favourable footspan:weight ratio (0.70 vs. 1.11). Female African Jacanas spend more time foraging than males, and they are more restricted than males in the choice of floating substrata on which they can walk without sinking (Tarboton, In press, a). From their less favourable wing-length:weight ratio I predict that flying will be energetically more costly to females than males, and this, coupled with the handicap imposed on their

foraging efficiency by their greater weight, could lead to higher female mortality and the observed male-skewed sex ratios.

The frequency with which female jacanas copulate with different males in a short space of time (Jenni 1974; this study) suggests that males had little guarantee of their paternity in the clutches that they incubated, and that sperm competition may be an important factor in selection for copulating behaviour. Sperm storage is well developed in birds (Birkhead *et al.* 1987) and the high frequency at which sexually active African Jacanas copulated ( $\bar{x} = 0.4X/h$ ) and the long duration of each copulation ( $\bar{x} = 47$  sec) probably maximise sperm availability for egg fertilization. Even longer copulations ( $\bar{x} > 60$  sec) occur in *Jacana spinosa* (Jenni 1974).

Dominant males guarded their mates from approaches by subordinate males until the third egg was laid and they began incubation. Since eggs are fertilized about 24 h before laying (Howarth 1974), other males copulating with the female after this would not affect the paternity of the fourth egg of the clutch. In contrast to the dominant male's exclusive access to the laying female, lower ranked males appeared less able to prevent other subordinates from copulating with her, and the clutches laid for these males probably had a higher incidence of mixed paternity. Dominant males were not excluded, however, from the possibility of receiving mixed paternity clutches. This could arise when a dominant male lost his initial clutch and reclaimed the female to lay a replacement clutch after she had been copulating with other males. Sperm competition theory would predict that dominant males would increase their copulation frequency when this occurred, and this was observed.

Cloacal pecking of females by males was sometimes observed during courtship sequences, but it was not the highly developed behaviour described for the Dunnock *Prunella modularis* which has been interpreted as being a means of ejecting competitor sperm from the female's cloaca (Davies 1985). In the case of the African Jacana such pecking only lasted a few seconds and its function was more likely to stimulate the female to copulation.

The African Jacana's well-known chick-carrying behaviour has been linked to its unusual bow-shaped, flanged radius by Fry (1983a) who suggested three possible functions for this structure:

to facilitate incubation (used for holding the eggs against the brood-patch), to facilitate chick-brooding/carrying, and to strengthen the wings for fighting. Although the chick brooding/carrying explanation appears the most plausible, Fry (1983a) pointed out two anomalies: some jacana species lack the modified radius yet wing-brood their chicks whereas females in species with this structure do not wing-brood. Based on the observed behaviour of the Lesser Jacana, Tarboton & Fry (1986) considered the most probable explanation for the modified radius to be its adaptiveness for fighting.

In African Jacanas, however, intraspecific fighting does not involve striking the opponent with wings. Fighting birds attempt to seize their opponents by the neck and force them under water (pers. obs.) and there is no apparent advantage to be gained in doing this by having bow-shaped or flanged radii. The wing-brooding/chick-carrying hypothesis becomes more convincing if these two behaviours are distinguished (Table 13). Thus with the exception of *Actophilornis albinaucha* for which data are lacking, all jacana species wing-brood their young whether or not they have modified radii. Not all species carry their young underwing, however: the three with modified radii (*Actophilornis africana*, *Metopidius indica* and *Irediparra gallinacea*) do, whereas two of the three without modified radii (*Hydrophasianus chirurgus* and *Jacana jacana*) do not. In the third species lacking a modified radius (*Microparra capensis*), the evidence that it wingcarries, rather than merely wing-broods its young is equivocal. A single observation of wing-carrying was reported in Tarboton & Fry (1986), although neither of us witnessed it during our observations of *Microparra* with young and I suggest that the distinction between brooding and carrying may not have been made in this report. In addition to clarifying the position with *Microparra*, it would also be instructive to determine whether *Actophilornis albinaucha* wing-carries its young: on the basis of its strongly modified radius (Fry 1983b) this hypothesis predicts that it does.

Just as all jacana species (for which data are available) wing-brood their young, so they all scoop their wings under their eggs while incubating (Table 13). Since chick-carrying appears restricted to those species with modified radii, I propose that this modification is a specific adaptation to facilitate chick-carrying, and that the three spe-

TABLE 13  
PRESENCE OR ABSENCE OF MODIFIED RADIUS AND ASSOCIATED BEHAVIOUR IN SEVEN SPECIES OF JACANIDAE

Species	Modified radius	Scoops up eggs during incubation	Chicks brooded under-wing	Chicks carried under-wing
<i>Actophilornis albinaucha</i>	Yes	?	Yes	Yes
<i>Actophilornis africana</i>	Yes	Yes	Yes	Yes
<i>Metopidius indica</i>	Yes	?	Yes	Yes
<i>Irediparra gallinacea</i>	Yes	?	Yes	Yes
<i>Hydrophasianus chirurgus</i>	No	Yes	Yes	No
<i>Jacana jacana</i>	No	Yes	Yes	No
<i>Microparra capensis</i>	No	Yes	Yes	*

\* Reported as 'Yes' on equivocal evidence.

cies that lack this behaviour are thus more primitive than the four in which it occurs. That females of species with modified radii also have this structure suggests that the uniparental care found in these is probably derived from a system of biparental care in which females also attended and carried the young.

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