Incubation behaviour of the African jacana

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In African jacanas all parental care is by males. The male's daytime attendance of the nest (= incubation constancy) averages 53% and is characterized by frequent, short 'on' and 'off' shifts in which he leaves the nest, on average, 35 times per day. Ambient temperatures affect both the incubation constancy and the duration of 'on' and 'off' shifts: on the coldest ($\bar{x}$ = 22,9°C) of 4 days of variable weather in which egg and ambient temperatures were monitored together with the male's incubation behaviour, the incubation constancy was 70,9%, the eggs were unattended 28,1%, the 'on' shifts were long ($\bar{x}$ = 22,5 min) and the 'off' shifts short ($\bar{x}$ = 8,4 min). In contrast, on the hottest day ($\bar{x}$ = 31,3°C) the eggs were unattended 56,5% of the day; they were incubated 6,9% and shaded 36,6%. Both 'on' ($\bar{x}$ = 4,7 min) and 'off' ($\bar{x}$ = 6,3 min) shifts were short. At night, when the eggs were constantly incubated, their temperature remained constant at 34,1°C (*SD* = 0,4; *n* = 69) whereas in daytime their temperature ranged between a daily mean of 33,2–37,1°C (*n* = 4 days) and between extremes of 27,0–39,6°C. On a hot day ($\bar{x}$ = 30,0°C) when the male was prevented from shading the test egg its temperature reached a lethal level (43,8°C) in 30 min. It is suggested that the high ambient temperatures prevailing in the African jacana's breeding range have facilitated the evolution of a uniparental care system in this species, but the males' unusual incubation behaviour associated with high temperatures may also have led to the high clutch predation rate found in this species.

Onder grootlangtone word die eiers sowel as die kuikens alleen deur die mannetjies uitgebroei en grootgemaak. Die daaglikse aandag aan die neste ('broeistandvastigheid') deur die mannetjies is gemiddeld 53% en word gekenmerk deur baie 'aan' en 'af' periodes waarvan elkeen van korte duur is. Die mannetjies verlaat die nes gemiddeld 35 keer per dag. Die omringende temperatuur beinvloed beide die broeistandvastighed en die tydsduur van die 'aan' en 'af' periodes: op die koudste ($\bar{x}$ = 22,9°C) van vier dae van wisselende weer, toe omringende temperatuur, die temperatuur van die eiers en die mannetjie se broeigedrag aangeteken is, was die broeistandvastigheid 70,9%, die eiers was vir 28,1% van die dag verlate, die 'aan' periodes was lank ($\bar{x}$ = 22,5 min) en die 'af' periodes was kort ($\bar{x}$ = 8,4 min). In teenstelling hiermee was die broeisel op die warmste dag ($\bar{x}$ = 31,3°C) 56,5% verlate; die mannetjie het vir 6,9% van die dag op die broeisel gesit en dit vir 36,6% in die skadu van sy liggaam gehou. Beide 'aan' ($\bar{x}$ = 4,7 min) en 'af' ($\bar{x}$ = 6,3 min) periodes was van korte duur. Snags, wanneer daar deurlopend op die eiers gesit was, het die temperatuur van die eiers konstant gebly by 34,1°C (*SD* = 0,4; *n* = 69) maar gedurende die dag het dit gemiddeld tussen 33,2–37,1°C gewissel met uiterstes van 27,0–39,6°C. Op 'n warm dag, toe die mannetjie verhoed is om die toetseier met sy liggaamskadu te beskerm, het die eier 'n dodelike temperatuur (43,8°C) in 30 min bereik. Daar word voorgestel dat die hoë omringende temperature wat in die broeigebied van die grootlangtoon voorkom die ewolusie van die versorging van die eiers en kleintjies deur net een ouer vergemaklik het, maar ook dat die buitengewone broeigedrag van die mannetjie gepaard met die hoë temperature, ook tot die hoë predasiekoers van die eiers onder hierdie spesie gelei het.

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In avian eggs the development of the embryo is primarily dependent on the egg temperature being maintained within the range 32–38°C (White & Kinney 1974; Drent 1975). Temperatures above this (40–48°C) are lethal to the developing embryo; below this the embryo may either develop abnormally, or, if the temperature remains below the 'physiological zero temperature' of 25–27°C, there may be no embryonic development at all (Drent 1975). The optimal incubation temperature varies by a few degrees between taxa, as does the tolerance of their eggs to sub-optimal temperatures. Charadriiformes, for example, have the highest mean incubation temperatures recorded (34,3°C), whereas Sphenisciformes have the lowest (30,7°C) (Webb 1987).

In all but a few bird species the maintenance of eggs within the optimal temperature range is achieved by the parent transferring its body heat to the eggs via its brood patch. The parent regulates the egg temperature by maintaining an incubation time-table according to the temperature gradient existing between the eggs and their immediate environment (White & Kinney 1974). However, parental attentiveness is not dictated solely by the thermal demands of the developing embryo, but also by the nutrient demands of the parent. In most species where the incubation is shared by the sexes, attentiveness or 'incubation constancy' (= per cent of daylight hours spent on the nest; Skutch 1962) is high, whereas in uniparental species it may be lower because of the parents' need to spend time foraging (White & Kinney 1974). In shorebirds with a biparental breeding system, for example, incubation constancy is between 95–99%, whereas in those having uniparental care this may be only 80–90% (Lofaldii 1985). In some shorebird species both forms of parental care occur. In the spotted sandpiper *Actitis macularia* some clutches are incubated solely by males, in which case incubation constancy is lower (74,8%) than in those clutches where females assist males with incubation (83,7%) (Maxson & Oring 1980). Similarly, uniparental sanderlings *Calidris alba* incubated for 81% of the day whereas biparental sanderlings incubated for 96% of the day (Pienowski & Green 1976). In the dotterel *Eudromias* *morinellus* most clutches are incubated by the male alone but in a few cases where females assisted the incubation constancy was not different (both 90%; Kalas 1986).

The jacanas, family Jacanidae, are a distinctive group of shorebirds in which at least four species exhibit role-reversed, uniparental male breeding systems (Johnsgard 1981) and unusually low incubation constancies. In the American jacana *Jacana spinosa*, males incubate for only 44% of the day, and shade the eggs for a further 5% (Jenni & Betts 1978); in the bronze-winged jacana *Metopidius indicus* two males incubated for 54,3% and 15,7% of the time observed (30 h and 34,5 h respectively: Mathew 1964) and in the pheasant-tailed jacana *Hydrophasianus chirurgus* males incubated between 13% (at midday) and 60–70% (morning and evening) (Hoffman 1950). In the African jacana *Actophilornis africana* Postage (1984) reported an incubation constancy of 50% based on 16 h observation. All four species are also 'restless sitters', making frequent changes between the incubation ('on') and recess ('off') shifts. In the American jacana 'on' shifts averaged 13,6 min and 'off' shifts 19,3 min (n = 115) (Jenni & Betts 1978) whereas in the African jacana these were, respectively, 12 min and 9,5 min (Postage 1984).

This unusual incubation behaviour, which is strikingly different from that found in most other shorebirds, is probably related to the unusual thermal environment surrounding their eggs. In contrast to many shorebird species which breed at high latitudes the jacanas are virtually restricted to the tropics and subtropics (Haymans, Marchant & Prater 1986) where ambient temperatures may be high during the breeding season. Their eggs are laid in exposed nests built on floating vegetation and they are often in close contact with water, the surface temperature of which may reach levels matching those considered optimal for incubation. The purpose of this study was to examine the effects of these and other variations on the thermal environment of the African jacana's nest, to relate these to the observed incubation behaviour of the male parent and to consider the role played by a thermally favourable nesting environment in the evolution of the advanced form of simultaneous polyandry that is found in this species (Tarboton 1992c and unpublished data).

Study area and methods

I studied the incubation behaviour of African jacanas nesting on a shallow dam on the farm Deelkraal on the floodplain of the Nyl River (24°40'S / 28°40'E) in the central Transvaal, South Africa, from 1980–88. When full, the dam was 11 ha in extent and was then partly covered with floating vegetation (mainly *Nymphaea, Ludwigia, Potamogeton*) and bordered by emergents (mainly *Cyperus, Polyganum, Leersia*). As many as 70 African jacanas frequented the dam, and up to 29 nested there (in a season), during those summers (August to March) in which it contained water; it was dry during two of the eight years.

Nest attendance behaviour totalling 169 h was observed at 26 nests for periods that lasted from 2–10,7 h. The time when the incubating bird left the nest and returned, and whether it shaded or incubated the eggs, was recorded. The terms 'on' and 'off' are used to describe shifts at and away from the nest, and 'on' time was further subdivided into time spent shading and incubating. Most observations were made using binoculars and telescopes from three elevated towers that overlooked the dam and from which virtually all the jacana nests on the dam were visible. From these viewing points up to eight nests were monitored simultaneously. Most of the incubating males under observation were colour-ringed and thus individually recognizable. In most clutches under observation the stage of incubation was known from their laying dates, or if these were unknown, this was estimated by immersing the eggs in water and comparing their rate of sinking or extent of floating with the results obtained from sample clutches in which the stage of incubation had been calibrated with their floating or sinking characteristics (Tarboton 1992c).

At one nest (which was placed on floating stems of willowherb *Ludwigia stolonifera* in 2 m deep water and 10 m from the shore) a temperature probe was inserted into one of the eggs of the four-egg clutch. The colour-ringed male (M07) attending this nest had incubated two previous clutches in the season, both of which failed. Five other probes were used to track the temperatures of the top and bottom of the nest, the water 100 mm below the nest, the air 50 mm above water alongside the nest, and the 'radiation' temperature (Figure 1). The temperatures at each site were measured at 3-min intervals using a multichannelled scanning telethermometer (Yellow Springs Instrument Company, model 47TD). These were recorded on a flatbed recorder (J.J. Lloyd Instruments, model CR552) with paper-feed set at 5 mm/min. Each day the chart recorder was calibrated by immersing the 'radiation' probe (which was located on the shore) into water heated to different known temperatures and marking these at the positions recorded on the chart. The temperature readings from the top and bottom of the nest invariably fell between the temperature of the water and air and to maintain clarity these have not been plotted in Figure 2 and Figures 4–7. The 'radiation' temperature was measured by a probe enclosed in a plastic sheath and placed on the shore in sunlight. During cloud-free periods its temperature exceeded the range of the chart (> 46°C). The

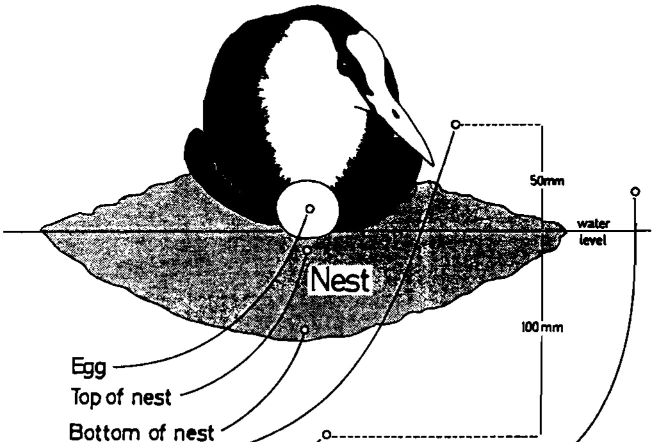

Figure 1 Location of temperature probes at an African jacana nest.

equipment was supplied with power from a portable generator sited 50 m from the nest. Ambient temperatures were recorded at 15-min intervals using a maximum and minimum thermometer placed in a shady position 35 m from the nest where a vehicle which served as a hide and instrument shelter was stationed.

The probe was inserted into the centre of the egg through a hole drilled through the shell that was just sufficient to allow its entry and it was secured to the shell with dental cement. Temperature measurements were made over five days (25–29 February 1989) using the same egg which, at the start, was on its fifth day of incubation. Temperatures were also recorded one night for 4 h (25–26 February) to establish a 'standard' egg temperature resulting from uninterrupted incubation (Figure 2). This 'standard' (34,1°C; *SD* = 0,4; *n* = 69 readings) was used to scale other temperatures in Figures 4–7. A total of 19 h of daytime temperature and simultaneous incubation activity was recorded.

The water temperature in Deelkraal Dam was measured monthly (100 mm below the surface) at 14 fixed points between January 1984 and March 1986 (Figure 3).

Results

The overall incubation constancy of African jacanas in this study was 53,1% (26 nests, 169 h). The average durations of 'on' and 'off' shifts were, respectively, 10,7 min (*SD* = 6,9; range = 0,2–39,2 min; *n* = 476) and 9,7 min (*SD* = 6,2; range = 0,6–54 min; *n* = 461). These are the same order of magnitude as those reported previously for this species (Postage 1984) but the 'off' shifts are shorter than those recorded in the American jacana (Jenni & Betts 1978). On average, incubating birds left the nest, usually to forage, 35× per day. These mean values mask a range of variation in the male's incubation behaviour which was affected by time of day, by temperature, and ultimately by weather conditions as is shown in the following examination of subsets of the data.

The effect of time of day on the male's incubation behaviour is shown in Table 1. Clutches were attended for a higher proportion of time (*ca* 65%) during the morning and evening than during the midday period (10h00–16h00) (*ca*

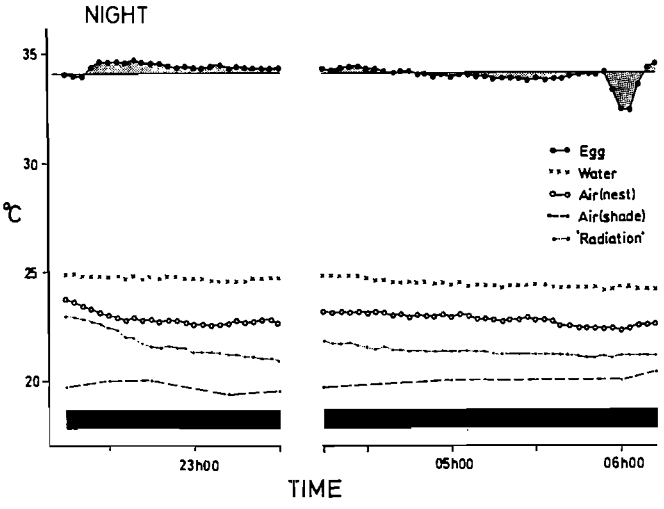

Figure 2 Temperatures at African jacana nest during continuous incubation at night: means of egg = 34,1°C; water = 24,6°C; air (nest) = 22,8°C; air (shade) = 21,0°C.

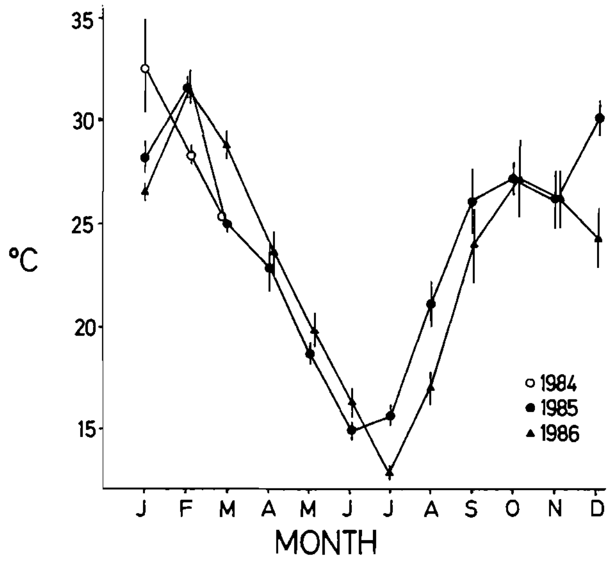

Figure 3 Monthly water temperatures ($\bar{x}$ ± 1 *SD*) on Deelkraal Dam during January 1984–March 1986.

Table 1 Effect of time of day on male African jacana's incubation behaviour (% 'ON' and 'OFF' and duration of 'ON' and 'OFF' shifts)

Time interval		05h00–08h00	08h00–10h00	10h00–12h00	12h00–14h00	14h00–16h00	16h00–18h00	Total
% time ON		66,9	63,6	48,4	43,2	46,4	58,3	53,1
Sample size (h)		12,75	24,98	15,42	18,55	11,02	7,13	89,85
% time OFF		33,1	36,4	51,6	56,8	53,6	41,7	46,9
Sample size (h)		6,32	14,3	16,47	24,35	12,75	5,1	79,29
Duration ON	— $\bar{x}$	15,6	13,3	9,3	7,8	9,8	10,0	10,7
(min)	— *SD*	5,2	7,4	5,2	5,9	6,5	7,5	6,9
	— *n*	43	108	83	97	96	49	476
	— range	3–26	1–39,2	0,3–24,5	0,2–30	0,3–28,6	0,3–34	0,2–39,2
Duration OFF	— $\bar{x}$	8,7	8,3	10,2	10,6	11,7	6,9	9,7
(min)	— *SD*	7,2	3,8	7,2	6,1	6,3	4,8	6,2
	— *n*	47	109	100	84	88	33	461
	— range	1,8–50	1–24	0,6–54	1–33	1–35,3	1–28,3	0,6–54

45%). One nest monitored for a portion of the night (22h13–23h34; 04h13–06h00) was continuously attended during this period and it is thus assumed that incubation is continuous after dark. 'On' shifts were shorter ($\bar{x}$ = 9,0 min) and 'off' shifts longer ($\bar{x}$ = 10,8 min) during the midday period than during the morning ($\bar{x}$ = 14,0 min and 8,4 min respectively; Z = -7,34 and 4,19 respectively; both $p < 0{,}001$, Mann-Whitney test) and evening ($\bar{x}$ = 10,0 min and 6,9 min respectively; Z = 0,60 and 3,98 respectively; not significant and $p < 0{,}001$, respectively, Mann-Whitney test).

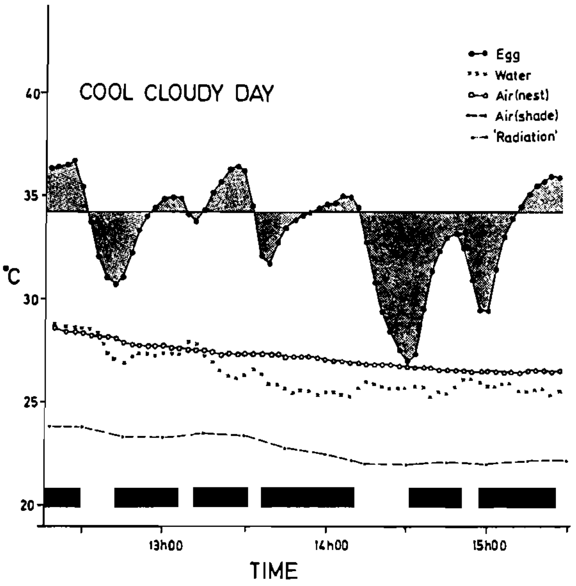

Figure 4 Temperatures at African jacana nest on a cool, cloudy day. Means of egg = 33,2°C; water = 27,2°C; air (nest) = 26,4°C; air (shade) = 22,9°C. Eggs incubated for 70,9% of the time (black bars).

This within-day variation in the incubation behaviour reflects the changes in water and ambient temperature in the vicinity of the nest as shown in Figure 5 where, on an average day, these gradually increased to a peak between 11h00–16h00 and then declined. Figures 4–7 illustrate how incubation behaviour varied between days of varying weather conditions. On a cool, overcast day (Figure 4) during which the mean shade temperature was 22,9°C, the male incubated for 70,9% of the time and the temperature of the eggs was, on average, below standard ($\bar{x}$ = 33,2°C). During his 'on' shifts the egg temperature went above standard, but fell below this each time he left the nest. During his longest 'off' period which lasted 21,3 min the egg temperature dropped 7,7°C to 27,0°C, close to physiological zero.

On a warmer, but mainly overcast day (Figure 5) during which mean shade temperature was 25,1°C, the male spent less time on the nest (58,4%) and the mean egg temperature (35,1°C) exceeded the standard. Virtually all 'on' time was spent incubating (56,6%) rather than shading (1,8%), and the latter occurred only during the midday period. Figure 6 illustrates the temperature profiles and incubation behaviour on a still hotter day when the mean shade temperature during the observation period was 28,1°C. The egg temperature never fell below the standard temperature during this period and averaged 37,1°C. From 10h36 onwards the eggs were attended for only 42% of the time and these 'on' periods were frequent and of short duration during which the eggs were shaded rather than incubated. When the male left the nest the egg temperature increased and once, when he was away for 8 min (at 12h30), reached 39,6°C. On a second hot, cloudless day (28 February) when the shade

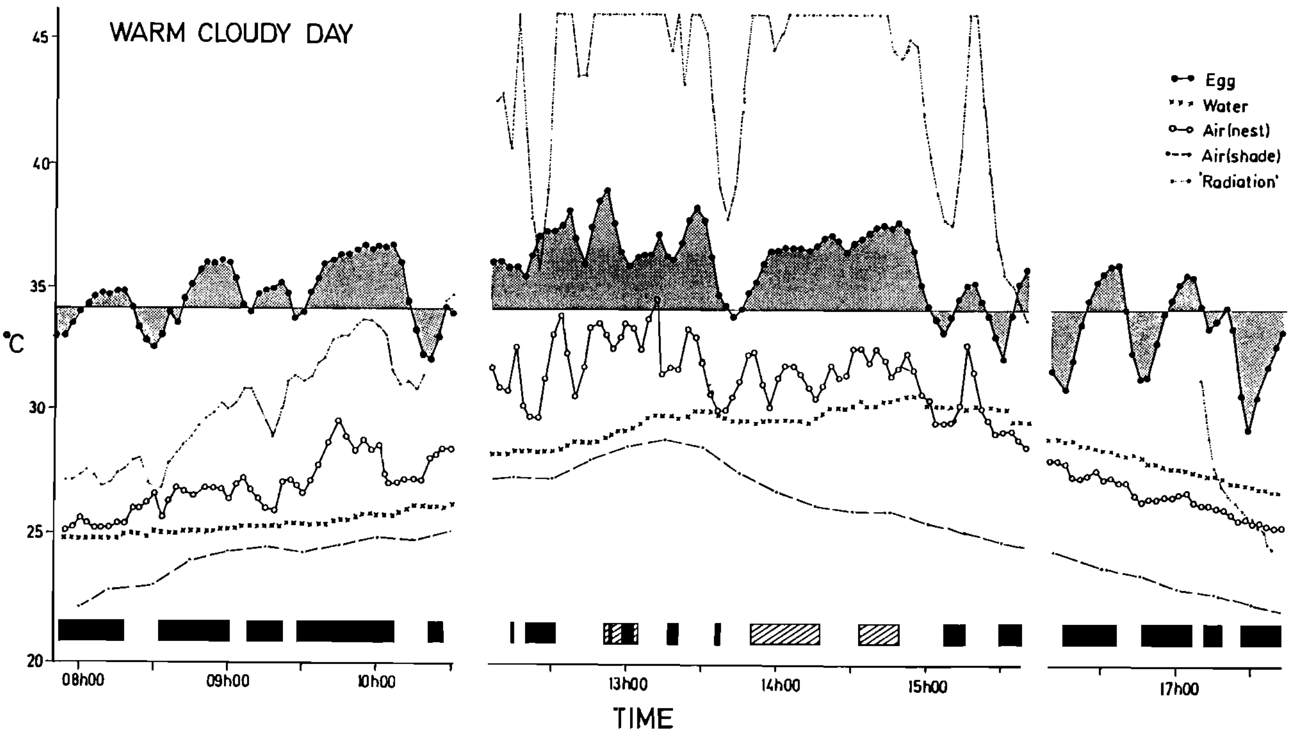

Figure 5 Temperatures at African jacana nest on a warm, cloudy day. Means of egg = 35,1°C; water = 27,8°C; air (nest) = 28,9°C; air (shade) = 25,1°C. Eggs incubated (black bars) 56,6% and shaded (hatched bars) 1,8% of time.

temperature between 11h30–12h00 was 30,0°C the male was deliberately kept off the egg containing the probe for 30 min (while the remaining three live eggs were kept in shade) during which time the male became increasingly anxious to return to its eggs, eventually approaching to within a meter of the observer in an attempt to reach the nest. The egg temperature reached a maximum of 42,3°C, which would normally be lethal.

On the hottest day monitored (Figure 7) when the mean shade temperature for the observation period was 31,3°C, the male attended the nest for 43,5% of the time, making frequent, short-duration visits to shade the eggs (36,6%)

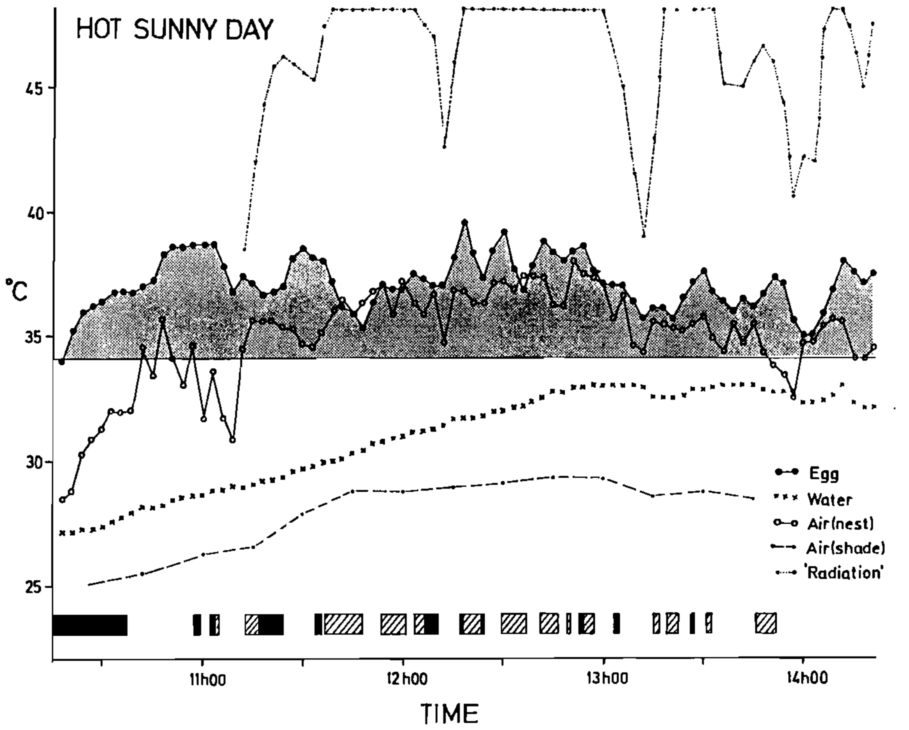

Figure 6 Temperatures at African jacana nest on a hot, sunny day. Means of egg 37,1°C; water = 31,0°C; air (nest) = 34,9°C; air (shade) 28,9°C. Eggs incubated (black bars) 22,7% and shaded (hatched bars) 24,5% of time.

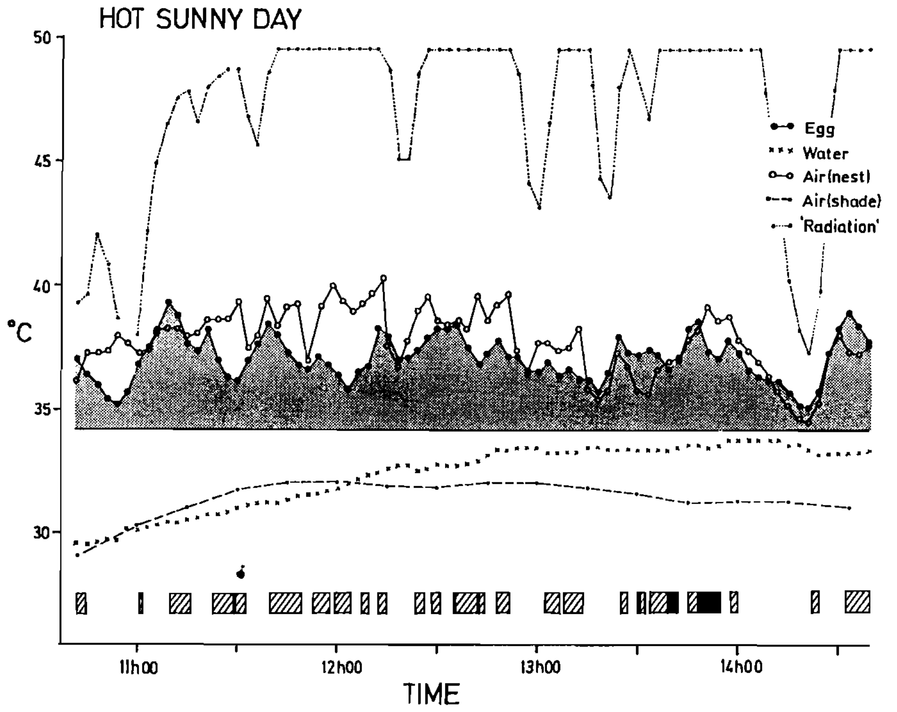

Figure 7 Temperatures at African jacana nest on a very hot, sunny day. Means of egg 37,1°C; water = 32,3°C; air (nest) = 37,8°C; air (shade) 31,3°C. Eggs incubated (black bars) 6,9% and shaded (hatched bars) 36,6% of time.

rather than to incubate them (6,9%). The egg temperature never fell below the standard and reached a maximum of 39,3°C.

In summary, the male's incubation behaviour ranged between two extremes: long 'on' shifts, short 'off' shifts and a high constancy on cool days and short 'on' and 'off' shifts, with a lower constancy, on hot days (Table 2). On cool days the water temperature ranged between 25–29°C and on hot days it ranged between 27–33°C. The range in air temperature at the nest for cool and hot days was, respectively, 25–34°C and 30–40°C.

To examine whether stage of incubation influenced the male's incubation behaviour, eight nests, in which clutches ranged from 2–22 days incubated, were monitored on two days, once in the morning (08h00–10h07) and once at midday (13h33–15h29). No detectable trend of increased or decreased constancy with advancing incubation was found (Spearman's Rank Correlation: am, $r = 0{,}25$; pm, $r = -0{,}41$; in both $p > 0{,}05$) nor was there a correlation between the duration of 'on' and 'off' shifts and advancing incubation (am 'on': $r = 0{,}57$; am 'off': $r = -0{,}18$; pm 'on': $r = 0{,}72$; pm 'off': $r = 0{,}68$; in all four $p > 0{,}05$; Spearman's Rank Correlations). The differences between the observed behaviours are attributable to time of day, as shown in Table 1.

Males differed in their incubation behaviour, as indicated in Figure 8. Male M91 was more attentive than male M53 as their respective incubation constancies of 57,3% ($SD = 2{,}05$; $n = 4$ days totalling 22 h) and 42,0% (SD 4,4; $n = 4$ days totalling 29,5 h) indicate (Mann-Whitney U test: $Z = 2{,}17$; $p = 0{,}029$). In 1985 these two males dominated all breeding on the dam, incubating six (M91) and seven (M53) clutches which were laid for them by five different females. M53 was repeatedly challenged during the season for the attention of his female by a third male (M72) whereas M91 faced no such challenges. This distraction may have been responsible for M53's lower nest attendance.

Table 2 Summary of male African jacana's incubation behaviour during different kinds of weather

	Type of day			
	Cool cloudy	Warm cloudy	Warm sunny	Hot sunny
% cloud cover	100	80–100	25–60	15–40
$\bar{x}$ air temp (shade)	22,9	25,1	28,1	31,3
$\bar{x}$ air temp. (at nest)	26,4	28,9	34,9	37,8
$\bar{x}$ water temp.	27,2	27,8	31,0	32,3
$\bar{x}$ egg temp.	33,3	35,1	37,1	37,1
% ON — total	70,9	58,4	47,2	43,5
— incubating	70,9	56,6	22,7	6,9
— shading	0	1,8	24,5	36,6
inc : shading ratio	100 : 0	97 : 3	48 : 52	16 : 84
% OFF — total	28,1	41,6	52,8	56,5
Duration of ON shift				
— $\bar{x}$	22,5	16,0	4,8	4,7
— SD	4,1	10,8	3,7	3,1
— n	5	15	17	21
Duration of OFF shift				
— $\bar{x}$	8,4	11,1	6,3	6,3
— SD	2,2	5,1	5,2	5,2
— n	4	16	18	21

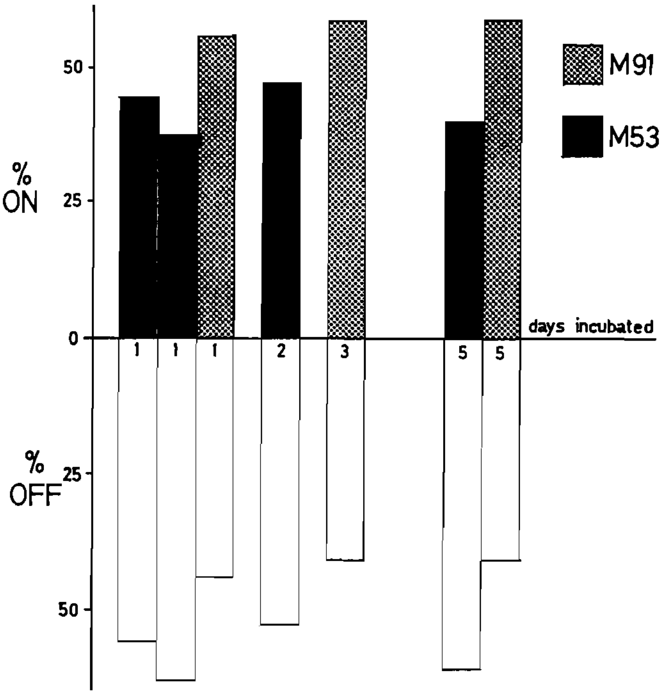

Figure 8 ON/OFF schedules of two males at some of their clutches at different stages of incubation (M91 = 22 h; M53 = 29,5 h).

Discussion

Shorebirds in which a single parent incubates face three sometimes conflicting objectives — to maintain favourable thermal conditions for the eggs, to satisfy their own nutrient and energy requirements, and to minimize the risk of revealing their nests to predators by their incubation behaviour. The first of these is dependent on weather, on the microclimate at the nest and on parental attentiveness (Webb 1987). Species nesting in low temperature environments (high latitudes/altitudes) adopt an incubation schedule that minimizes the risk of the eggs chilling: the eggs are attended for a high proportion of the time and the 'off' shifts are timed that the temperature of the eggs remains above their 'physiological zero' (e.g. Norton 1972; Lofaldii 1985; Kalas 1986). In high temperature environments the greater risk to uniparental breeding species is that unattended eggs will reach lethally high temperatures. In the climatic regime of this study African jacana eggs were exposed to risk in both directions: as shown, egg temperatures ranged between extremes of 27,0–39,6°C, and daily mean egg temperatures ranged between 33,2–37,1°C, despite the male's attentiveness, his incubation constancy varying between 43,5–70,9%. His average constancy of 53,1% is exceptionally low when compared with those reported for other uniparental shorebirds nesting in more temperate climates, e.g. painted snipe *Rostratula benghalensis* 80,4% (Komeda 1983), sanderling *Calidris alba* 81% (Pienowski & Green 1976), pectoral sandpiper *Calidris melanotos* 85% (Norton 1972), great snipe *Gallinago media* 90,3% (Lofaldii 1985) and dotterel

Table 3 The number of African jacana egg-laying records per month at different latitudes

		Number of egg-laying records per month													% Between
Region	Latitude	J	A	S	O	N	D	J	F	M	A	M	J	*n*	Nov–Mar
Natal[1]	27°S–31°S	0	0	0	1	5	7	16	6	4	0	0	1	39	97
Nyl floodplain[2]	24°S	0	4	6	26	42	51	73	40	12	2	0	0	256	85
Zimbabwe[3]	15°S–23°S	7	12	9	10	16	12	27	41	32	10	6	5	187	68
Malaŵi[4]	10°S–17°S	2	8	3	2	3	5	0	8	7	2	1	7	48	48
East Africa[5]	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 Incubation schedule of male African jacana (M07) in relation to ambient (= shade) temperature

Ambient temperature (°C)*	Time of day (h)	% Off	% On	% Incubating	% Shading	Incub : shading ratio	Sample size (min)
23,4	12–14	25,2	74,8	74,8	0	100:0	101
22,1	14–16	33,7	66,3	66,3	0	100:0	87
26,4	10–12	48,9	51,1	30,1	21,0	59:41	104
29,1	12–14	56,5	43,5	15,8	27,8	36:64	112
30,5	10–12	53,0	46,9	1,3	45,6	3:97	72
31,9	12–14	52,3	47,7	10,6	37,1	22:78	120
31,3	14–16	78,1	21,9	5,6	16,2	26:74	39

* This is the mean of all shade temperatures recorded within the indicated 2-h period.

Charadrius morinellus 90% (Kalas 1986). It is reasonable to assume that the jacana's relatively low incubation constancy meets the thermal requirements for embryo development and that incubating males have more time available to them for foraging (on average, 46,9% of the day) than their temperate counterparts. Elsewhere (Tarboton 1992a) I have shown that non-breeding males foraged, on average, for 69,5% of the day so, despite their low nest attendance, breeding males may still at times be subject to stress with respect to foraging time.

Although the male's attentiveness (% incubation) decreases significantly with increasing ambient temperature (Table 4; Spearman's $r = -0{,}82$; $p = 0{,}044$) his visits to the nest, though of shorter duration, become more frequent. Similar behaviour occurs in the Egyptian plover *Pluvianus aegyptius* (Howell 1979). This behaviour carries an increased risk of attracting predators to the eggs: observing male African jacanas' movements on hot days was a technique I used to locate nests and it may be exploited in a similar way by diurnal nest predators such as the purple gallinule *Porphyrio porphyrio* and Nile monitor *Varanus nilotica*. The failure rate of clutches is high in the African jacana ($\bar{x}$ = 75%) and predation is the suspected main cause of egg loss (Tarboton 1992c). Thus a hot climate which may favour the selection of a uniparental breeding system may also carry a higher cost in egg loss to predators. High egg loss, and the compensation for this by increased egg production, has been identified as an important component in selection for role reversal and polyandry in other shorebird species (Maxson & Oring 1980; Osborne 1982; Jenni & Betts 1978).

A second jacanid, the lesser jacana *Microparra capensis*, occurs in the Afrotropical region, and in places breeds alongside and in the same thermal environment as the African jacana (Urban, Fry & Keith 1986). In contrast to the African jacana, it is monogamous, the sexes share the incubation equally, the incubation constancy is high ($\bar{x}$ = 82%), its 'on' shifts are long ($\bar{x}$ = 39 min) and its 'off' shifts are short ($\bar{x}$ = 6 min) (Tarboton & Fry 1986). Tarboton & Fry (1986) attribute this species' monogamy, shared incubation and different nest attentiveness to its smaller egg size compared with that of the African jacana and hypothesize that the thermal properties (i.e. more rapid heat flux) of its small eggs necessitate a high incubation constancy that is achievable only through biparental care. In the absence of a precursory uniparental breeding system the evolution of role reversal and polyandry in this species is not possible.

The African jacana has a mainly tropical and subtropical distribution (Urban *et al.* 1986) and the extent of its breeding season varies according to latitude (Table 3). In the south of its range (27–31°S) the breeding season is confined to midsummer (97% of Natal's egg-laying records fall between November and March), but this becomes progressively extended with decreasing latitude so that close to the Equator (10°S 5°N) egg-laying occurs in every month without a seasonal peak. I suggest that the African jacana's uniparental breeding system is the primary cause of this breeding season gradient. In year-round thermally benign (equatorial) climates males can meet the nest-attentiveness demands required for successful hatching, whereas at increasing latitudes, with increased seasonality and colder winters, successful incubation by one parent is only achievable in the warmer months.

The mean water temperature on Deelkraal Dam was lowest (below 20°C, Figure 3) during the three mid-winter months May–July, the same months in which no egg-laying occurred on the floodplain (Table 3). To maintain egg temperatures in cold weather within the range considered optimal for incubation, males needed to increase their nest attendance to more than 70% (Table 2), and they probably sacrificed feeding time to do this. Relatively few clutches laid early in the breeding season (August to early October) were successful; if they hatched, they had a longer than average incubation period (Tarboton 1992c), a lower fecundity, and the chicks' development was retarded. Thus in 1987 five early-laid clutches (totalling 20 eggs) which escaped predation hatched 0, 1, 1, 2 and 3 young. The eggs that failed to hatch (13/20) all contained dead, partially developed embryos which probably died as a result of insufficient male attendance during the cold spells of weather that occurred in this early summer. In contrast, clutches laid later in the same summer (1987/88) which escaped predation had a high fecundity (Tarboton 1992c). Five of the seven early-hatched young reached maturity but each took longer than usual to do this.

Factors such as food availability undoubtedly play an important role in determining the timing and duration of the breeding season as well (Lack 1968), but these were not investigated. What is of special significance in this study is that, despite variable thermal conditions and their effect on incubation requirements, the African jacana's uniparental male care system is inflexible: females do not help males incubate during unfavourable conditions, even if their eggs are sacrificed by his inability to cope.

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